Passage and survival of adult Snake River sockeye salmon within and upstream from the Federal Columbia River Power System: 2008-2017

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Report of research to

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Executive Summary

Sockeye salmon *Oncorhynchus nerka* originating in the Sawtooth Valley of Idaho represent the southernmost spawning population of the species. With a history of essentially no wild anadromous returns since the 1990s, this evolutionarily significant unit (ESU) has the highest level of protection under the U.S. Endangered Species Act. Large releases of hatchery smolts and relatively high ocean survival have led to an increased number of returning adults since 2008. The ability to detect tagged individuals throughout their return migration has made it possible to investigate factors that influence upstream survival of these fish. Here, we analyze these factors to support decision-making strategies that will continue recovery of this population.

In our initial report to the U.S. Army Corps of Engineers in 2014, *Passage and survival of adult Snake River sockeye salmon within and upstream from the Federal Columbia River Power System*, we examined patterns in migration of Snake River sockeye from 2008 to 2013. Here we provide an update to include return years 2014-2017. In the present analysis, we examined data from all years, noting any refinements in our understanding since previous reports.

As in the previous report, we explored factors influencing fallback and survival of adult migrants from three major sources: 1) juvenile characteristics, such as hatchery origin and downstream migration history; 2) adult migration characteristics, such as timing and fallback; and 3) environmental conditions from Bonneville Dam to the Sawtooth Valley. We also compared patterns in Snake vs. upper Columbia River sockeye. The two ESUs from the upper Columbia River, Lake Wenatchee and Okanogan River, are self-sustaining. Where migration of these populations overlap, they provide a valuable contrast to Snake River sockeye.

Additionally, we explored the extent to which environmental conditions that cause high mortality in sockeye can be predicted prior to the start of the migration. These forecasts could be used to trigger transportation of adults to spawning grounds. We also characterized the relative benefits in potential spawner numbers of transporting adults from Bonneville, Ice Harbor, and Lower Granite Dam. Key findings from this analysis are listed below:

Adult detection efficiency

- Adult detection efficiencies during 2014-2017 were generally high (>95%), similar to 2008-2013. However, 2017 had the lowest detection efficiency of all years. As in previous years, adult detection efficiency was lower at Ice Harbor than at other dams (89% in 2017).

Migration timing and survival statistics

- Median arrival dates at Bonneville Dam were near average in 2017, whereas they were the earliest on record in 2016. While fish began arriving earlier than average in 2015, the run was protracted in the lower river, which caused a delay in median run timing, such that the median was later than average (similar to 2014, 2011, and 2010). Upper Columbia sockeye consistently arrived at lower Columbia River dams 5-6 d earlier than Snake River sockeye.

- Migration survival from Bonneville Dam to the Sawtooth Valley was extremely low in 2015 (~1.3%). Survival in 2016 and 2017 was slightly above the long-term average, at ~41 and ~37% respectively, despite being warmer than average. Survival in 2014 was very near average at 35%. Of fish detected at Bonneville from 2008-2017, a total of 27% reached the Sawtooth Valley, although survival increased to 38% when data from 2015 were excluded. In 2015, the majority of unusual mortality occurred downstream from McNary Dam. Upper Columbia sockeye consistently exhibited higher migration survival than Snake River sockeye, even under the same environmental conditions.

Influences on survival and fallback

- Anomalously high river temperatures during the 2015 migration likely contributed substantially to the low survival observed in that year. As described in previous analyses and confirmed here, migration survival decreases most rapidly as temperatures approach 18°C at Bonneville Dam. A mean temperature of 22°C occurred during the peak of the run. Across all years, upper Columbia sockeye encountered lower average temperatures due to earlier migration timing, but they also had higher migration survival than Snake River sockeye when exposed to the same temperatures.

- Low survival in 2015 was also associated with the highest juvenile transportation rate of all study years (54%). Sockeye that had been transported downstream as juveniles experienced more fallbacks, lower survival, and greater sensitivity to temperature during their adult migration than those that had migrated in-river as juveniles. An additional factor that contributed to lower survival was a higher fallback rate. We had limited power to quantify the impact of hatchery rearing due to the low number of wild fish in this population. Nonetheless, the combination of juvenile transportation, increased fallback, and hatchery origin may all contribute to lower survival of Snake than upper Columbia River sockeye at the same temperatures.

- Sockeye encountered temperature differentials up to 5.9°C between the entrance and exit of fish ladders in 2016 and 2017. The highest temperature differentials occurred at Lower Monumental Dam in 2016 and were associated with a lower probability of survival to Lower Granite Dam. While peak temperature differentials were smaller in magnitude at Lower Granite Dam (2.5°C), fish that encountered larger differentials at this dam exhibited longer dam passage times, a higher frequency of fallbacks, and reduced upstream survival. Temperature differentials were lower and the associated responses were weaker at Ice Harbor Dam.

  However, fish that experienced the highest differentials also had other conditions that made survival less likely, especially seasonally late arrival and high cumulative temperature exposure. These latter factors were stronger predictors of survival when compared directly. However, ladder temperature differentials likely contribute to these cumulative effects. Higher-resolution studies of fish behavior within the ladder and immediately after exiting the fishway would provide greater power to separate short-term and cumulative effects.

Predictability of low survival and the potential benefits of adult transportation

- We demonstrated skill at forecasting the mean temperature experienced by Snake River sockeye during their migration period 20 d prior to the median run date. We were also successful in predicting when the annual runs would begin. These two tools could be useful in making decisions about whether transportation is needed to avoid catastrophic run failures and when it should start.

- Consistent with previous results, theoretical modeling of the number of spawners expected following adult transportation showed that transport from Bonneville Dam could provide considerably more benefit than transport from Ice Harbor or Lower Granite. This conclusion was strengthened greatly by record adult mortality in the lower Columbia in 2015. If conditions similar to those in 2015 become more common in the Columbia River as a consequence of climate change, developing the capacity to transport from Bonneville Dam may become necessary to avoid similar die-offs.

Contents

Introduction

Robust sockeye salmon populations support major salmon fisheries throughout British Columbia and Alaska. However, in the U.S. Pacific Northwest, Snake River sockeye at the southern extent of its range is critically endangered (Ford et al. 2015). After successive population crashes, this evolutionarily significant unit (ESU) bottomed out in the 1990s, when less than a dozen anadromous sockeye returned to the Sawtooth Valley. Fortunately, a careful breeding program minimized the loss of genetic heterogeneity from inbreeding over two decades of intensive captive rearing (Kalinowski et al. 2012). Gradual increases in the number of hatchery fish released, combined with favorable ocean conditions, have resurrected the anadromous component of the run to the Snake River.

Snake River sockeye salmon historically spawned in a variety of lakes in the Sawtooth Valley in central Idaho (Bjornn et al. 1968; Chapman et al. 1990). They still undergo the most extensive freshwater migration of any sockeye population, traveling over 1,500 river kilometers to spawn at elevations above 2,000 m (Waples et al. 1991). These fish experience substantial and variable rates of mortality during the rigorous spawning migration, and such mortality could inhibit the population from becoming self-sustaining, as well as the availability of anadromous broodstock. Factors influencing migration success for adult Snake River sockeye salmon were identified and reported by Crozier et al. (2014) and (2015) for adult return years 2008-2014. Direct and indirect hydrosystem effects such as fallback and juvenile transport, along with environmental conditions such as water temperature, spill, and flow were identified as influential factors.

In this report, we updated previous analyses of fallback and survival for these adults with new data through 2017. Similar to previous reports, our primary goal was to characterize the upstream migration from Bonneville Dam to the Sawtooth Valley. We analyzed detections of passive integrated transponder (PIT) tags at major dams on the Columbia and Snake River, as well as detections from in-stream detection systems near Salmon and Stanley, Idaho, and at a weir near the Sawtooth Hatchery. Additionally, we compared survival and fallback between Snake and upper Columbia River sockeye migrating through the lower Columbia River from Bonneville to McNary Dam.

In supplemental biological opinions issued in 2008 and 2010, the National Marine Fisheries Service and Action Agencies recommended studying the potential of transporting adult sockeye salmon to increase migration survival (NOAA Fisheries 2008; NOAA Fisheries 2010). The *Trap and Haul Emergency Procedures and Feasibility*

Plan at Lower Granite Dam (Kozfkay et al. 2017) was completed in 2017, outlining proposed operations at Lower Granite Dam. This plan does not propose transportation from Ice Harbor (or any other dam) at this time, but supports a pilot study to test the feasibility of other options for further investigation.

River temperature during migration was previously identified as an important environmental factor limiting migration survival (Crozier et al. 2014), and is considered as an important indicator in the plan (Kozfkay et al. 2017). Specifically, previous reports showed high sensitivity to temperature, with survival diminishing most rapidly at temperatures near 18°C (Crozier et al. 2015). Crozier et al. (2014) also estimated the potential increase in survival in scenarios in which transportation was triggered when temperature thresholds were exceeded on a daily basis. However, this approach is logistically difficult because trapping fish at high temperature induces high mortality in itself, and the trap is generally closed under these conditions. Therefore, we explore a different approach here than in the previous report.

Formal study objectives focused on analysis of data from 2014-2017 and the potential to identify low-survival probabilities in advance of the run:

Objective 1. Estimate annual PIT-tag detection efficiency through the Federal Columbia River Power System (FCRPS) and Salmon River from 2014-2017 for adult Snake River sockeye salmon.

Objective 2. Estimate annual conversion rates through the FCRPS from 2014 to 2017 for adult Snake River sockeye salmon.

Objective 3. Estimate annual conversion rates for adult Snake River sockeye from Lower Granite Dam to the Sawtooth Valley from 2014 to 2017.

Objective 4. Estimate annual adult migration characteristics including migration timing, travel time, and fallback/reascension rates from 2014 to 2017 for Snake River sockeye salmon and upper Columbia sockeye.

Objective 5. Identify covariates, including migration characteristics, origin, genetic history, and temporal and environmental factors that affected adult migration survival and dam fallback from Bonneville to McNary Dam during 2014-2017 for Snake River sockeye as well as for upper Columbia sockeye for comparison.

Objective 6. Identify migration temperature metrics/thresholds that indicate the likelihood of low survival/conversion rates, potentially necessitating transport of adult sockeye salmon from the FCRPS to the Eagle Fish Hatchery. Model the potential increase in migration survival to the Sawtooth Valley with transportation from different potential trap locations.

In addition, although our formal objectives focused on 2014-2017, we extended all analyses to include additional years whenever sufficient data were available to do so. Summary statistics were possible for data from 2008-2017, but low sample sizes in 2008-2010 made these years unreliable for some analyses. Furthermore, we included analyses of adult Upper Columbia River sockeye passing through the Lower Columbia River. These analyses were used to compare migration characteristics and influences on survival and fallback with those of adult Snake River sockeye through the shared portion of the migration corridor.

Methods

Study Fish Database

Our database consisted of fish tagged as juveniles in the Snake or upper Columbia River and subsequently detected as adults at mainstem dams between 2008 and 2017. Ultimately, we included detection histories from 2,219 adults from the Snake River sockeye ESU, and 3,750 sockeye from the upper Columbia River (Table 1).

To develop individual detection histories, we queried the PIT-Tag Information System database (PTAGIS 2018) for juvenile tag files from 2006 to 2017 and interrogation files from 2008 to 2017. We included only Snake River and upper Columbia sockeye: PTAGIS species code 4, run codes 2, 5, or R, and rear codes H, U, and W. We used river kilometer (rkm) of the juvenile release site to identify fish originating from the Snake (≥ 522 rkm) and upper Columbia River Basin (≥ 639 rkm). We excluded fish tagged in the lower Columbia River.

We used a maximum size criterion (200 mm) to identify fish tagged as juveniles, based on a clear discontinuity in reported lengths above and below this cutoff and on communications with tagging personnel. Fish tagged above Lower Granite Dam that met the other criteria were assumed to be juveniles even if they were missing a length measurement. To identify returning adults, we collated data from all fish detected in adult fish ladders at least one year after the juvenile migration year.

Detections at dams included those from Bonneville, McNary, Ice Harbor, Lower Granite, Priest Rapids, Rock Island, and Rocky Reach during 2008-2017, from The Dalles during 2013-2017, and from Lower Monumental and Little Goose during 2014-2017. In-stream monitoring systems in the Salmon River were located at Eleven Mile Creek (rkm 437, PTAGIS code USE) and Iron Creek (rkm 460, PTAGIS code USI). We refer to combined detections from these two sites as the "upper Salmon" site.

Fish detected as adults anywhere in the Sawtooth Valley were considered successful in completing their migration. Sawtooth Valley detection sites included the Sawtooth Hatchery, Redfish Lake, and Valley Creek (VC1 and VC2). We included the Valley Creek detection site because it lies *en route* to historical spawning grounds in Stanley Lake (Bjornn et al. 1968; Chapman et al. 1990). Detection at Valley Creek represented successful completion of the most challenging parts of the migration, which is the primary focus of this report. However, spawning and broodstock collection areas were a bit further upstream, at Redfish Lake and the Sawtooth weir.

We further queried PTAGIS for recapture and mortality events at Redfish Lake, Pettit Lake Creek, and Sawtooth Hatchery. These mortality events would not necessarily be recorded as detections, yet the fish would have reached the Sawtooth Valley and thus would have been considered successful in their migration for our purposes.

Table 1. Detection numbers at each dam for adult Snake River and upper Columbia River sockeye PIT-tagged as juveniles.

	Snake River									
Year	Bonneville	The Dalles	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite	Upper Salmon	Sawtooth	Total
2008	14	--	10	10	--	--	10	--	3	14
2009	23	--	16	17	--	--	17	--	11	23
2010	40	--	34	30	--	--	31	--	24	40
2011	516	--	343	316	--	--	332	--	252	520
2012	122	--	70	67	--	--	64	--	40	123
2013	205	170	138	121	--	--	91	38	29	206
2014	343	290	214	204	213	205	199	119	120	347
2015	679	430	100	60	50	32	27	5	8	687
2016	183	157	132	126	126	125	124	80	75	183
2017	74	58	46	44	46	43	42	20	28	76

	Upper Columbia River							
	Bonneville	The Dalles	McNary	Priest Rapids	Rock Island	Rocky Reach	Wells	Total
2008	45	--	35	41	34	22	22	46
2009	326	--	244	257	232	71	42	329
2010	957	--	752	770	713	248	140	963
2011	651	--	395	441	371	106	87	658
2012	572	--	408	403	339	128	99	575
2013	172	148	139	133	114	71	62	179
2014	313	290	262	259	84	154	148	314
2015	413	359	249	217	173	141	116	420
2016	146	133	121	120	111	70	67	148
2017	115	111	102	95	84	58	57	117

Covariates for Analysis

We explored relationships between various covariates and conversion rates/fallback. Covariates fell into three distinct categories related to the sockeye life history, including juvenile characteristics, aspects of the adult migration, and environmental conditions during the adult migration.

Juvenile covariates

Juvenile covariates included fish origin, migration history, and fish age. Fish origin was defined as either "hatchery" or "wild" based on designation in PTAGIS. Juvenile migration history was defined as "in-river" or "transported." Transported fish were those the last juvenile detection site at the entrance to a barge holding raceway (summarized by Ben Sandford, NOAA fisheries, personal communication). We assumed that all smolts migrated as yearlings, and thus used the number of years in the ocean as a proxy for fish age. We defined ocean years as the difference between the adult and smolt migration years. Origin and migration history were analyzed as factors, while fish age was a continuous variable.

Adult migration covariates

We also explored how various aspects of the adult migration related to migration fate. For adult migration covariates, we considered arrival timing, travel time within the hydrosystem, fallback statistics, and harvest as continuous variables. We defined day of arrival at the beginning of a reach as the first day a fish was detected at the farthest downstream dam within that reach. We calculated travel time within the hydrosystem as the difference between day of first detection at Bonneville and day of first detection within a reach of interest. This covariate was thus only relevant when analyzing reaches upstream of McNary Dam. We also examined an effect of fish being diverted into the Lower Granite Dam sampling trap as a factor variable (trapped or not trapped) on survival from Lower Granite to the Sawtooth Valley.

Fallback at a dam occurs when a fish ascends an adult fish ladder and then falls back downstream of the dam. Fallback can occur over multiple routes, such as through the turbines or over spillways, which are not monitored for PIT-tags. We therefore used a proxy developed previously for identifying fallbacks (Burke et al. 2004). Briefly, we classified a fish as having fallen back if it was detected moving upstream in an adult ladder and then detected again after a lag of more than 6 h either in that same ladder, in a different ladder at the same dam, or at a downstream dam. Long delays between detection sites within a ladder would count as a fallback as long as the fish was not detected moving downstream within the ladder. However, at most sites detection coils are very close together, such that previous work found that 6 h was a relatively good proxy for true fallbacks, as identified by radiotelemetry (Burke et al. 2004). We used a program using these criteria developed specifically to infer fallback from detections of PIT-tagged fish (Tiffani Marsh, NOAA Fisheries, personal communication).

We tallied the total number of unique fish that fell back and the total number of fallbacks. Following Boggs et al. (2004), when divided by the total number of fish in the sample, these two indices produced a *fallback percent* (unique fish that fell back/total number of fish), and *fallback rate* (total number of fallback events/ total number of fish). Alternative definitions of fallback, such as those published in DART (CBR 2018), require detection at specific entrance and exit coils. Due to imperfect detection at individual coils, these requirements reduced the number of fish considered in their analysis. However, a shorter delay requirement (2 h instead of our 6 h criterion) would increase the number of fish considered to have fallen back. Thus, the absolute number and rate of fallback is expected to be different for the different methodologies. However, to characterize general patterns, we compared annual variation in fallback rates between the two methods using fallback rates queried from DART (CBR 2018).

When including fallback as a covariate in the survival analysis, we summed all fallbacks that occurred for a fish at downstream dams. For example, when analyzing survival from Ice Harbor to Lower Granite, we summed all fallbacks detected at Bonneville, McNary, and Ice Harbor. We did not include dams that did not have data from all years in this covariate.

We derived our index of catch from estimates of combined tribal and non-tribal harvest within Zone 6 (roughly from Bonneville to McNary Dam) summarized by the Columbia River Inter-Tribal Fish Commission staff (Stuart Ellis, personal communication). These estimates were not spatially explicit within Zone 6. In certain years (2014-2017), catch data were reported as a combined sum of gillnet and platform in weekly increments. In other years (2008-2013), platform catch (usually in weekly or longer increments) and gillnet catch (2-3 d out of a week) were reported separately. There was also a small yearly sport catch estimate, which we distributed equally in weekly increments over that year's gillnet and platform period.

We combined all sources of fishing mortality into weekly catch estimates. We therefore expanded gillnet catches to apply to the entire week around the opening. When reporting periods were longer than one week, we used linear interpolation to spread out the catch over the reporting period, then re-aggregated it into weekly sums. The longer reporting periods had smaller catch, so the error introduced by this method had a small effect relative to gillnet catches. Although this approximation was not ideal, the index still captured the general seasonal and annual pattern of fishing effort. Each PIT-tagged fish was then assigned a weekly catch associated with passage day at Bonneville Dam.

Environmental covariates

Daily averages of temperature, flow, spill, and percentage of dissolved gas were collected at all dams by the U.S. Army Corps of Engineers and distributed by the Columbia River Data Access in Real Time project (CBR 2018). For each fish, we used values measured at each project on the day of first detection at that project. We prioritized data from the water quality monitoring station from the tailrace of each project (project codes CCIW, TDDO, MCPW, IDSW, and LGNW) when available. In cases where data was not available from the tailrace, we used data reported for the forebay (project codes BON, TDA, MCN, IHR, LWG, PRD, RIS).

For temperature specifically, we utilized finer-scale data at McNary, Ice Harbor, and Lower Granite Dam. The U.S. Army Corps of Engineers measures temperature along a vertical line, or "string" in the forebay at some dams at a series of depths (USACE 2018). We used the daily mean temperature measured at the 0.5-m depth to estimate reservoir surface temperature (monitoring sites: MCN_S1, IHR_S1, LWG-S1). We compared these string temperatures with those from the water quality monitoring stations described in the previous paragraph, and they were highly correlated in most cases, although the relationship varied by season.

We excluded a small number of individual temperature readings that were highly anomalous for the season and recorded at only one dam. To identify anomalous readings, we calculated average temperature across all years for each calendar day at each dam, and then examined individual readings that differed from this long-term mean by more than 10°C. If the anomaly was not supported by evidence from nearby sites, we replaced the anomalous value by linear interpolation. Temperatures above 30°C were considered errors and interpolated.

Missing data from 1 to 3 d were filled in by interpolation. There were more gaps in the string temperature data than in data from water quality monitoring stations. However, these gaps tended to occur at times of year when there was no stratification, so string temperatures were very similar to water quality monitoring station temperatures. Similarly, temperatures at water quality monitoring stations were highly correlated among dams. Therefore, for longer series of missing data in all datasets, gaps were filled by regression against the nearest available station.

We analyzed two temperature metrics as covariates for reach survival. First, we used the temperature experienced on the day of passage at a dam. Second, we calculated a cumulative temperature metric, in which daily temperatures that had accrued between entering the hydrosystem and entering the reach of interest were summed. Like the travel time estimate, the cumulative temperature index requires successful completion of a reach; thus, it is only useable as a covariate for reaches upstream of McNary Dam. To calculate the cumulative temperature ($T_{cumulative}$), we assumed that all days in the reach (D) were spent at the mean of temperatures from the downstream (T_{down}) and upstream (T_{up}) dams:

$$T_{cumulative} = D * \left(\frac{T_{down} + T_{up}}{2}\right)$$

We summed reaches as the fish moved upstream, so cumulative temperature for the reach from Lower Granite to Sawtooth would be the sum of $T_{cumulative}$ from Bonneville to McNary, McNary to Ice Harbor, and Ice Harbor to Lower Granite.

To explore the effect of temperature gradients experienced in fish ladders, we calculated ladder temperature differentials as the difference between the ladder entrance and exit temperature at the hour and location a fish was first detected at a dam. We used water temperatures collected by the U.S. Army Corps of Engineers at ladder entrances and exits on an hourly basis in 2016 and 2017 at McNary, Ice Harbor, Lower Monumental, Little Goose and Lower Granite dams, and 2017 at The Dalles. We downloaded these data from the Fish Passage Center (http://www.fpc.org/river/Q_ladderwatertempgraph_multipleyears.php). For each ladder we utilized that following loggers for entrance and exit temperatures respectively:

The Dalles North	TDAANEN1 and TDAANMD6
McNary North	MCNANEN1 and MCNANEX1
McNary South	MCNASEN1 and MCNASEX1 (2016) or MCNASMD6 (2017)
Ice Harbor North	IHRANEN1 and IHRANEX1
Ice Harbor South	IHRASMD1 and IHRASEX1
Lower Monumental N	LMNANEN1 and LMNANEX1
Lower Monumental S	LMNASEN1 and LMNASEX1
Little Goose South	LGSASEN1/ LGSASEN2 and LGSASEX1
Lower Granite South	LWGASEN1 and LWGASEX1

All entrance and exit times were rounded to the nearest hour. We also explored temperature differentials between first entrance and last exit, but this often occurred on different days and hence confounded seasonal temperature patterns with in-ladder temperature gradients.

Data Analysis

Objectives 1-3: estimates of detection probability and survival

To estimate reach-specific survival from Bonneville to the Sawtooth Valley and detection efficiencies at dams for Snake River sockeye, we used the Cormack-Jolly-Seber (CJS) mark-recapture model implemented in R with the Marked package (Laake et al. 2013). We assumed that the migration corridor was linear and that failure to reach the Sawtooth Valley was equivalent to mortality. Therefore, we consider CJS model results to be estimates of true survival rather than apparent survival (*sensu* Schaub and Royle 2014). Sockeye were assigned a pseudo-detection history below Bonneville (always 1) that was comparable to the juvenile release history. These model estimates included the following assumptions (Pledger et al. 2003):

1. All fish in the population had the same probability of being detected at dams,
2. All detections were recorded correctly and PIT tags were not lost, and
3. The detection probability and survival probability of each fish was independent of other fish.

Although we cannot test these assumptions independently, exploration of the data revealed no biases.

We compared models that explored a single year effect across all reaches as well as an interaction effect between year and reach. We also considered a hatchery effect as a factor variable. We selected the model with the lowest rank based on Akaike information criterion (AIC, Burnham and Anderson 2002). Utilizing the selected model. we estimated detection efficiencies for Bonneville, The Dalles (starting in 2013), McNary, Ice Harbor, Little Goose (starting in 2014), Lower Monumental (starting in 2014), Lower Granite, Salmon River (starting in 2013), and above Lower Granite, as well as observed survival for each reach between these dams. We assumed 100% detection probability at Sawtooth because recovery at the hatchery is very thorough, and no detectors exist upstream with which to model detection efficiency at the hatchery.

Objective 4: estimated migration characteristics

We calculated summary statistics for arrival day (first detection at a dam) and travel times for each reach (first detection day at the downstream dam to the first detection at the upstream dam). We compared these statistics across dams for Snake and Upper Columbia River sockeye. Additionally, we calculated and compared patterns in fallback, including *fallback percent* and *fallback rate* using standard functions in R (R Core Team 2013).

Objective 5: covariate analyses of survival and fallback

Model development—We fit generalized linear models to investigate which environmental, juvenile, and adult migration covariates best predicted fallback and survival respectively. We modeled observed survival using a logit-link (i.e., logistic regression models) rather than CJS-modeled survival with covariates because detection rates were very high (>0.95). Consequently, observed survival was generally within the SE of the CJS estimate. The maximum difference in any reach-by-year combination was 0.09, which equals the maximum standard error of the CJS model estimates.

There were also complications of jointly modeling covariates within the CJS model. For example, multiple reaches in this analysis had distinct environmental conditions and could not be considered a single environment. This had the effect of greatly enhancing the number of factors in the model. Furthermore, some factors, such as catch, are only relevant for certain parts of the migration. In sum, we concluded that independent models of each reach would be more straightforward to interpret, would include only minor loss of accuracy, and thus would be more useful. We assumed that missed detections were not biased in relation to the covariates.

For the covariate analysis, we utilized data from fish detected at Bonneville Dam (Table 1). For survival, we ran separate models for reaches from Bonneville to McNary (upper Columbia and Snake River populations), McNary to Ice Harbor, Ice Harbor to Lower Granite, and Lower Granite to Sawtooth. None of the models were overdispersed. To describe the probability of fallback, separate models were run for each dam, including Bonneville, The Dalles, McNary, Ice Harbor, and Lower Granite. Some of these models were overdispersed, so we used the quasi-Poisson link for fallback models.

For all survival and fallback covariate models we utilized the *dredge* function in the MuMIN package in R (Barton 2018) to run models with all possible covariate combinations and up to 10 covariates in a single model. We considered quadratic terms for temperature and day as data exploration found that these variables had non-linear relationships with survival and fallback. We ranked models by AIC and produced a model-average object, where importance denotes the proportion of top models that contained the variable, weighted by relative support for the model. We also reported conditional significance for each variable, which denotes whether the coefficient was significant (P <0.05) among models that included the variable. We reported model coefficients from the model averages, conditional significance, and variable importance.

Environmental covariates vary seasonally and thus are often correlated. The strongest linear correlations were found between temperature and day. Flow and spill were also highly correlated with each other. To avoid problems with collinearity that would violate assumptions of regression analysis, we excluded one of any two covariates from the same model with a correlation coefficient greater than 0.7. All covariates were standardized by subtracting the mean and dividing by the standard deviation prior to model fitting.

***Ladder temperature differentials*—**Caudill et al. (2013) found that temperature gradients within adult fish ladders at Snake River dams can exceed 4°C, with Lower Granite Dam showing the largest temperature differentials (ladder exit-ladder entrance). Large temperature differentials were associated with Chinook and steelhead passage times nearly twice as long as they would be without the differential, and longer passage times that accumulate over the course of the migration were associated with lower migration survival (Caudill et al. 2007; Caudill et al. 2013).

To avoid such large temperature differentials and their impacts, sprayers were installed in 2016 at Lower Granite and Little Goose Dam to cool the surface water near the ladder exit. The U.S. Army Corps of Engineers also measured water temperatures at multiple locations within the fish ladder to quantify temperature differentials above and below the diffuser.

We conducted several analyses to determine the magnitude of temperature differentials that sockeye experienced in 2016 and 2017, and whether we could detect any dam-passage delays, increased fallbacks, or lower subsequent survival in response to elevated differentials. Ladder temperature data were available in these years for a total of 260 fish. Ladder temperature differentials were taken as the difference between the ladder exit and entrance temperature at the time of first detection. At Little Goose there were two entrances to one ladder (loggers EN1 and EN2). Entrance EN2 generally had higher temperature differentials, though we tested relationships with both measurements.

The original data describing fish behavior used radio-tagged fish, which tracked individual fish much more precisely than our PIT-tag data. Using PIT-tag data, we can summarize cumulative time between first and last detection at a dam, fallback status, and survival through the upstream reach. Total passage time, defined as first to last detection at a dam, can include backing out of a ladder, delay within a ladder, or exiting the top of a ladder followed by reascension of the same or a different ladder at the same dam. Backing out of a ladder would not have qualified as a fallback if downstream movement was detected within the ladder, but the other behaviors may have also qualified as a fallback, for example if the delay occurred between detection sites within a ladder.

Although we explored total passage time at all seven dams with PIT detection in 2016 and 2017, we had too few fish with multiple detections at most dams to produce a suitable distribution of passage times for analysis. At The Dalles, McNary, Lower Monumental, and Little Goose, 50-80% of passage times were less than one minute. Times were highly skewed at Ice Harbor as well, but 20% of passage times there were at least 1 hour. In contrast, 98% of passage times were at least 1 hour, and the median passage time was 7 hours at Lower Granite, where detection sites have more separation.

We tested three hypotheses at dams. First, for Lower Granite only, we tested whether total passage time, defined as the number of minutes from first to last detection, was significantly related to the ladder temperature differential at the time of first detection, as well as other covariates assessed by Caudill et al. (2013). We compared models that included ladder temperature differential, tailrace temperature (i.e., water quality at monitoring stations downstream), forebay temperature (i.e., vertical string temperature at 0.5 m), and time of day, including a quadratic form for hour. Passage time was log-transformed. We reported AIC comparison of models and variables that were significant.

Second, we tested whether a fallback was more likely to occur in the face of higher temperature differentials at McNary, Ice Harbor, Lower Monumental, Little Goose, and Lower Granite. We used logistic regression with a binomial response variable: whether the fish fell back or not.

Third, at the same five dams we tested whether survival through upstream reaches, as defined in the *Covariate models of fallback and survival* section, was correlated with ladder temperature differential. We note that warmer forebay temperatures are also expected to increase fallback and decrease survival, and because higher ladder temperature differentials are associated with warmer forebay temperatures, these two factors co-vary. In our dataset, these two predictors always had a correlation lower than 0.7, and thus could potentially be differentiated statistically. Nonetheless, they were probably both biologically relevant.

Additionally, we replaced reservoir temperatures with ladder temperature differentials in covariate models for reach survival from Lower Granite and Ice Harbor dams for 2016 and 2017 utilizing the full list of covariates described above to determine if ladder temperature differentials improved model fit over other factors during these years. Many factors affect survival, especially over longer periods, so a non-significant result in this test did not necessarily mean that these differentials had no effect. Rather, they might have contributed to other stronger signals or had short-term (sublethal) effects. Nonetheless, we found it useful to include magnitude of the ladder temperature differential effect within the context of our larger analysis of migration survival.

Objective 6: adult transport temperature thresholds and benefit ratios

Our analysis of transportation effects represented an alternative approach to that described by Crozier et al. (2015), where transportation was triggered on a daily basis if daily river temperature surpassed a specified threshold. In contrast, for this analysis we wanted some indication of whether temperatures might exceed physiological tolerance levels before the run started. We then applied the transportation sampling/survival scenario to the entire run for that year, not just to the fish that passed on an exceptionally hot day. The purpose of this analysis was to provide managers a tool that could be applied more predictably and identify advance warning signals that could be useful in anticipating the need for transportation in a given year.

Based on individual models, we know that most temperature-related mortality during the adult migration can be predicted by temperatures experienced by fish at either Bonneville or Ice Harbor Dam (see results section below and Crozier et al. 2015), even if mortality occurs far upstream. Therefore, we focused on predicting temperatures during the mean run period at these two dams. We defined the mean run period as the 20-d period centered on the long-term mean of annual median dates of arrival at each dam from 2008 to 2017 (30 June at Bonneville and 7 July at Ice Harbor).

We first assessed whether the mean run temperature was a good predictor of annual population survival to the same extent it had been at the individual level. For this analysis, we used a more flexible modeling framework than Crozier et al. (2015) in order to characterize any sort of non-parametric relationship. Specifically, we used generalized additive models (GAMs), which we fit with the package *mgcv* in R (Wood 2006). We used smoothed terms with a maximum of three knots in all models to avoid overfitting.

Next, to allow managers a temporal "cushion" to organize transport operations, we explored the ability to predict mean run temperature in advance. For these "cushion models" we analyzed a longer time series of environmental data, from 2000 to 2017, to provide increased confidence in our relationships. As with mean run period, predictive periods were 20 d long. We tested two cushions of 10 and 20 d for prediction periods. Thus, the predictive period was 20 d long starting either 30 or 40 d before and ending either 10 or 20 d before the beginning of the mean run period (i.e., 20 or 30 d before the median run date).

We tested whether 1) mean temperature during the predictive periods was significantly related to mean temperature during the mean run period and 2) whether mean temperature during the predictive periods was significantly related to annual population survival using linear regression models.

Finally, we analyzed the predicted increase in migration survival given transportation scenarios at Bonneville, Ice Harbor Dam, and Lower Granite Dam, respectively, for each year with a sufficient sample size (2011-2017). We lacked data on which to base scenario survival and sampling rates, and no specific sampling rate was enumerated by Kozfkay et al. (2017), so we used a scenario provided by USACE for modeling. Thus, in our scenarios we assumed that 20% of the population in each year would be transported and that 80% of those fish would survive to spawn in the Sawtooth Valley. The 20% of individuals selected for transportation and the 80% survival of those selected for survival were randomly chosen from the PIT tag data with 100 iterations for each year performed. The estimate of migration survival to spawning was then the mean of the 100 iterations.

We calculated a benefit ratio for spawners for each year with transportation. The transport benefit ratio was defined as predicted survival to the Sawtooth Valley with transportation divided by the estimated true survival for that year. To explore whether there was a particular threshold temperature that would be most beneficial as a trigger for transport, we compared results for benefit ratios with various temperature thresholds.

Results

Objective 1: Detection Efficiency

A comparison of CJS models indicated that survival varied across years differently in different reaches, because all models with 99% of AIC weight included a reach-by-year interaction (Appendix Table 1). Some of the top models suggested that survival was different for hatchery vs. wild fish, but AIC differed by less than 2 when origin was added to the model, so there was not strong support for this term. All of the top 99% of models included additive effects of reach and year on detection efficiency. As with survival, the hatchery/wild factor had a slight but non-significant effect on detection efficiency. These data adequately fit CJS model assumptions based on goodness of fit testing: $\chi^2 = 7.49$, $p = 0.112$ (Gimenez et al. 2017). We therefore reported the detection efficiencies and survivals from the top CJS model:

$$\phi(\sim -1 + reach \times year)\, p(\sim -1 + reach + year)$$

where ϕ is the survival component and p is the detection efficiency.

Modeled detection efficiencies through the FCRPS during 2014-2017 were similar to those during 2008-2013 (Figure 1). Detection efficiency was 95% or higher at all dams except Ice Harbor. Detection at Ice Harbor averaged 93% with a minimum of 89% in 2017 (Table 2). Detection was low (56-85%) at the in-stream monitoring sites compared to the dams, as expected generally for these two environments.

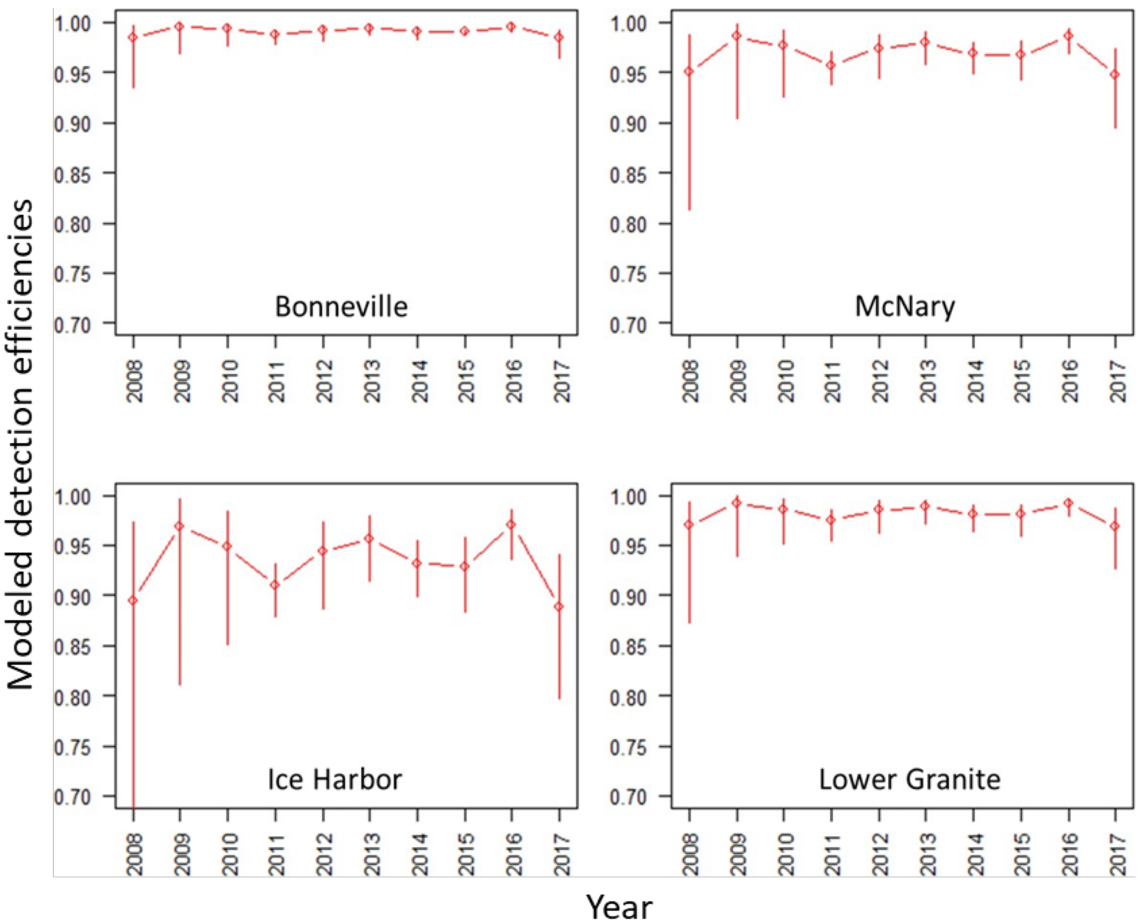


Figure 1. CJS-modeled detection efficiencies with 95% confidence intervals for Bonneville, McNary, Ice Harbor, and Lower Granite dams for 2008 to 2017.

Table 2. Estimated mean detection probabilities (%) for adult Snake River sockeye salmon (SEs in parentheses). Upper Salmon column reflects combined detections from the two in-stream PIT-tag monitoring systems on the mainstem Salmon River.

	Mean estimated detection probability of adult sockeye salmon (%)							
Year	Bonneville	The Dalles	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite	Upper Salmon
2008	98.4 (1.2)	--	95.1 (3.5)	89.3 (7.1)	--	--	97.4 (2.1)	--
2009	99.6 (0.4)	--	98.6 (1.4)	96.8 (3.1)	--	--	99.3 (0.8)	--
2010	99.3 (0.5)	--	97.6 (1.4)	94.7 (3.0)	--	--	98.8 (0.8)	--
2011	98.7 (0.3)	--	96.0 (0.8)	91.2 (1.3)	--	--	97.9 (0.7)	--
2012	99.2 (0.3)	--	97.5 (1.0)	94.3 (2.1)	--	--	98.7 (0.7)	--
2013	99.4 (0.2)	99.1 (0.4)	98.1 (0.7)	96.6 (1.6)	--	--	99.0 (0.5)	82.9 (4.4)
2014	99.1 (0.3)	98.8 (0.5)	97.2 (0.7)	93.8 (1.3)	99.2 (0.5)	98.9 (0.4)	98.5 (0.5)	78.7 (3.2)
2015	99.0 (0.0)	98.6 (0.6)	96.8 (0.6)	92.9 (0.9)	98.7 (0.9)	98.3 (0.7)	98.3 (0.5)	75.6 (6.4)
2016	99.6 (0.2)	99.2 (0.3)	98.6 (0.6)	96.9 (1.2)	99.4 (0.4)	99.2 (0.3)	99.3 (0.4)	85.1 (3.2)
2017	98.3 (0.7)	96.8 (1.3)	94.7 (1.9)	88.6 (3.6)	97.7 (1.4)	96.9 (1.3)	97.2 (1.3)	57.5 (6.5)

Objectives 2-3: Adult Migration Survival Estimates

Mean estimated survival from Bonneville Dam to Sawtooth was 28% during 2014-2017, compared with 37% during 2008-2013. Estimated survival was near the 2008-2017 average in 2014, 2016, and 2017; however, survival in 2015 was extraordinarily low. Only 1% of fish detected at Bonneville reached the Sawtooth Valley in 2015 (8 PIT-tagged fish, Figure 2, Table 1).

The lowest survival estimates across all reaches assessed for 2014-2017 were in 2015, including 15% from Bonneville to McNary Dam followed by 33% from Lower Granite to Sawtooth, 43% from Ice Harbor to Lower Granite, and 62% from McNary to Ice Harbor (Table 3 & Figure 3). To calculate cumulative survival, we multiplied the point estimates of CJS-modeled survival over sequential reaches.

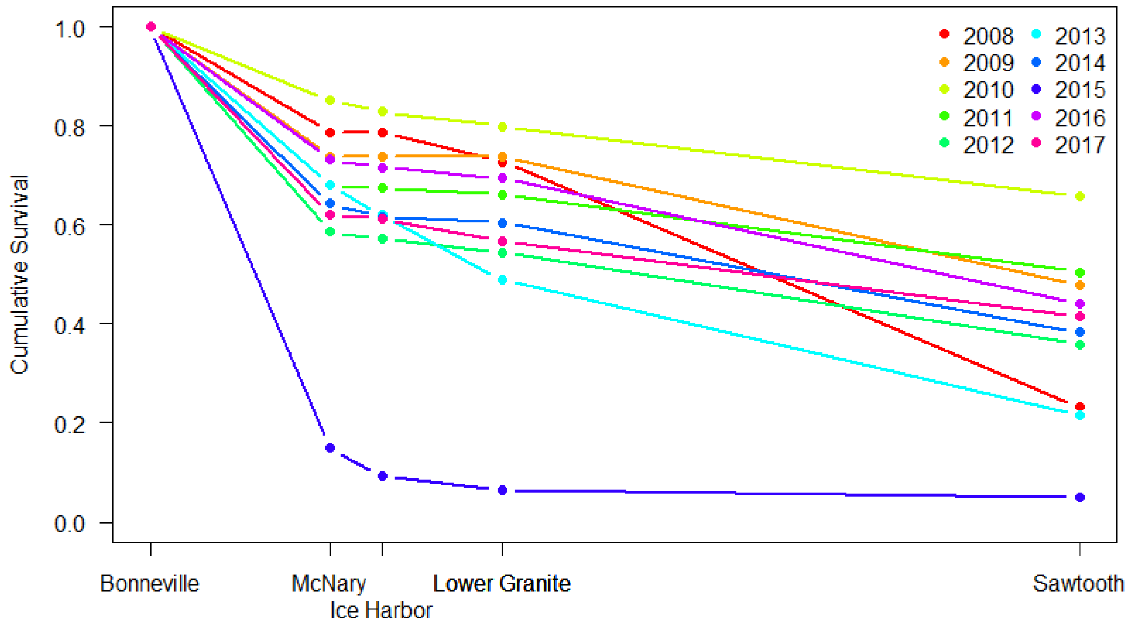


Figure 2. Cumulative survival probabilities from Bonneville Dam to the Sawtooth Valley for Snake River sockeye salmon based on CJS model. Reaches are scaled by distance from Bonneville Dam.

Table 3. Estimated survival by reach and year for PIT-tagged Snake River sockeye salmon. CJS model estimates shown with SEs in parentheses.

	Mean estimated survival (%)					
Year	Bonneville to The Dalles	The Dalles to McNary	Bonneville to McNary	McNary to Ice Harbor	Ice Harbor to Lower Monumental	Lower Monumental to Little Goose
2008	--	--	78.6 (1.1)	100.0 (0.2)	--	--
2009	--	--	73.9 (9.2)	100.0 (0.0)	--	--
2010	--	--	85.1 (5.7)	97.3 (3.0)	--	--
2011	--	--	68.1 (2.0)	99.1 (0.6)	--	--
2012	--	--	58.6 (4.4)	97.6 (2.0)	--	--
2013	83.6 (2.6)	81.4 (3.0)	68.1 (3.3)	91.0 (2.6)	- -	- -
2014	84.7 (2.0)	76.0 (2.5)	64.3 (2.6)	95.8 (1.4)	99.1 (0.7)	96.7 (1.2)
2015	63.3 (1.9)	23.8 (2.9)	15.0 (1.4)	61.5 (5.1)	77.2 (5.4)	65.9 (6.7)
2016	87.0 (2.5)	84.2 (2.9)	73.2 (3.3)	97.9 (1.3)	98.4 (1.1)	97.7 (1.3)
2017	77.1 (4.9)	81.0 (5.2)	62.0 (5.6)	98.9 (2.3)	100 (0.0)	95.9 (3.0)
Average	79.1 (2.8)	69.3 (3.3)	64.7 (3.9)	93.9 (1.9)	93.7 (1.8)	89.1 (3.1)

	Little Goose to Lower Granite	Ice Harbor to Lower Granite	Lower Granite to Upper Salmon	Upper Salmon to Sawtooth	Lower Granite to Sawtooth
2008	--	92.6 (9.0)	--	--	29.5 (14.3)
2009	--	100 (0.0)	--	--	64.7 (11.6)
2010	--	93.9 (4.4)	--	--	77.2 (7.6)
2011	--	97.1 (1.0)	--	--	74.2 (2.4)
2012	--	92.9 (3.3)	--	--	61.2 (6.1)
2013	--	71.8 (4.1)	49.0 (5.7)	64.9 (7.7)	31.6 (4.9)
2014	97.2 (1.2)	94.1 (1.8)	73.2 (3.5)	81.8 (3.6)	59.6 (3.5)
2015	82.1 (6.8)	42.9 (6.4)	34.4 (9.5)	85.8 (1.3)	33.0 (9.0)
2016	98.5 (1.1)	94.8 (2.0)	75.6 (4.2)	80.0 (4.5)	60.3 (4.0)
2017	95.7 (3.2)	91.4 (4.6)	91.4 (8.2)	73.6 (9.0)	66.8 (8.0)
Average	93.4 (3.1)	86.5 (3.1)	64.7 (6.2)	77.2 (5.2)	58.7 (6.3)

In years other than 2015, estimated survival was roughly proportional to distance, although the slop for mortality per km was steeper in the reach from Bonneville to McNary reach than in Snake or Salmon River reaches. Excluding 2015, average estimated survival was lowest in the reach from Lower Granite to Sawtooth (58%), followed by the reach from Bonneville to McNary (70%), Ice Harbor to Lower Granite (92%), and McNary to Ice Harbor (97%). Estimated survival was also relatively low in 2013, at only 73% from Ice Harbor to Lower Granite and 32% from Lower Granite to Sawtooth. Estimated survival from Bonneville to the Sawtooth Valley averaged 34% across all years.

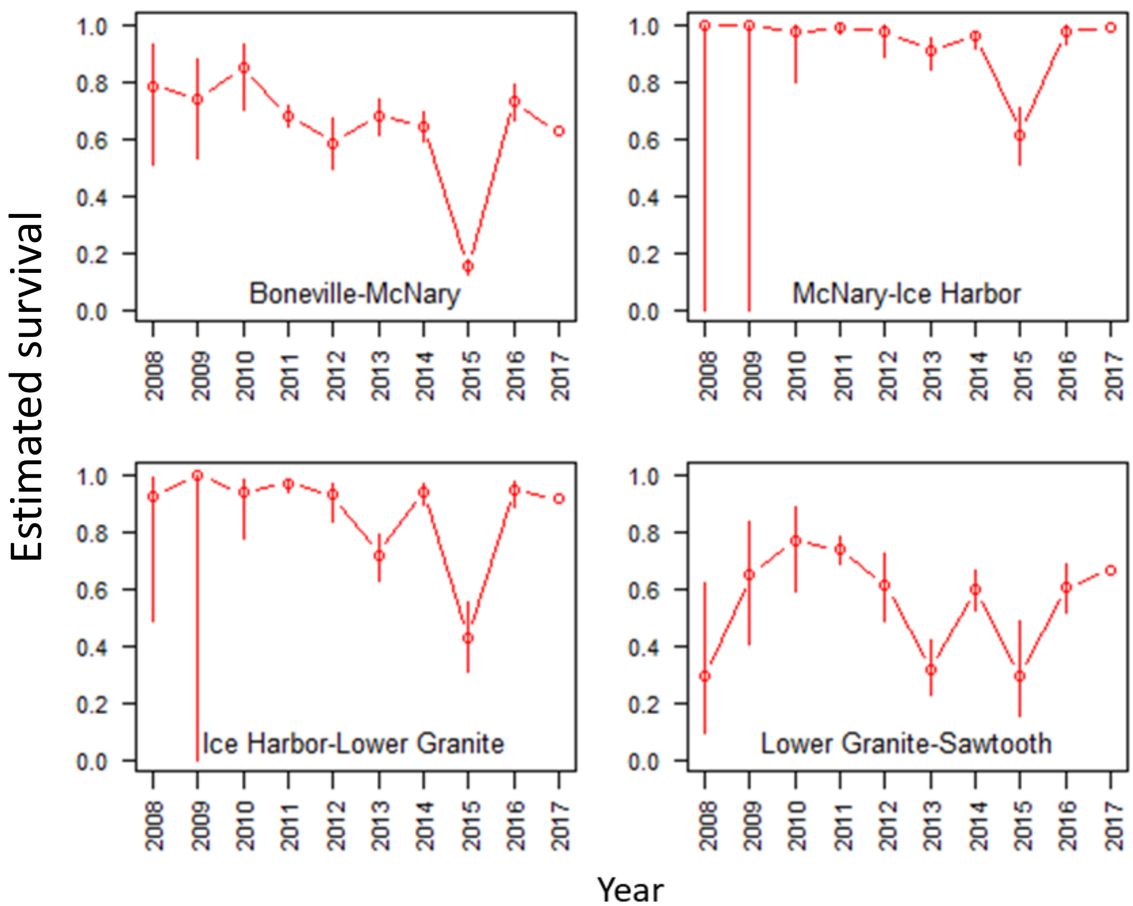


Figure 3. Estimated survival for Snake River sockeye salmon by reach from 2008 to 2017. Shown are CJS model estimates with 95% confidence intervals for Bonneville to McNary, McNary to Ice Harbor, Ice Harbor to Lower Granite, and Lower Granite to the Sawtooth Valley.

Objective 4: Migration Characteristics

Migration timing and travel time

Snake River sockeye arrived at each dam over a window of about 4 weeks (Figure 4). Across all years, 95% arrived at Bonneville between 17 June and 11 July, and the interquartile range was between 25 June and 5 July (Table 4). On average, 50% of the run had passed Lower Granite Dam by 12 July and 95% by 20 July. Average travel time was 12 d from Bonneville to Lower Granite Dam and 52 d from Bonneville to Sawtooth (Table 5). Thus, there was also about a 4-week period of arrivals at Lower Granite Dam, which occurred about 2 weeks after the arrival period at Bonneville Dam (essentially all of July). Arrival at the Sawtooth weir continued throughout August.

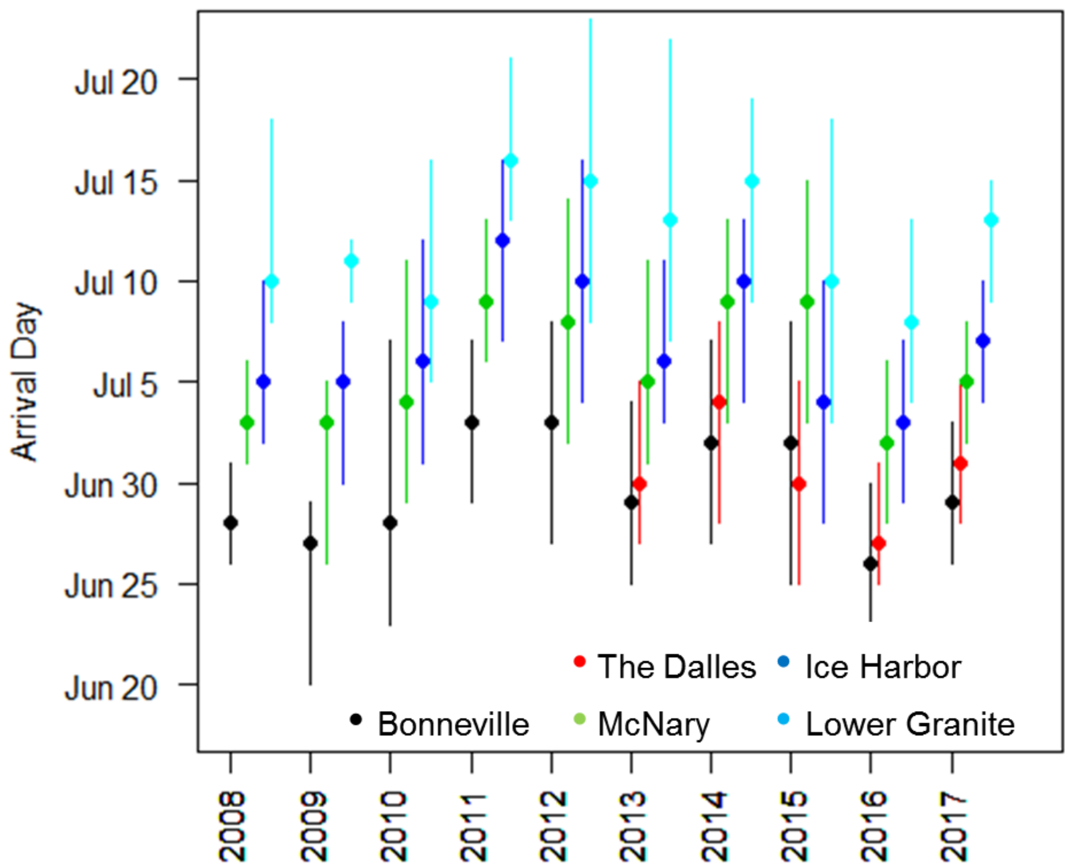


Figure 4. Median date of arrival at Columbia and Snake River dams for Snake River sockeye from 2008 to 2017. Whiskers show 50% quantile intervalsr.

Table 4. Median arrival date at dams by year for Snake and Columbia River sockeye populations. Dates encompassing the 25th-75th quantiles are shown in parenthesis.

	Median date of arrival						
	Snake River sockeye salmon						
	Bonneville	The Dalles	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
2008	6/28 (6/26-7/01)	--	7/03 (7/01-7/06)	7/05 (7/02-7/10)	--	--	7/10 (7/08-7/18)
2009	6/28 (6/21-6/30)	--	7/04 (6/27-7/06)	7/06 (7/01-7/09)	--	--	7/12 (7/10-7/13)
2010	6/29 (6/24-7/08)	--	7/05 (6/30-7/12)	7/07 (7/02-7/13)	--	--	7/10 (7/06-7/17)
2011	7/04 (6/30-7/08)	--	7/10 (7/07-7/14)	7/13 (7/08-7/17)	--	--	7/17 (7/14-7/22)
2012	7/03 (6/27-7/08)	--	7/09 (7/02-7/14)	7/10 (7/04-7/16)	--	--	7/15 (7/08-7/23)
2013	6/30 (6/26-7/05)	7/01 (6/28-7/06)	7/06 (7/02-7/12)	7/07 (7/04-7/12)	--	--	7/14 (7/08-7/25)
2014	7/03 (6/28-7/08)	7/05 (6/29-7/09)	7/10 (7/04-7/14)	7/11 (7/05-7/14)	7/12 (7/06-7/15)	7/13 (7/08-7/17)	7/16 (7/10-7/20)
2015	7/03 (6/26-7/09)	7/01 (6/26-7/06)	7/10 (7/05-7/16)	7/05 (6/29-7/11)	7/01 (6/27-7/07)	7/01 (6/29-7/08)	7/11 (7/04-7/19)
2016	6/26 (6/23-6/30)	6/27 (6/25-7/01)	7/02 (6/28-7/06)	7/03 (6/29-7/07)	7/05 (7/01-7/09)	7/06 (7/02-7/11)	7/08 (7/04-7/13)
2017	6/30 (6/27-7/04)	7/02 (6/29-7/06)	7/06 (7/03-7/09)	7/08 (7/05-7/11)	7/09 (7/07-7/12)	7/12 (7/09-7/15)	7/14 (7/10-7/16)
	Upper Columbia River sockeye salmon						
	Bonneville	The Dalles	McNary	Priest Rapids	Rock Island	Rocky Reach	Wells
2008	6/23 (6/20-6/27)	--	6/28 (6/24-7/01)	7/03 (6/30-7/05)	7/06 (7/04-7/11)	7/06 (7/05-7/09)	7/09 (7/07-7/11)
2009	6/25 (6/21-6/28)	--	7/01 (6/28-7/05)	7/05 (7/02-7/09)	7/09 (7/06-7/13)	7/11 (7/08-7/17)	7/13 (7/08-7/17)
2010	6/23 (6/20-6/27)	--	6/29 (6/26-7/03)	7/03 (6/30-7/07)	7/07 (7/04-7/11)	7/07 (7/05-7/11)	7/10 (7/07-7/13)
2011	6/29 (6/25-7/04)	--	7/06 (7/01-7/10)	7/11 (7/07-7/15)	7/16 (7/11-7/19)	7/15 (7/12-7/20)	7/18 (7/15-7/22)
2012	6/25 (6/21-6/30)	--	7/02 (6/27-7/07)	7/08 (7/05-7/13)	7/12 (7/09-7/17)	7/13 (7/10-7/18)	7/16 (7/12-7/21)
2013	6/25 (6/19-6/30)	6/26 (6/21-7/02)	6/30 (6/24-7/05)	7/05 (7/01-7/09)	7/08 (7/04-7/12)	7/09 (7/06-7/13)	7/12 (7/08-7/17)
2014	6/30 (6/24-7/05)	7/02 (6/26-7/07)	7/05 (6/29-7/10)	7/08 (7/03-7/13)	7/10 (7/07-7/15)	7/13 (7/09-7/18)	7/15 (7/10-7/19)
2015	6/24 (6/19-7/01)	6/25 (6/21-7/01)	6/26 (6/22-6/30)	6/29 (6/25-7/02)	7/01 (6/28-7/05)	7/02 (6/28-7/06)	7/04 (7/01-7/08)
2016	6/22 (6/17-6/28)	6/23 (6/18-6/29)	6/26 (6/22-7/01)	6/29 (6/26-7/05)	7/02 (6/29-7/08)	7/02 (6/29-7/09)	7/04 (7/01-7/10)
2017	6/24 (6/19-6/29)	6/26 (6/21-7/01)	6/29 (6/25-7/04)	7/03 (6/29-7/07)	7/08 (7/04-7/11)	7/09 (7/05-7/11)	7/10 (7/07-7/14)

Table 5. Median travel time (d) by reach between dams for the Snake and upper Columbia River sockeye from 2008 to 2017. Time from the 25th to 75th quantile is shown in parentheses.

	Travel time (d)					
	Snake River sockeye salmon					
	Bonneville to McNary	McNary to Ice Harbor	Ice Harbor to Lower Granite	Lower Granite to Sawtooth	Bonneville to Lower Granite	Bonneville to Sawtooth
2008	5.1 (4.8-5.5)	1.5 (1.4-1.7)	4.6 (4.1-5.4)	41.7 (38.3-51.3)	11.6 (10.9-12.2)	51.0 (48.5-61.8)
2009	6.3 (4.9-7.4)	2.0 (1.7-2.3)	5.9 (4.5-6.8)	43.2 (35.8-47.0)	14.0 (12.3-15.3)	57.1 (48.2-59.8)
2010	5.3 (4.5-6.0)	1.9 (1.5-2.5)	4.4 (3.8-5.5)	36.4 (34.2-39.4)	12.1 (10.3-13.4)	47.8 (45.2-52.6)
2011	6.0 (5.3-6.9)	1.9 (1.6-2.2)	5.0 (4.2-6.4)	39.9 (35.0-49.2)	13.0 (11.9-15.1)	54.0 (47.5-63.5)
2012	5.8 (5.3-6.5)	1.9 (1.6-2.7)	5.0 (3.9-6.8)	40.5 (33.6-54.3)	12.9 (11.7-15.0)	51.6 (46.0-64.2)
2013	5.4 (4.9-6.7)	1.7 (1.4-2.1)	6.8 (4.8-15.5)	42.7 (38.4-63.7)	15.1 (11.8-24.1)	55.2 (51.1-80.6)
2014	5.2 (4.5-6.2)	1.7 (1.4-2.0)	5.0 (4.1-7.5)	37.1 (33.8-44.9)	13.0 (10.7-15.8)	49.2 (44.7-56.5)
2015	5.9 (4.9-8.7)	2.3 (1.8-3.0)	9.1 (7.0-18.9)	45.7 (39.6-53.0)	18.0 (13.6-25.2)	63.3 (53.2-68)
2016	4.9 (4.1-6.0)	1.8 (1.4-2.8)	5.1 (4.2-6.7)	41.1 (35.0-61.5)	12.1 (10.3-14.3)	53.4 (46.3-73.9)
2017	5.2 (4.3-6.1)	1.9 (1.2-2.1)	5.1 (4.3-6.2)	43.5 (37.6-48.3)	12.2 (10.9-13.4)	55.5 (49.0-62.9)
	Bonneville to The Dalles	The Dalles to McNary	Ice Harbor to Lower Monumental	Lower Monumental to Little Goose	Little Goose to Lower Granite	
2013	1.9 (1.6-2.3)	3.7 (3.1-4.8)	--	--	--	
2014	1.8 (1.5-2.3)	3.4 (3-4.4.0)	1.3 (1.0-2.0)	1.3 (1.0-1.9)	2.2 (1.6-4.3)	
2015	2.0 (1.4-5.8)	4.1 (3.4-6.7)	3.1 (2.1-4.9)	2.2 (1.6-3.2)	4.3 (2.5-12.6)	
2016	1.6 (1.3-2.0)	3.1 (2.8-4.1)	1.6 (1.1-2.5)	1.4 (1.1-2.0)	2.1 (1.6-3.0)	
2017	1.9 (1.1-2.2)	3.3 (3.1-4.0)	1.3 (1.1-2.3)	1.1 (0.9-2.1)	2.1 (2.0-3.0)	

Table 5. Continued.

	Travel time (d)					
	Upper Columbia River sockeye salmon					
	Bonneville to McNary	McNary to Priest Rapids	Priest Rapids to Rock Island	Rock Island to Rocky Reach	Rocky Reach to Wells	Bonneville to Wells
2008	5.4 (4.5-7.8)	4.9 (4.2-5.9)	3.5 (3-4.3)	1.0 (0.8-1.7)	2.4 (2.1-3.2)	18.6 (16.8-23.1)
2009	5.5 (5-6.6)	4.1 (3.7-4.8)	3.5 (2.8-4.6)	1.0 (0.9-1.6)	2.1 (1.9-3)	15.5 (14.2-17.2)
2010	5.3 (4.7-6.1)	4.1 (3.9-4.8)	3.3 (2.8-4.2)	0.9 (0.8-1)	2.1 (1.6-3.1)	15.8 (14.2-18.7)
2011	6.0 (5.3-6.9)	5.1 (4.6-6.3)	3.9 (3.1-4.9)	1.1 (0.9-1.5)	2.4 (1.9-3.2)	18.6 (16.1-20.6)
2012	5.8 (5.1-6.6)	6.9 (5.3-8.8)	3.9 (3-4.9)	1.5 (1-2.1)	2.7 (2.1-3.2)	20.8 (18.4-23.7)
2013	5.0 (4.6-5.7)	5.0 (4.2-6.2)	3.0 (2.4-4)	1.0 (0.9-1.4)	2.0 (1.6-2.4)	17.0 (14.7-19.1)
2014	4.8 (4.3-5.3)	3.8 (3.2-4.2)	3.2 (2.3-4.5)	0.9 (0.8-1.2)	1.7 (1.4-2)	14.1 (12.9-15.8)
2015	4.6 (4.1-5.3)	3.3 (3-3.9)	2.9 (2.3-3.9)	1.1 (0.9-1.3)	1.8 (1.4-2.5)	13.6 (12.6-16.3)
2016	4.2 (3.9-4.9)	3.6 (3.3-4.1)	3.0 (2.6-3.7)	1.0 (0.8-1.2)	1.9 (1.6-2.3)	14.2 (12.8-15.8)
2017	5.2 (4.2-6.2)	4.7 (3.9-5.2)	3.2 (3-4.1)	1.1 (0.9-1.8)	2.1 (1.9-3)	16.9 (14.3-18.9)

Travel time of Snake River sockeye was fairly consistent across years, with the exceptions of 2015 in the Lower Columbia River and 2013 and 2015 in the Snake (Table 5). In the reach from Bonneville to McNary Dam, median travel time varied by only about 1 d across years (4.9-6.3 d). However, migration was slower in 2013 and 2015. For example, the 75th percentile migrated through the Lower Columbia River over 9 d in 2016 vs. 5-6 d in other years. Similarly, in 2013 and 2015, respectively, the 75th percentile reached Lower Granite from Ice Harbor Dam in 15.5 and 18.9 d.

In both 2013 and 2015, slower migration corresponded to periods of high temperature, which might have caused fish to alter migration behavior, perhaps by looking for thermal refugia or simply waiting for cooler water. There do not appear to be many thermal refugia in the Snake River, although slightly cooler areas have been identified near the Lyons Ferry Hatchery and Palouse River mouth (Keefer and Caudill 2015).

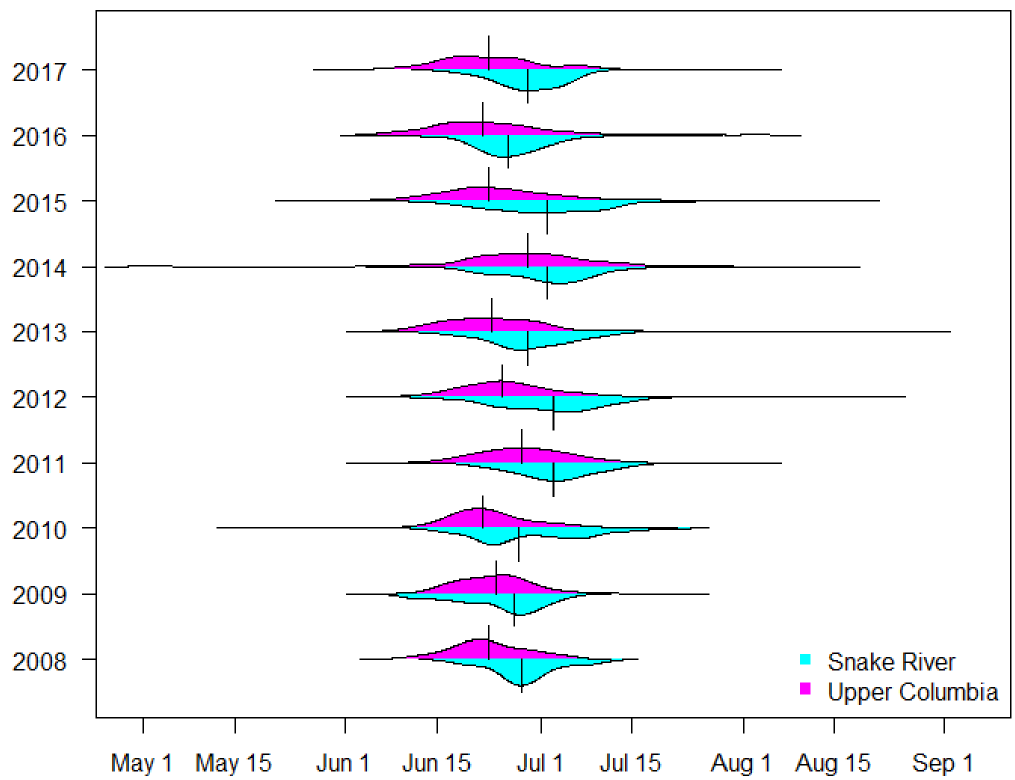


Figure 5. Distribution of arrival dates at Bonneville Dam for Snake and Upper Columbia River sockeye, 2008-2017. Vertical lines indicate median passage date for the population.

Snake River sockeye arrive at Bonneville, The Dalles, and McNary Dam later than Upper Columbia River sockeye. Snake River sockeye arrived an average of 5 d later than Upper Columbia sockeye at Bonneville (30 vs. 25 June; Figure 5) and The Dalles (1 July vs. 26 June), and 6 d later at McNary (6 July vs. 30 June; Table 4).

Fallback percentages

For Snake River sockeye, fallback percent was highest at most dams in 2015 (Figure 6, Appendix Table 2) when it peaked at The Dalles with a record of 28.8%. Over one-quarter of Snake River sockeye also fell back at Lower Monumental in 2015 and at Lower Granite during 2012-2014. Upper Columbia River sockeye, on the other hand, had no trouble at The Dalles, with a max fallback percent of 2.7% in 2013.

Snake River sockeye consistently exhibited higher fallback percent than upper Columbia sockeye (Figure 6). From 2008 to 2017, respective average fallback percentages for Snake and upper Columbia River sockeye were 6.7 and 3.8% overall and 2.9 and 1.9% at McNary Dam. For Upper Columbia sockeye, mean fallback percent did not exceed 5% at any dam, and rarely exceeded this percent in individual years.

We examined a linear regression of the number of fish that fell back using our method vs. the method of the Columbia Basin Research group reported on DART (CBR 2018). Fallback percentages showed high correlation ($r^2 \geq 0.97$) at The Dalles, Ice Harbor, Lower Monumental, and Little Goose Dam. Fallback percentages were most similar at Lower Monumental and Little Goose (average rates were equal, $r^2 \geq 0.9$). Only two years of fallback estimates were available for Lower Granite Dam, but our percentages were somewhat higher (1-4% higher) than those reported by CBR (2018). The largest differences across methods were seen at McNary Dam, where no fallbacks were reported under the CBR criteria, and at Bonneville Dam, where percentage were equal between methods from 2008 to 2012. At Bonneville during 2013-2017, fewer fish met the CBR criteria than met ours. In general, however, annual variation was similar across methods.

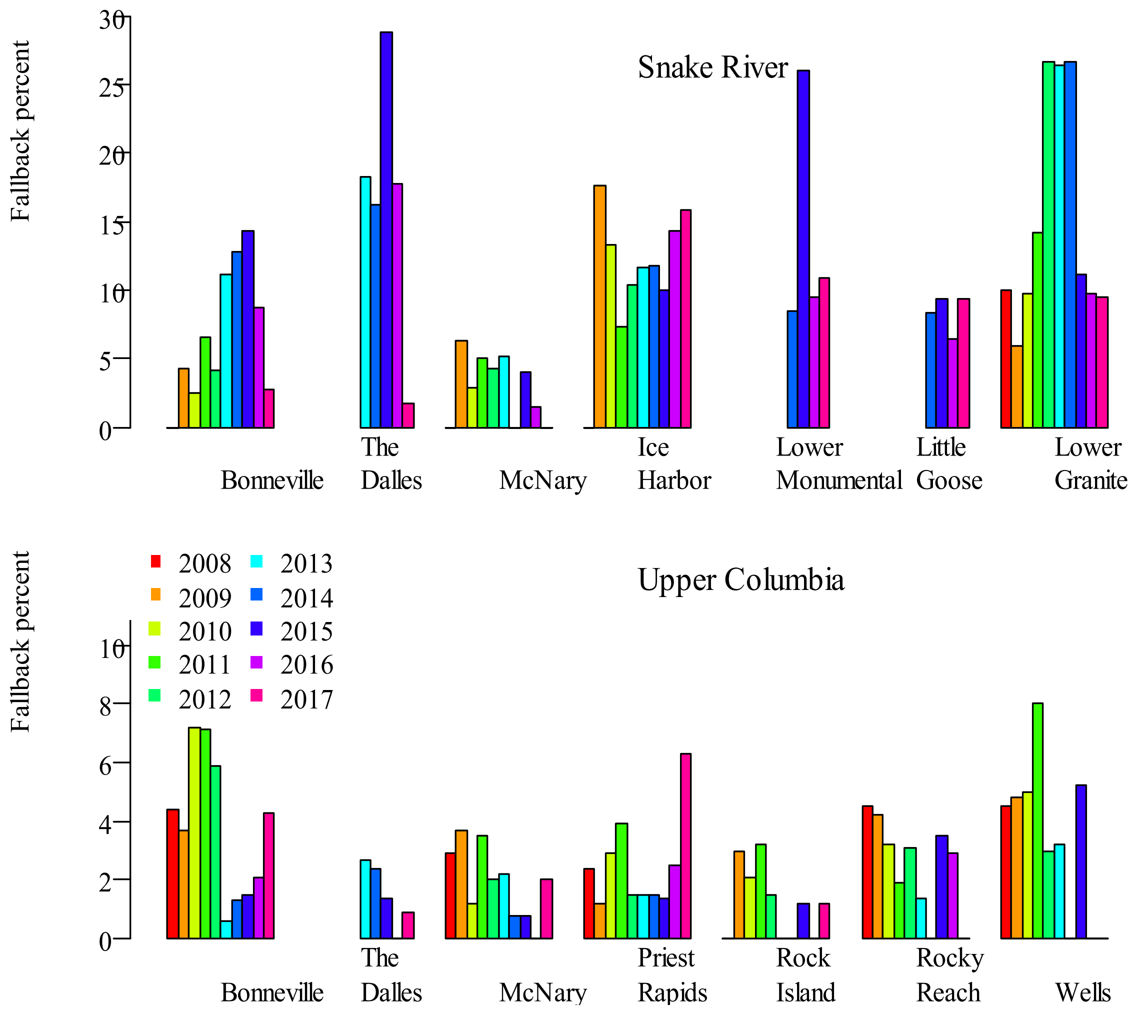


Figure 6. Percent fallback (unique fish) at dams for Snake River and upper Columbia River sockeye.

Objective 5: Covariate Analyses of Survival and Fallback

Covariates affecting adult migration survival

Temperature upon reach entry and cumulative temperature were the most important predictors of observed migration survival for Snake River sockeye across all years of data, 2008-2017. Temperature was highly significant for all reaches. The quadratic temperature term had an importance of 1 for all reaches except that from Lower Granite to Sawtooth, where it was replaced by day and either cumulative temperature or travel time (Tables 6 and 7, Figure 7). Note that quadratic terms always had the associated linear term in the model, which was the standard polynomial equation. However, the linear terms could occur without their associated quadratic terms. Thus, when the importance of the linear term exceeded that of the quadratic term for the same factor, support for a linear relationship was indicated.

Variables with correlation coefficient over 0.7 were not included in the same model (Appendix Table 3). Although model averaging tables included covariates that were highly correlated, among correlated pairs, the variable with higher importance was generally the better predictor. Temperature and flow were generally strongly correlated, but from Lower Granite to Sawtooth, flow was a slightly better predictor of observed survival. Because temperatures at Lower Granite Dam are regulated by controlled releases of cooler water from Dworshak Dam, they may not represent the conditions fish experienced during most of the migration to the Sawtooth Valley. Thus flow might have been a better predictor of survival because it was more strongly correlated with temperature in the Salmon River.

Transportation had a substantial effect on survival for Snake River sockeye in the reach from Bonneville to McNary, but this effect was reduced in reaches upstream. Observed survival rates were within the confidence intervals of survival estimates for most years in all reaches. Most models captured the majority of annual variation in observed survival (R^2 = 0.86-0.92) and did even better when compared with CJS estimates of survival (R^2 = 0.87-0.97).

The Lower Granite-Sawtooth model for Snake River had lower R^2 values (R^2 = 0.48 and 0.49, respectively compared with observed and estimated survival), but this annual estimate did not account for low sample sizes in some years. Observed survival estimates in a few years were outside model-predicted confidence estimates, but note the large confidence estimates on the observations (Figure 8). The top five survival covariate models that were utilized in model averages are shown with their AICc rank in Appendix Table 4. Note that the all models accounting for the top 95% of AIC weight were included in the model average.

Table 6. Covariate model results for survival in the reach from Bonneville to McNary Dam for adult Snake River and upper Columbia River sockeye. Asterisks represent significant coefficients ($P < 0.05$). Note, quadratic terms were considered for *temperature* and *day* but not other variables.

Bonneville to McNary (Snake River fish)			Bonneville to McNary (Upper Columbia River fish)		
	Coefficient	Importance		Coefficient	Importance
(Intercept)	0.4679*	NA	(Intercept)	1.2216*	NA
Temperature^2	-0.7173 *	1	Temperature^2	-0.2618*	1
Temperature	-0. 8991*	1	Temperature	0.0964	1
Fallback	-0.3336*	1	Age	-0.2762*	1
Transport	-0.3126*	1	Spill	-0.2587*	1
Age	-0.2164*	1	Day	-0.2123*	1
Catch	-0.1038*	0.84	Day^2	0.0467*	0.94
Day	-0.0632	0.60	Fallback	-0.0420	0.64
Spill	0.0292	0.33	Catch	0.0134	0.34
Day^2	0.0231	0.53	Hatchery/wild	-0.0140	0.31
Hatchery/wild	0.0183	0.36			

Table 7. Results from covariate models of survival in Snake and Salmon River reaches for Snake River sockeye. Asterisks represent significant coefficients ($P < 0.05$). CumT = cumulative temperature. Only covariates with importance greater than 0.3 are shown. Note, quadratic terms were considered for *temperature* and *day*.

McNary to Ice Harbor			Ice Harbor to Lower Granite		
	Coefficient	Importance		Coefficient	Importance
(Intercept)	2.2862*	NA	(Intercept)	2.707*	NA
Temperature	-0.6369*	1.00	Temperature	-0.8184*	1.00
Temperature^2	-0.4860*	1.00	Temperature^2	-0.4512*	1.00
Age	0.2518*	1.00	Fallback	-0.2449*	0.86
CumT	-0.5329*	0.99	CumT	-0.4021*	0.86
Travel time	0.1287	0.59	Day	-0.0815	0.52
Transport	-0.0924	0.53	Age	0.0632	0.48
Day	-0.0742	0.50	Transport	0.0665	0.40
Spill	-0.0964	0.43	Travel time	-0.0262	0.35
Hatchery/wild	-0.0357	0.40	Gas	0.0254	0.29
Fallback	-0.0374	0.38	Day^2	0.0346	0.26
			Hatchery/wild	-0.0095	0.26

Lower Granite to Sawtooth		
	Coefficient	Importance
(Intercept)	0.5540*	NA
Day	-0.4353*	1.00
Flow	0.5688*	0.97
Detected at trap	-0.1046*	0.84
Spill	0.2792*	0.82
Fallback	-0.1428*	0.82
Age	0.1016	0.73
Day^2	-0.1285	0.66
CumT	-0.2976*	0.56
Travel time	-0.2798*	0.43
Transport	-0.0075	0.27
Hatchery/wild	-0.0057	0.26

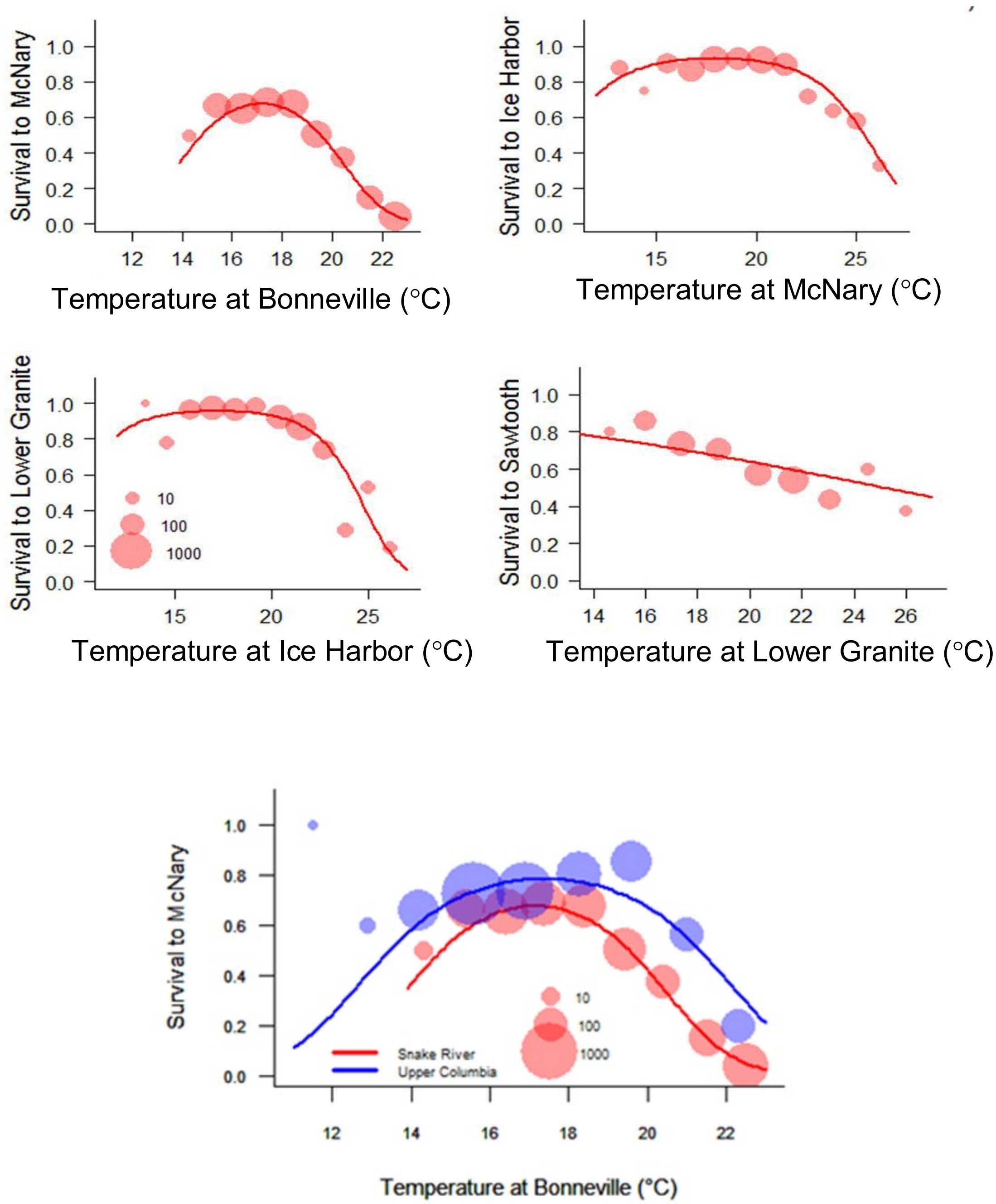


Figure 7. Observed survival vs. temperature in Columbia and Snake River reaches with model fit (line) for Snake River sockeye. Size of circles represents sample sizes of fish in each temperature bin. Data in top left panel shown again in comparison with upper Columbia sockeye in lower panel.

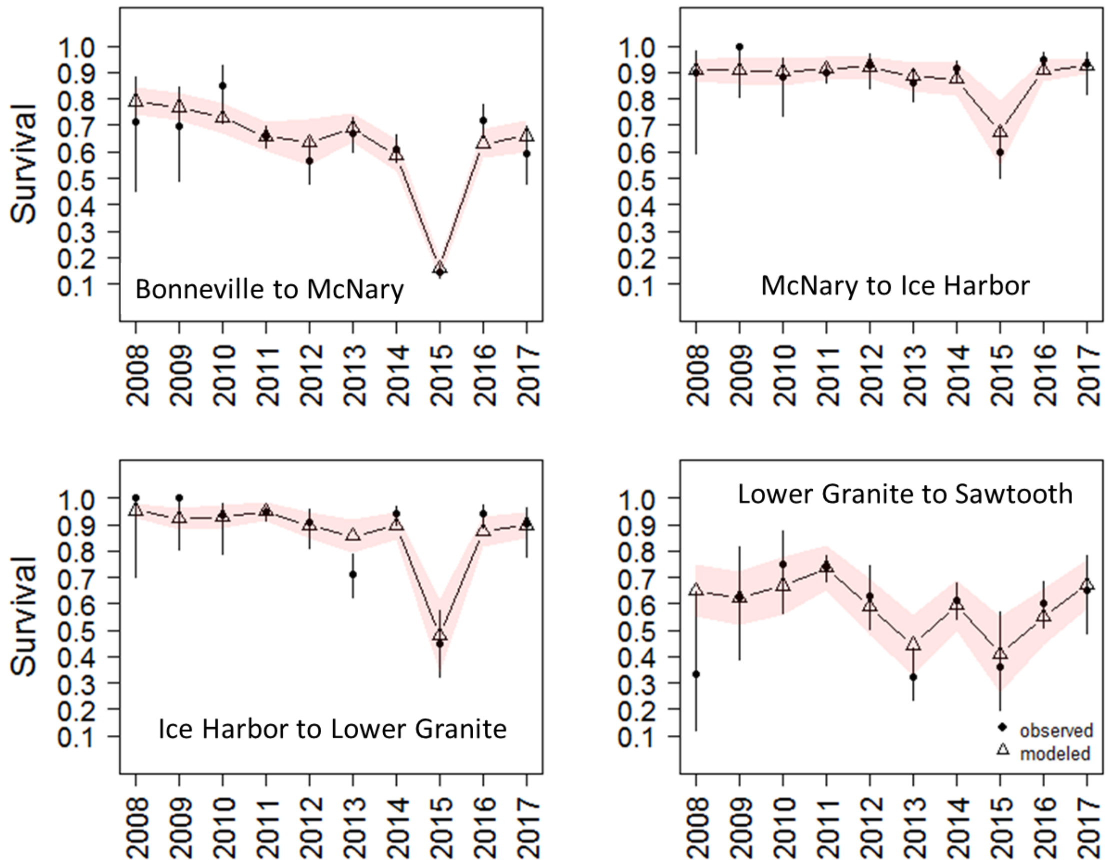


Figure 8. Observed survival and covariate-model predictions in the reaches from Bonneville to McNary, McNary to Ice Harbor, Ice Harbor to Lower Granite, and Lower Granite to Sawtooth for Snake River sockeye. For each model prediction, 95% confidence limits are shown in the shaded area. Whiskers show confidence limits for observed survival based on sample size using the binomial distribution.

Covariates affecting fallback percentages

Similar to the analysis of survival, we used the model average to rank predictors of fallback for Snake River sockeye at Bonneville, The Dalles (2013-2017), McNary, Ice Harbor, and Lower Granite Dam, utilizing all available data from 2008 to 2017. While the Bonneville and The Dalles models described the majority of annual variation in fallbacks (R^2 = 0.72 and 0.88 respectively) and the Ice Harbor and Lower Granite models were moderately successful (R^2 = 0.34 and 0.31 respectively), the McNary model described little annual variation (R^2 = 0.02), potentially due to low numbers of fallbacks at this dam. The most important predictors of fallback were temperature or day of arrival, travel time or cumulative temperature, and juvenile transportation history (Table 8). The preference among these correlated variables varied by dam. Relationships with day of arrival and temperature were both better described with the inclusion of a quadratic component. Temperature and day of arrival were both significant at all dams except for McNary. In general, fallbacks increased with temperature up to about 20°C at Bonneville (Figure 9) and Ice Harbor Dam, and to about 22°C at Lower Granite before decreasing at higher temperatures. Adults that were transported as juveniles were substantially more likely to fall back at Columbia River dams, particularly at Bonneville (Figure 9 and Table 8). However, transportation had a minor effect on fallbacks at the Snake River dams.

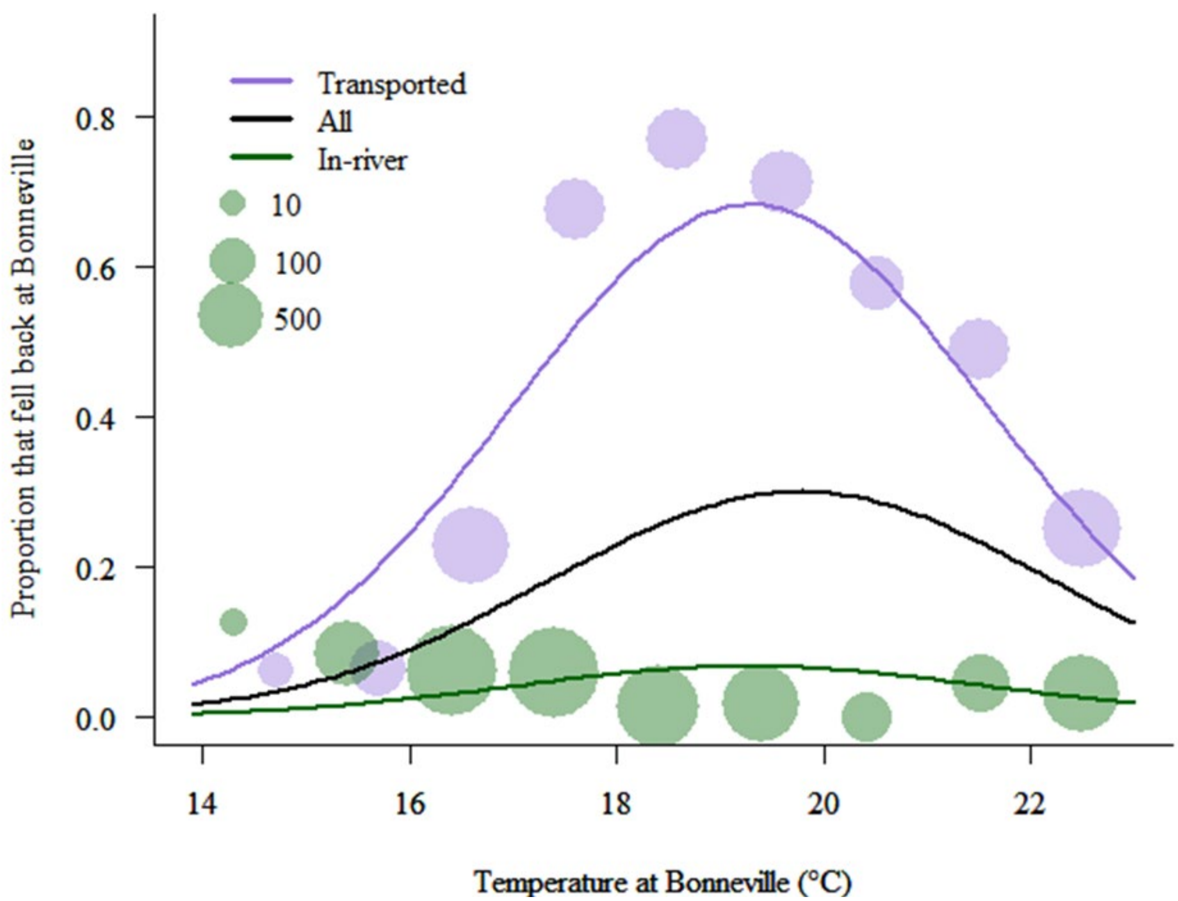


Figure 9. Observed fallback in relation to temperature at Bonneville Dam and model fit (central red line). Outer lines depict the juvenile transport effect, with the bottom line depicting fallback for non-transported fish and the top line depicting fallbacks for transported fish.

Table 8. Covariate model results of top predictors of fallback in Snake River sockeye. Asterisks indicate significant coefficients ($P < 0.05$). CumT = Cumulative temperature; BOMN fallback = sum of fallbacks at Bonneville and McNary; BOIH fallback = sum of fallbacks at Bonneville, McNary and Ice Harbor Dam.

Bonneville	Coefficient	Importance	The Dalles	Coefficient	Importance	McNary	Coefficient	Importance
(Intercept)	-2.1599	NA	(Intercept)	-2.1498*	NA	(Intercept)	-3.4863*	NA
Transport	1.1081*	1	Temperature	-0.0089	1	Transport	0.4580*	0.9393
Hatchery/wild	-1.1587	0.7645	Temperature^2	-0.2633*	1	Travel time	0.1998*	0.7149
Temperature	0.1598*	0.6093	Transport	1.6134*	1	Temperature	-0.2141	0.5364
Temperature^2	-0.3145*	0.6093	Travel time	0.2754*	1	Temperature^2	-0.2535	0.4448
Day	-0.0807*	0.3907	BO fallback	0.0350*	0.7361	Hatchery/wild	-0.5628	0.3516
Spill	-0.1612*	0.3907	Age	0.0171	0.3412	Day	0.0078	0.3501
Age	0.0159	0.3386	Gas	-0.0005	0.2441	Gas	-0.0976	0.3383
Day^2	0.0004	0.0892	Hatchery/wild	-0.0005	0.2184	Fallback	-0.1292	0.3334

Ice Harbor	Coefficient	Importance	Lower Granite	Coefficient	Importance
(Intercept)	-4.1508	NA	(Intercept)	-1.5067*	NA
BOMN fallback	0.9407*	1	Day	0.4710*	1
Day^2	-1.0052*	1	Flow	-0.5581*	0.8928
Day	0.6879	1	Spill	0.1554*	0.796
Travel time	0.5309*	0.8845	CumT	-0.1789*	0.5996
Gas	-0.1435	0.4276	Day^2	-0.0249	0.3892
Temperature	-0.0941	0.3527	Age	-0.0204	0.3604
Transport	-0.0846	0.3439	Travel time	-0.1274*	0.3597
Hatchery/wild	-0.5574	0.3073	Transport	0.0248	0.3434
Temperature^2	0.1771*	0.2744	BOIH fallback	-0.0207	0.3091
Spill	0.1453	0.2694	Hatchery/wild	-0.0033	0.2565
Age	0.0066	0.2586	Temperature	0.0514*	0.1072
Flow	0.118	0.2151	Temperature^2	-0.0235*	0.0991

Travel time from Bonneville was an important and significant predictor of fallback at The Dalles, McNary, and Ice Harbor Dams (Table 8). Travel time and cumulative temperature were correlated variables and were essentially equally useful for explaining fallback at Lower Granite Dam. Number of fallbacks increased with longer travel time at McNary and Ice Harbor, but decreased with travel time/cumulative temperature at The Dalles and Lower Granite. When cumulative temperature or travel time were regressed against fallback by themselves, the coefficients were positive, as expected. However, both became negative after accounting for flow at Lower Granite.

Fish transported as juveniles were more likely to fall back than in-river migrants at Bonneville (Figure 9), The Dalles, and McNary Dam, but not at the Snake River dams (Table 8). Fish also had a higher fallback rate if they had fallen back at previous dams. Hatchery vs. wild origin was highly important at Bonneville Dam but was not significant. Spill was significant but unimportant at Bonneville Dam, with a negative effect on fallback. Fish age was neither important nor significant at any dam.

Ladder temperature differentials

We examined patterns in ladder temperature differentials in 2016 and 2017. The greatest temperature differentials during a sockeye ascent occurred at Lower Monumental (5.9°C, Figure 10), followed by Little Goose (2.7°C), Lower Granite Dam (2.5°C, Figure 10), McNary (1.5°C), Ice Harbor (1.2°C), and The Dalles (0.4°C). The largest median temperature differentials were also at Lower Monumental (0.6°C). While the greatest differentials tended to occur in August, when reservoirs are most stratified and surface temperatures are highest, temperature differentials occurred at Lower Monumental throughout the run and at cooler temperatures. In general at other dams, only a small number of late arriving fish experienced the highest differentials.

Ladder temperature differentials at McNary Dam were not significant predictors of fallback at McNary or of survival to Ice Harbor, Lower Granite, or Sawtooth. Ladder temperature differential at Ice Harbor Dam was not a significant predictor of fallback at Ice Harbor or of survival to Lower Granite. Neither measure of ladder temperature differentials (EN1 or EN2) at Little Goose was a significant predictor of fallback or survival.

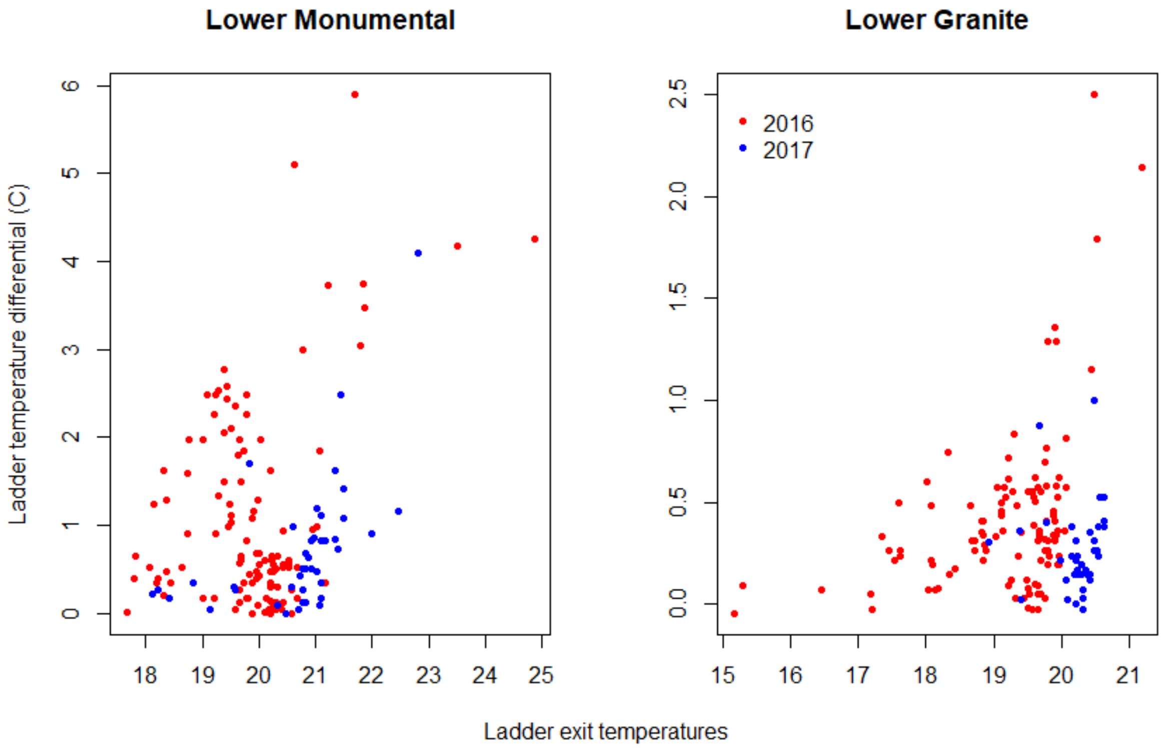


Figure 10. Ladder temperature differential at Lower Granite Dam compared with forebay temperature LWG-S1, measured upstream from the sprinkler. Despite forebay temperatures of over 22°C in 2017, ladder differentials stayed within 1°C, whereas in 2016 the differential reached 2.5°C.

Table 9. Model comparison of passage time as a function of ladder temperature differential (LTD), and other covariates. Time of day was tested as either a linear (hour) or quadratic term (hour^2). The degrees of freedom (df) and delta AIC scores are shown for separate model comparisons at Lower Granite and Ice Harbor Dam.

		ΔAIC	
Model	df	Lower Granite	Ice Harbor
Passage time ~ LTD	3	0.0	0.5
Passage time ~ tailrace temperature	3	7.2	1.3
Passage time ~ forebay temperature	3	7.3	1.3
Passage time ~ LTD + hour	4	1.6	2.4
Passage time ~ LTD + hour^2	5	0.4	0.0
Passage time ~ LTD + hour^2 + tailrace temp	6	2.4	1.3

While not a significant predictor of fallback, ladder temperature differential at Lower Monumental had a negative relationship with survival to Lower Granite and to Sawtooth (Appendix Figure 1), though only survival to Lower Granite was significant ($\chi^2_{1, 170}$ = 11.1, P = 0.001). However, despite large temperature differentials at Lower Monumental in both 2016 and 2017, only 9 of 172 fish detected at Lower Monumental were not detected at Lower Granite, suggesting high survival in this reach during these years.

At Lower Granite, the model of passage time as a function of ladder temperature differential had a lower AIC than models with either tailrace or forebay temperatures (Table 9), and ladder temperature differential was the only significant variable tested ($F_{1,164}$ = 7.47, P = 0.007, Figure 11). Adding time of day made a very small difference (ΔAIC $\leq$ 0.5), and the coefficient on hour was not significant (P > 0.05).

Ladder temperature differential at Lower Granite was a significant predictor of fallback at Lower Granite ($\chi^2_{1, 164}$ = 6, P = 0.014, Figure 11), whereas other temperature metrics were not significant. Similarly for survival to Sawtooth, ladder temperature differential was significant ($\chi^2_{1, 164}$ = 8.5, P = 0.004). When all variables found to be important in the covariate model were considered, ladder temperature differential was included among the top models based on AIC weight. More specifically, models that included this term accounted for 32% of AIC weight (Table 10). However, the coefficient on this term was not significant when averaged over the models that included it (Table 10).

Table 10. Model-average results for survival from Lower Granite to Sawtooth for the years 2016 and 2017. Asterisks represents significant coefficients (P < 0.05).

Lower Granite to Sawtooth	Coefficient	Importance
(Intercept)	0.5179	NA
Day	-0.7665*	0.7111
Day^2	-0.3056	0.5477
Flow	0.0491	0.3020
Transport	-0.0452	0.2968
Temperature	0.0595	0.3740
Temperature differential	-0.0643	0.3182
Hatchery/wild	-0.0205	0.2582
Age	-0.0008	0.2372
Fallback	0.0087	0.2469
Cumulative temperature	-0.2064*	0.1800

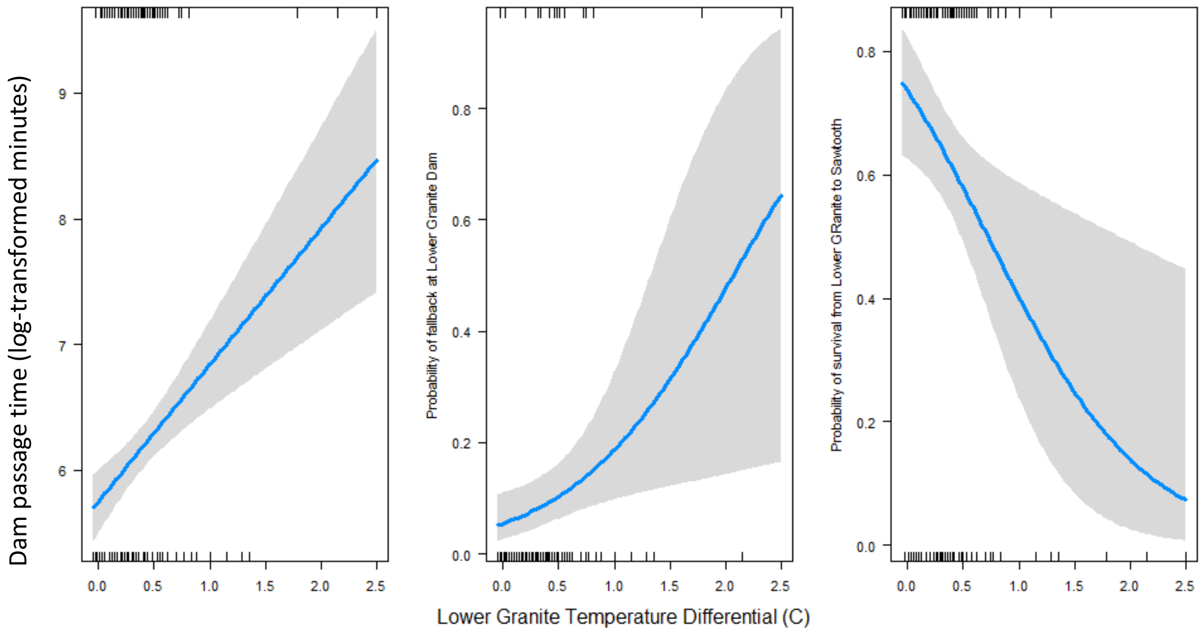


Figure 11. Modeled relationships with 95% confidence area in grey between ladder temperature differential at Lower Granite Dam and dam passage time (left), probability of fallback (middle), and survival to Sawtooth (right).

In summary, ladder temperature differential was a significant predictor of passage time at Lower Granite, the only dam with an adequate distribution of passage times for analysis. Ladder temperature differential significantly increased fallback at Lower Granite, but not at other dams. Finally, ladder temperature differential was a significant predictor of survival from Lower Monumental to Lower Granite and from Lower Granite to Sawtooth. However, for Lower Granite it was not a stronger predictor than other factors previously identified in the survival models. One possible reason for this result could be that ladder temperature differentials contributed to those other factors, but were not exclusively responsible for them. For example, a delay caused by ladder temperature would also have elevated the cumulative temperature exposure, which was significant. Cumulative delays throughout the hydrosystem also led to later arrival at Lower Granite Dam, which was also a significant predictor of upstream survival. Ladder temperature differentials could therefore be influencing overall survival through various mechanisms, although the direct effects might be sublethal.

Objective 6: Adult Transport Thresholds and Benefit Ratios

Temperature during mean run periods vs. survival by reach

Mean run periods that we selected (20-d periods centered on the mean of the median run dates) incorporated the majority of the run in all years (Figure 12). The mean run period occurred from 21 June to 10 July at Bonneville Dam and from 28 June to 17 July at Ice Harbor. Consistent with individual models, mean temperature during this standardized period was a strong predictor of annual survival for the population as a whole (Figure 13; Bonneville to Ice Harbor: generalized cross validation (GCV) = 0.010, deviance explained = 91.3%, and Ice Harbor to Lower Granite: GCV = 0.021, deviance explained = 77.2%).

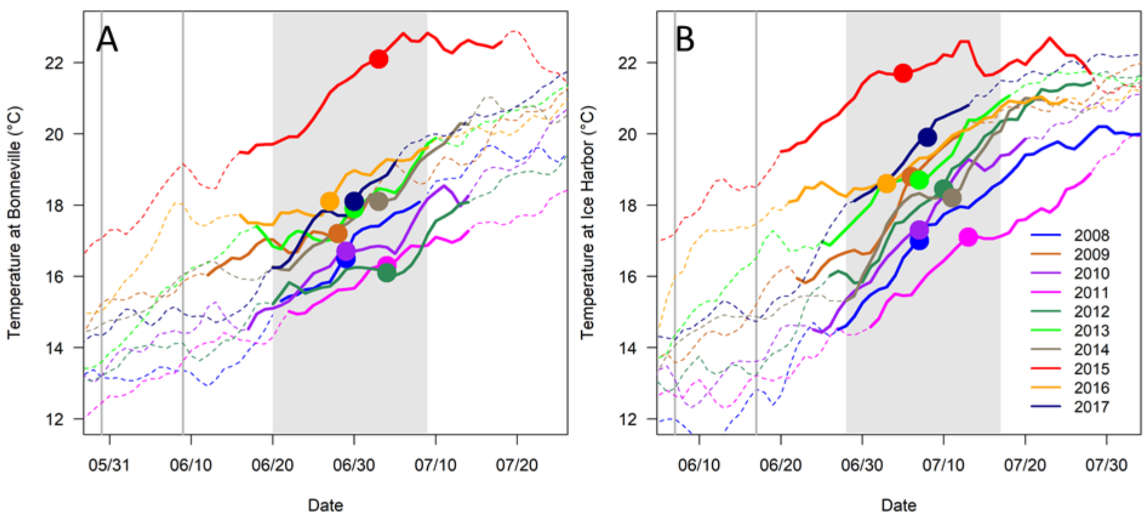


Figure 12. Timing of the adult Snake River sockeye run by year vs. river temperature at Bonneville (A) and Ice Harbor (B) dams. Colored lines represent river temperature in each year. Solid colored segments represent 0.025-0.975 quartiles of the run past each dam and circles indicate the median passage date. Shaded areas represent 20-d mean run periods, and vertical grey lines show the end of the two forecasting periods.

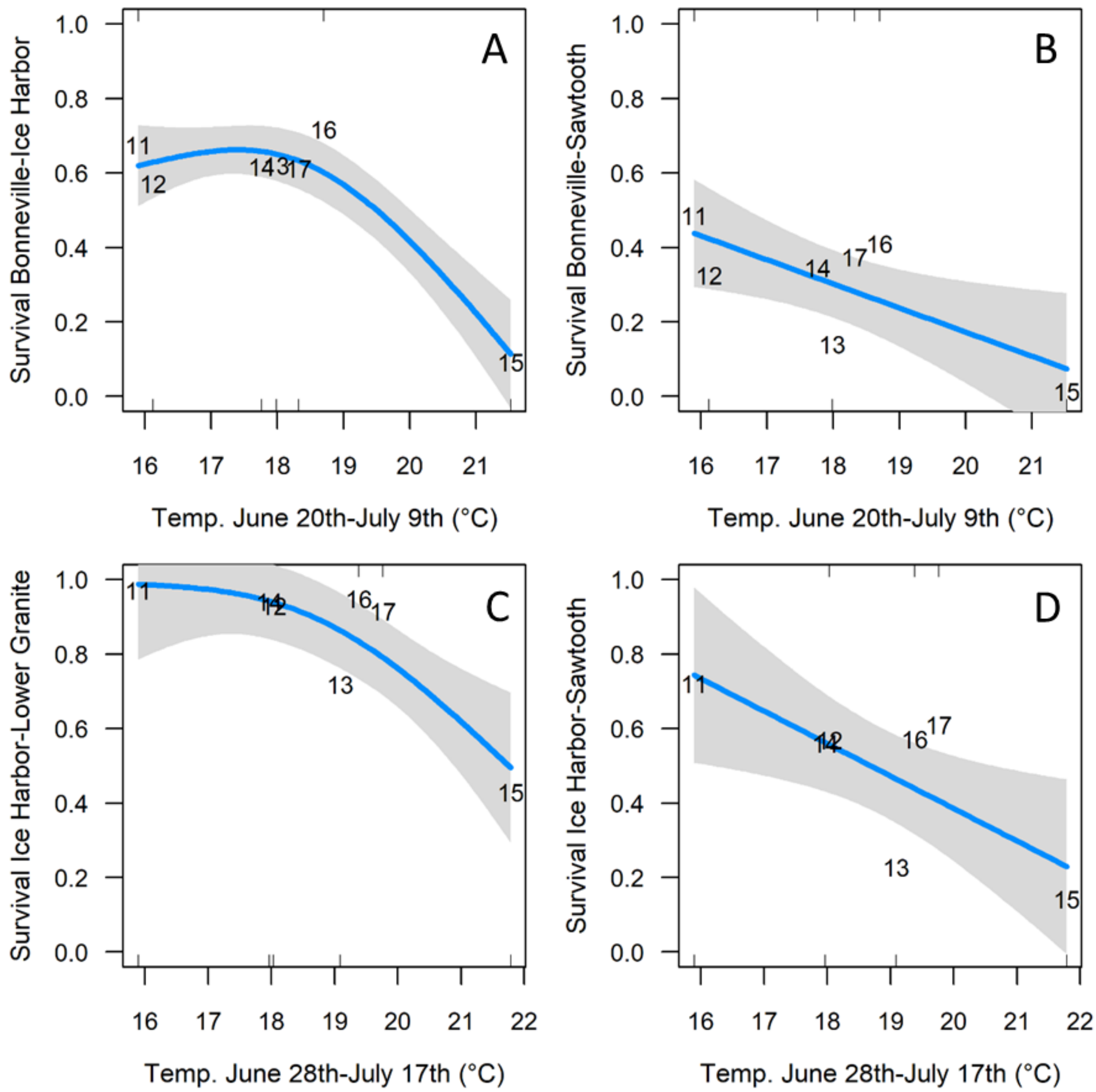


Figure 13. Mean run period temperatures vs. reach survival from Bonneville to Ice Harbor (A), Ice Harbor to Lower Granite, (C) and from Bonneville and Ice Harbor to the Sawtooth Valley (B and D). Lines the model predictions, and shaded areas indicate 90% confidence intervals. Numbers 0-17 represent years 2000-2017 where 1 = 2001, 2 = 2002…, 17 = 2017 and show observed survival in that year.

Mean temperature during mean run periods also had a strong relationship with survival from respective dams to the Sawtooth Valley, though variability was higher in this relationship (Figure 13 B and D; Bonneville to Sawtooth, GCV = 0.021, deviance explained = 54%; Ice Harbor to Sawtooth, GCV = 0.035, deviance explained = 55%). While migration survival in most years was well described by forecast models, survival in 2013 was lower than predicted from Ice Harbor through the Sawtooth Valley, while survival in 2016 was higher than predicted in all modeled reaches.

The deviation in 2016 might have resulted from a relatively early run. Although anomalously high temperatures in 2015 created a gap in the data range available for this annual analysis, the shapes of these relationships were similar to those from individual analyses, which included fish experiencing the full range of temperatures (Figure 7).

Predicted temperature during mean run periods

We used mean river temperature during the 20-d periods ending 10 and 20 d in advance of the beginning of the mean run periods to predict mean temperatures during the mean run periods. These predictive cushion models predicted subsequent temperatures with good accuracy (Figure 14). Ten-day cushion models for reaches from Bonneville to Ice Harbor (root mean square error (RMSE) = 0.60, $R^2 = 0.77$, $P < 0.001$, Figure 15A) and from Ice Harbor to Lower Granite (RMSE = 0.68, $R^2 = 0.77$, $P < 0.001$, Figure 15C) were more accurate than 20-d cushion models (RMSE = 0.70, $R^2 = 0.69$, $P = 1.92\text{e-}06$, Figure 15B, RMSE = 0.74, $R^2 = 0.72$, $P < 0.001$, Figure 15D). Nevertheless, the 20-d advance models retained high predictive value.

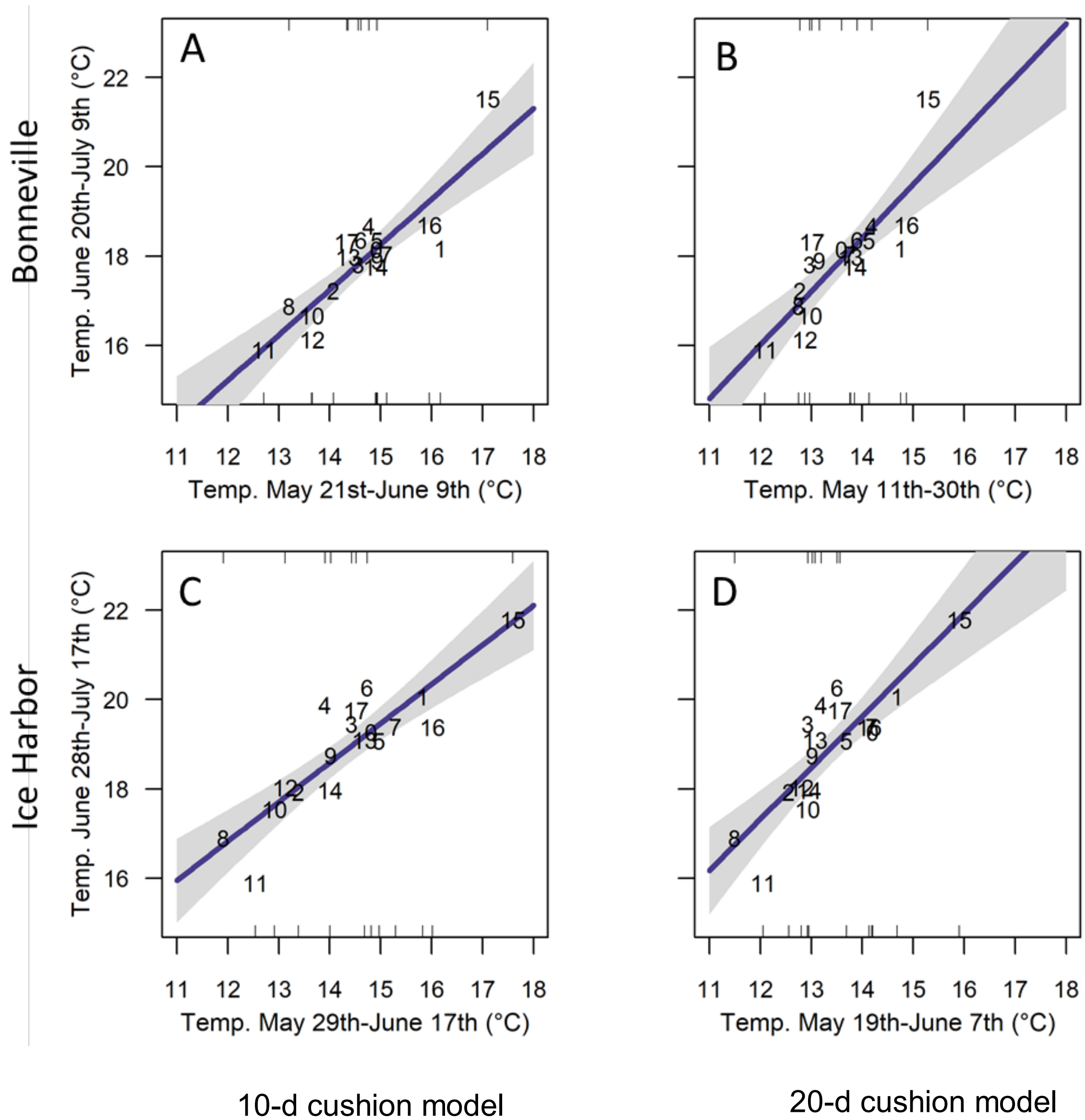


Figure 14. Plots showing 10-d (A and C) and 20-d (B and D) cushion period mean river temperatures (x axes) vs. mean river temperature during mean run periods (y axes) of Snake River sockeye at Bonneville and Ice Harbor. Fit lines and confidence intervals for linear models describing relationships between variables are shown. Numbers 1-17 represent years 2001-2017, where 1 = 2001, 2 = 2002,…, 17 = 2017.

Predicted migration survival from temperature forecasts

As described above, we found strong relationships between river temperature during cushion periods and river temperature during mean run periods, as well as between river temperature during mean run periods and migration survival. Accordingly, we modeled migration survival directly utilizing river temperatures during the prediction cushion periods (Figure 15).

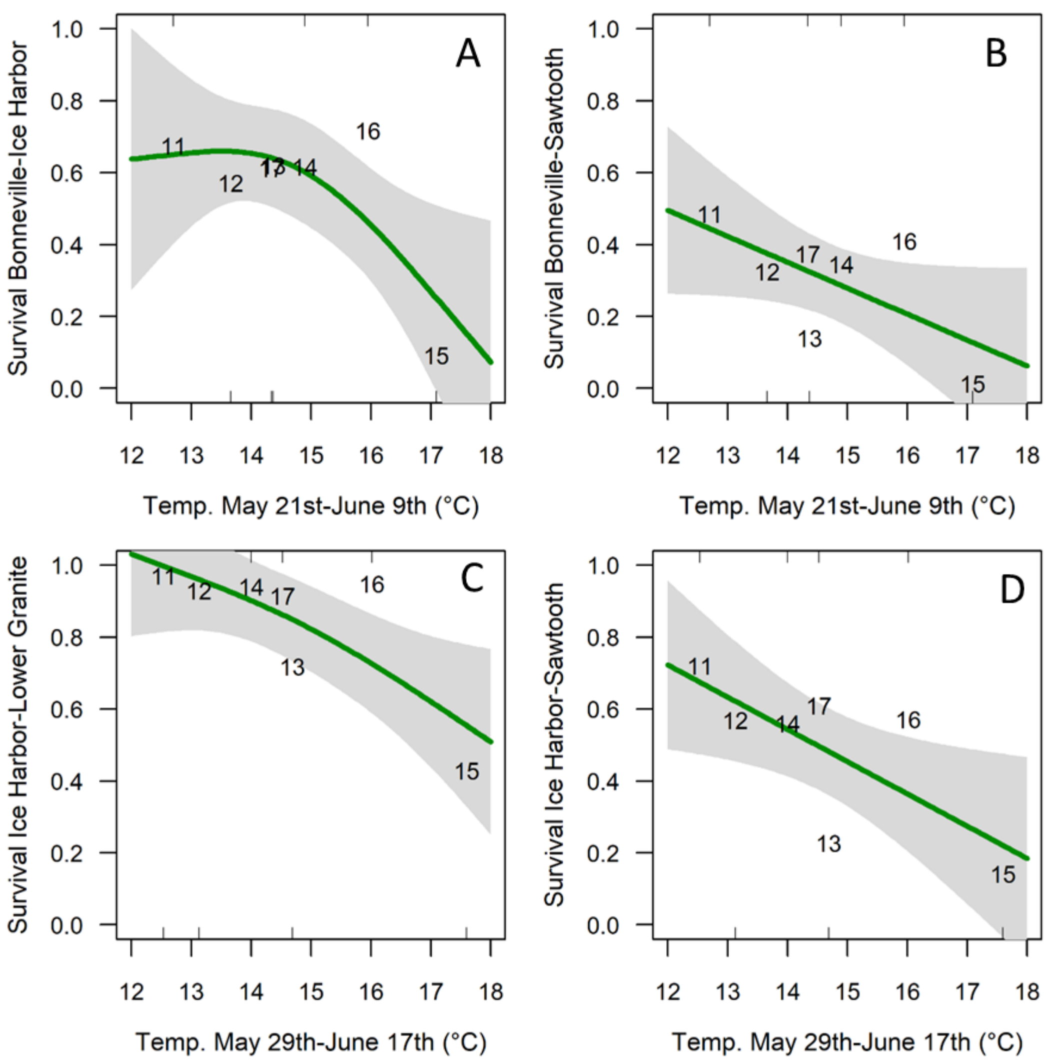


Figure 15. Plots showing 10-d cushion period mean river temperature vs. reach-specific survival of adult Snake River sockeye from Bonneville to Ice Harbor and Sawtooth (A and B respectively) and from Ice Harbor to Lower Granite (C and D respectively). Fit lines and confidence intervals for GAM models describing relationships between variables are shown. Numbers represent points for specific years; 1 = 2001, 17 = 2017, etc.

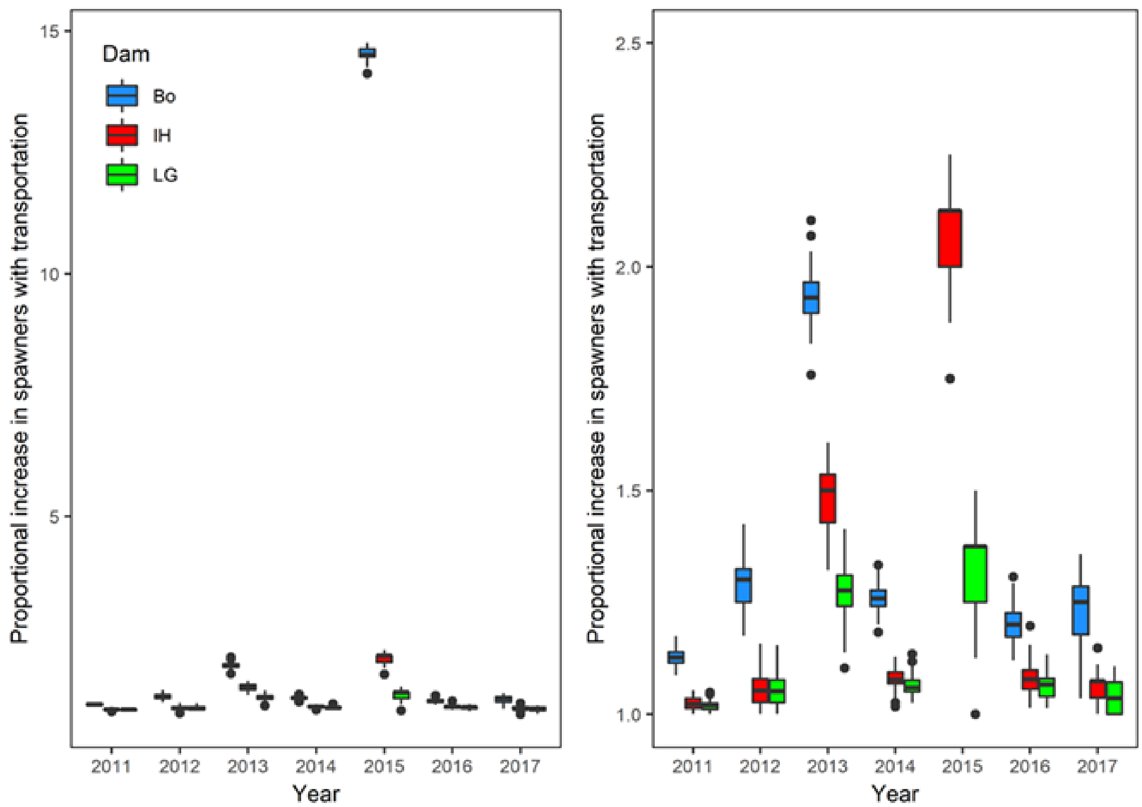
Ten-day cushion models were fairly accurate in predicting reach-specific survival (Bonneville to Ice Harbor, GCV = 0.037, deviance explained = 62.6 %, Figure 15A; Ice Harbor to Lower Granite, GCV = 0.028, deviance explained = 62.7%, Figure 15C) and survival from Bonneville and Ice Harbor to the Sawtooth Valley (Bonneville to Ice Harbor, GCV = 0.028, deviance explained = 40.4 %, Figure 15A; Ice Harbor to Lower Granite, GCV = 0.037, deviance explained = 51.7%, Figure 15C).

Adult transport benefit ratios

We modeled the potential benefit of adult transportation from Bonneville, Ice Harbor and Lower Granite on survival to the Sawtooth Valley for years with sufficient sample sizes (2011-2017, Figure 16). Survival increased with transportation in all cases based on the assumption that 20% of the run was transported with 80% transportation survival. The transport benefit ratio was defined as estimated survival with transportation divided by observed survival to Sawtooth. For transportation from Bonneville, the benefit ratio ranged from a low of 1.1 in 2011 to an outlier high of 14.5 in 2015. For transportation from Ice Harbor, the benefit ratio ranged from a low of 1.0 in 2011 to a high of 2.1 in 2015 with similar but slightly lower benefit from Lower Granite.

After 2015, the next highest benefit ratio was for 2013, with estimates of 1.9 from Bonneville and 1.5 for transport from Ice Harbor. While all survival proportions were above 1.1 with transportation from Bonneville, in 2013 and 2015, survival proportions were above 1.1 only with transportation from Ice Harbor.

Given predictions from 10- and 20-d cushion models, years that would have triggered transportation at different threshold temperatures are shown in Table 11. Temperatures were sufficiently high in 2015 that all reasonable thresholds (16-20°C) would have triggered transportation. However, because 2013 and 2016 were slightly inverted in their temperature/survival relationships, there was no clear winner in the ability to pick out the lowest-survival years overall. In order to capture the low-survival year of 2013, transportation in 2016 and 2017 would also have been triggered. However, because survival in those later years was higher than expected, the benefit ratio was relatively low. Additional work will be needed to separate out these years if greater predictability is required.



Dam	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	Average
Bonneville	1.13	1.29	1.94	1.26	14.53	1.20	1.23	1.34
Ice Harbor	1.02	1.06	1.48	1.08	2.06	1.08	1.05	1.13
Lower Granite	1.02	1.05	1.28	1.06	1.32	1.06	1.02	1.08

Figure 16. Predicted transport benefit ratios with transportation from Bonneville, Ice Harbor, and Lower Granite dams by year. Both panels show the same information, but the right panel has a smaller range on the y-axis to better illustrate variation in results from most years. Box and whisker plots show the median (horizontal line) and interquartile range (box) and 1.5 × the interquartile range (vertical lines) from 100 iterations of randomly selected fish.

Table 11. Outcome of the trigger decision by year for various temperature thresholds. If transport was triggered, the expected transport benefit ratio is shown for Bonneville and Ice Harbor Dams.

Threshold for transportation (°C)	2011	2012	2013	2014	2015	2016	2017
	Transportation from Bonneville Dam						
	Benefit ratio						
	1.13	1.29	1.94	1.26	14.53	1.20	1.23
	10-d cushion model triggers transport						
16	NO	YES	YES	YES	YES	YES	YES
17	NO	NO	YES	YES	YES	YES	YES
18	NO	NO	NO	YES	YES	YES	NO
19	NO	NO	NO	NO	YES	YES	NO
20	NO	NO	NO	NO	YES	NO	NO
21	NO	NO	NO	NO	NO	NO	NO
	20-d cushion model triggers transport						
16	YES	YES	YES	YES	YES	YES	YES
17	NO	YES	YES	YES	YES	YES	YES
18	NO	NO	YES	YES	YES	YES	NO
19	NO	NO	NO	NO	YES	YES	NO
20	NO	NO	NO	NO	NO	NO	NO
21	NO	NO	NO	NO	NO	NO	NO
	Transport from Ice Harbor Dam						
	Benefit ratio						
	1.02	1.06	1.48	1.08	2.06	1.08	1.05
	10-d cushion model triggers transport						
16	YES	YES	YES	YES	YES	YES	YES
17	YES	YES	YES	YES	YES	YES	YES
18	NO	NO	YES	YES	YES	YES	YES
19	NO	NO	YES	NO	YES	YES	YES
20	NO	NO	NO	NO	YES	YES	NO
21	NO	NO	NO	NO	YES	NO	NO
	20-d cushion model triggers transport						
16	YES	YES	YES	YES	YES	YES	YES
17	YES	YES	YES	YES	YES	YES	YES
18	NO	YES	YES	YES	YES	YES	YES
19	NO	NO	NO	NO	YES	YES	YES
20	NO	NO	NO	NO	YES	NO	NO
21	NO	NO	NO	NO	YES	NO	NO

Run-timing prediction

The ability to predict run timing could help determine when to initiate transportation operations in order to capture the largest proportion of the run, and improve our ability to predict survival. We explored the relationship between temperature and flow with different quantiles of the run passing Bonneville. From 2011to 2017, initiation of the run at Bonneville, as measured by the 0.025 quantile, ranged from 14-21 June with a mean date of 17 June (Table 4; 2008-2010 excluded due to low sample sizes).

Mean river discharge at Bonneville Dam during 21-30 May (20-day cushion period) was a strong linear predictor for initiation of the run (Figure 17; RMSE = 1.04, $R^2 = 0.85$, $P = 0.003$). This metric also predicted the 0.25 quartile of the run with fair accuracy (RMSE = 1.57, $R^2 = 0.55$, $P = 0.057$). However, median date was less strongly related to this metric (RMSE = 2.91, $R^2 = 0.11$, $P = 0.474$).

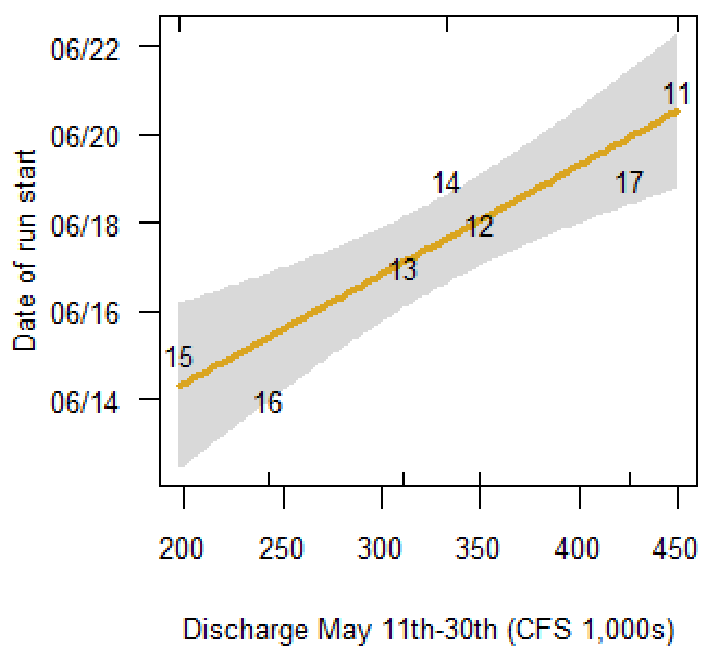


Figure 17. Plot showing the relationship between mean discharge at Bonneville during the 20-d cushion period (11-30 May) and the start of the adult Snake River sockeye population run as measured by the estimated 0.025 quantile at Bonneville for years 2011-2017.

Discussion

Patterns in migration survival and fallback

Migration survival of Snake River sockeye throughout the FCRPS in 2014, 2016, and 2017 demonstrated reach-specific patterns and overall survival similar to that seen in earlier years (2008-2013). However, migration survival in 2015 was much lower than in any year previously observed. Survival from Bonneville to the Sawtooth Valley was estimated at ~1% in 2015 compared to 14% in 2013, the next lowest year. Most adult mortality in 2015 occurred between Bonneville and McNary Dam, where ~85% of all Snake River sockeye were estimated to have perished. Fallback rates at most dams were also highest in 2015 (Figure 6). In contrast to the Snake River ESU, upper Columbia sockeye experienced a more modest drop in survival in the Bonneville-to-McNary reach during 2015, as well as lower-than-average fallback rates.

High river temperatures appear to have been the primary driver of low survival in 2015. In that year, even fish that had not been transported as juveniles had only 25% survival from Bonneville to McNary Dam and only 3% survival from Bonneville Dam to the Sawtooth trap. River temperatures at Bonneville were around 22°C during the median run date in 2015 compared to just over 18°C during the next warmest year (Figure 12). Results from covariate analysis suggest that river temperature during migration is a large component of survival through dams on the lower Columbia and Snake River: temperature had an importance of 1 in model averaging for all reaches between dams.

This extended the role of temperature spatially from our previous analysis, in which temperature was primarily relevant in the Snake and Salmon Rivers. The increased importance of temperature on migration survival through the Lower Columbia River seen in this study was a largely a consequence of the extensive mortality observed in 2015.

Regarding temperatures experienced during the adult migration, 2015 was an outlier (Figure 12). Nonetheless, survival of individual fish, given migration temperatures, followed the relationship previously described (Crozier et al. 2015), where higher mortality occurred above 18°C at Bonneville and above 21°C at McNary and Ice Harbor Dam. Other factors not included in our models may have possibly contributed to particularly low rates of survival in 2015; for example, unique fishery events, the condition of fish upon river entry, or high rates of pinniped injury.

However, the mortality event of 2015 was consistent with our previous conclusion that expected increases in global and regional temperatures will likely depress survival of this endangered ESU. With climate change, increases in air temperature and earlier snowpack runoff are predicted for the Pacific Northwest (e.g., Wu et al. 2012). Thus, years similar to 2015 are likely to become more common (Mantua et al. 2010).

Upper Columbia River sockeye arrived slightly earlier than average in 2015, and this early timing allowed them to avoid the worst of the high river temperatures (although they still experienced very high temperatures upstream from McNary Dam). In contrast, median run timing for Snake River sockeye was later than average. For the Snake River population, the median arrival date at Bonneville in 2015 was estimated to be 3 July. This was 8 d later than the median arrival date at Bonneville for Upper Columbia River sockeye in 2015 and 3 d later than the mean median arrival date during 2008-2017 (Table 4).

Additionally, the duration of the run through Bonneville Dam was prolonged for Snake River sockeye in 2015. While fish actually began showing up earlier than normal (Figure 12), the run lasted over 33 d as measured by the time between the 0.025-0.975 quantiles. In contrast, the population passage period at Bonneville for these fish was 24 d on average during 2008-2017. This suggests that fish stalled the migration in the lower Columbia in 2015, likely either due to temperature stress, or possibly seeking temperature refugia in cold-water tributary confluences.

The latter half of the run progressed more slowly from Ice Harbor to Lower Granite Dame during exceptionally warm periods in both 2013 and 2015. Although we do not have travel times to the intermediate dams for 2013, in 2015 the delay occurred between Little Goose and Lower Granite Dam. This reach lacks cool-water tributaries where migrating adults seek thermal refuge, as described for Chinook salmon and steelhead (Keefer et al. 2018). Thus, temperatures in this reach appear to present a largely unmitigated block to migration, with little opportunity for advantageous behavioral thermoregulation.

However, in the reach from Bonneville to McNary, Snake River sockeye had lower survival and higher fallback percentages than upper Columbia sockeye at the same migration temperatures (Figure 7 and Appendix Table 2). Within this reach, Snake River sockeye survival appears to decline rapidly when temperatures at Bonneville exceed 18°C, whereas Upper Columbia sockeye appear to tolerate temperatures up to 20°C. Differences in thermal performance during the spawning migration across sockeye populations have been noted previously in a study of Fraser River sockeye. Eliason et al. (2011) found variability in physiological performance among populations at different temperatures, suggesting that populations with more challenging migratory environments had higher aerobic scopes and cardiac capacities. However, Snake River sockeye have a discernably more strenuous migration than upper Columbia sockeye, as measured by distance and elevation, and they have historically experienced high temperatures in the Snake River prior to hydrosystem development. Additional factors appear to be at play in explaining the poorer performance of Snake River sockeye.

Substantially higher fallback rates may be one reason that Snake River sockeye experience lower survival at the same migration temperatures as upper Columbia River sockeye. Fallbacks increase travel time and thus temporal exposure to river conditions that may cause physical trauma and stress. This explains why covariate models of migration survival consistently found negative effects of fallback on reach-specific survival rates (Tables 6 & 7). In 2015, fallback rates of Snake River sockeye exceeded 25% at multiple dams on the Columbia River.

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As with survival, the high temperatures experienced by fish in 2015 likely contributed to temperature replacing flow, spill and gas from the previous report (Crozier et al. 2015) as a primary variable in the covariate analysis of fallbacks for the lower Columbia River dams (Table 8). Fallback rates at Bonneville Dam increased with temperature up to about 20°C before decreasing at higher temperatures, possibly as a consequence of low survival to reascension at temperatures above 20°C (Figure 9).

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Results suggest that juvenile transportation of Snake River sockeye, which does not occur for upper Columbia sockeye, contributes to higher fallback rates and lower migration survival. In our dataset from 2011-2017, the percent of adult fish transported as juveniles ranged from a low of 9% in 2012 to a high of 54% in 2015. The high rates of juvenile transportation among adults returning in 2015 contributed to lower adult migration survival during this year. Transported juvenile salmon have been shown in other studies to have higher stray rates, likely as a consequence of interruptions to olfactory imprinting, which reduces the directional homing sense (Keefer and Caudill 2014). Snake River Chinook salmon also experience decreased adult migration survival and increased fallbacks among fish that were transported as juveniles (Crozier et al. 2017). The best balance between the advantages and disadvantages of juvenile transportation for Snake River sockeye thus depends on carryover effects throughout the life cycle (Gosselin et al. 2018).

Note that our results might underestimate the effects of ladder differentials due to a limited ability to track passage time at dams and determine when, exactly, a fish delayed its migration, backed out of a ladder, or fell back over a dam due to their ladder experience rather than some other cause, such as reservoir conditions. Better estimates of passage time and behavior at all dams would have provided a more robust analysis, comparable to Caudill et al. (2013). However, our results are consistent with theirs, indicating that ladder temperature differentials have a detectable effect. Reducing these differentials might have contributed to the relatively high survival in 2017.

Estimated benefit of adult transportation

The success of a transportation program would depend on the actual sampling and survival rates that could be reliably achieved, as well as the ability to minimize unintended negative effects, such as mixing of different populations. Nonetheless, given the potential for high temperatures to become more common as a consequence of climate change, consideration of adult transportation from Bonneville may become a necessary management option. Transport from Bonneville Dam has not been seriously considered before because upper Columbia sockeye vastly outnumber Snake River sockeye. Therefore, in the absence of a PIT-tag sorting technique, identification of Snake River sockeye is not feasible. Additional logistical challenges would need to be overcome in order to selectively transport these adults.

However, particularly high mortality during 2015 in the reach from Bonneville to McNary Dam implied that transportation from Bonneville during this year would have considerably increased survival to the Sawtooth Valley. Indeed, our estimates indicated that transport in 2015 would have increased survival by over 14.5 times, from an estimated 8 tagged fish (Table 1) to about 115 tagged fish. As hatchery production of Snake River sockeye expands, larger numbers of fish could be PIT-tagged so that an adult separation-by-code system at Bonneville could become more feasible. We modeled benefit ratios of adult transport from Bonneville so that managers can consider the potential of developing this capacity.

In contrast, transport from Ice Harbor in 2015 might have doubled observed survival, but its mitigation of the primary mortality event that occurred in that year would have been minimal. Even when the high mortality rates of 2015 were excluded, transportation from Bonneville produced a substantially higher average estimated increase in spawners than transportation from Ice Harbor across study years (34 vs. 13%; Figure 16). The size of this increase was due to consistently high rates of mortality in the reach from Bonneville to McNary (Figure 2).

Despite river temperatures that were slightly warmer during 2016-2017 than during 2013 (Figures 13), migration survival in 2016-2017 was substantially higher than in 2013. Consequently, despite our accurate predictions of temperature during the mean run period, there was no temperature threshold that captured years with low observed survival and excluded years with normal survival (Table 11). Exploration of the specific factors that caused migration delays in 2013 could improve model forecasting.

The differences between 2013 and 2016-2017 show the importance of additional factors identified in our individual covariate models. These differences might also reflect improvement in passage conditions, such as cool water sprays at the upstream end of fish ladders. Other important factors, such as the rate of juvenile transportation, can be known in advance of the run and used to predict survival. Additionally, the condition of fish upon arrival from the ocean is likely to affect their ability to withstand strenuous conditions, and could be studied further.

Overall, when temperatures were as high as those seen in 2015, river temperature appeared to be the dominant factor leading to high mortality, with impacts exacerbated by high juvenile transportation rates. High temperature differentials within fishways also exacerbated these conditions, leading to slower dam passage, higher fallback percentages, and lower upstream survival from Lower Granite Dam. Fish were likely unable to avoid prolonged exposure to detrimental temperatures during 2015.

Forecast models predicted that 2015 would be anomalously warm, with mean temperatures at or above 20°C. Temperatures of 20°C or higher indicate a warming level that is clearly detrimental for migration survival as suggested by analyses at both the individual (Figure 7) and population level (Figure 13). Thus in future years similar to 2015, low migration survival could likely be predicted in advance (Figure 15). Such forecasts would allow time to organize transportation operations to ensure sufficient survival of anadromous sockeye for broodstock.

Conclusions

In conclusion, we found that high river temperatures in recent years (2014-2017) were a greater threat to sockeye salmon than in previous years. This threat is likely to continue to increase due to anthropogenic climate change. The functional relationship between survival and temperature remained the same as previously reported, but river temperatures were anomalously high in 2015. In that year, the earliest migrants survived, but the majority of the run stalled in the lower river, where they encountered lethal temperatures.

At a given temperature, Snake River sockeye continued to display higher fallback rates and lower survival than upper Columbia River sockeye. Snake River sockeye barged as juveniles were much more likely to fall back and less likely to survive passage through the Lower Columbia River. This explains a portion of the differential survival between Snake and Upper Columbia River sockeye, as well as the low survival in 2015. The prevalence of hatchery fish in the population and later arrival at Bonneville Dam also contribute to higher mortality rates for Snake River sockeye.

High temperatures during the migration period can be predicted based on river temperatures prior to the beginning of the run. Hence, temperatures prior to the migration period could be used as an indication of when adult transportation might be beneficial. However, because of the recent phenomenon of exceptionally high temperatures in both the Columbia and the Snake Rivers, long-term planning that considers transportation from Bonneville Dam would be even more beneficial than indicated in our previous report.

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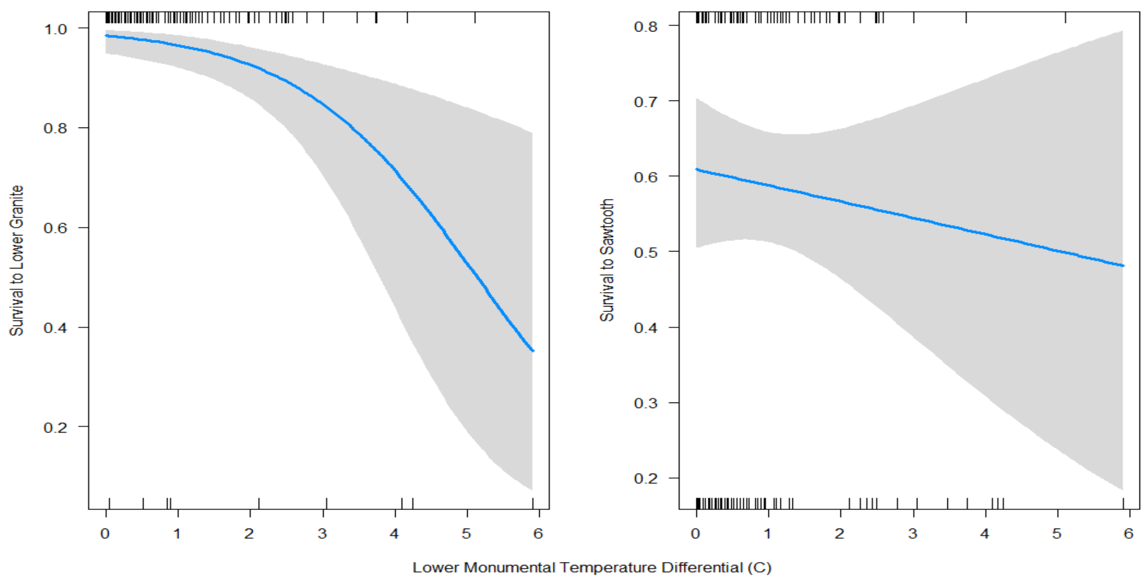
Appendix



Appendix Figure 1. Modeled relationships with 95% confidence area in grey between ladder temperature differential at Lower Monumental and survival to Lower Granite (left) and the Sawtooth Valley (right).

Appendix Table 1. Selection table for Cormack-Jolly-Seber models for survival (ϕ) and detection efficiency (p) compared by AIC. K is the degrees of freedom in the model. Hatchery vs. wild = hw.

Model	K	AIC	ΔAIC	Weight
ϕ(~-1 + reach × year) p(~-1 + reach + year)	75	5906.47	0.00	0.45
ϕ(~-1 + reach × year + hw) p(~-1 + reach + year)	76	5907.82	1.35	0.23
ϕ(~-1 + reach × year) p(~-1 + reach + year + hw)	76	5908.05	1.57	0.21
ϕ(~-1 + reach × year + hw) p(~-1+reach+year+hw)	77	5909.41	2.93	0.10
ϕ(~-1 + reach × year) p(~-1 + reach)	66	5914.44	7.96	0.01
ϕ(~-1 + reach + year) p(~-1 + reach + year)	30	5922.03	15.56	0.00
ϕ(~-1 + reach + year) p(~-1 + reach)	21	5922.23	15.75	0.00
ϕ(~-1 + reach + year + hw) p(~-1 + reach + year)	31	5923.23	16.76	0.00
ϕ(~-1 + reach + year + hw) p(~-1 + reach)	22	5923.42	16.94	0.00
ϕ(~-1 + reach + year) p(~-1 + reach + year + hw)	31	5923.62	17.14	0.00
ϕ(~-1 + reach + year + hw) p(~-1+ reach + year + hw)	32	5924.84	18.36	0.00
ϕ(~-1 + reach × year + hw) p(~-1 + reach)	67	5951.71	45.23	0.00
ϕ(~-1 + reach × year) p(~-1 + reach × year)	120	5972.45	65.97	0.00
ϕ(~-1 + reach × year + hw) p(~-1 + reach × year)	121	5973.80	67.32	0.00
ϕ(~-1 + reach × year) p(~-1 + reach × year + hw)	121	5974.16	67.69	0.00
ϕ(~-1 + reach × year + hw) p(~-1 + reach × year+ hw)	122	5975.52	69.04	0.00
ϕ(~-1 + reach + year) p(~-1 + reach × year)	75	5985.33	78.86	0.00
ϕ(~-1 + reach + year + hw) p(~-1 + reach × year)	76	5986.45	79.97	0.00
ϕ(~-1 + reach + year) p(~-1 + reach × year + hw)	76	5987.17	80.69	0.00

Appendix Table 2. Fallback statistics: percentages (number of fish that fell back/number of fish detected) and rates (total fallbacks/number of fish detected) for Snake River and upper Columbia sockeye at dams in the Columbia River hydrosystem.

Year	Number of fish detected	Total number of fish that fell back	Total number of fallbacks	Fallback percent	Fallback rate
Snake River					
Bonneville Dam					
2008	14	0	0	0.0	0.0
2009	23	1	1	4.3	4.3
2010	40	1	1	2.5	2.5
2011	516	34	44	6.6	8.5
2012	122	5	7	4.1	5.7
2013	205	23	57	11.2	27.8
2014	343	44	113	12.8	32.9
2015	679	97	155	14.3	22.8
2016	183	16	36	8.7	19.7
2017	74	2	2	2.7	2.7
The Dalles Dam					
2013	170	31	52	18.2	30.6
2014	290	47	80	16.2	27.6
2015	430	124	222	28.8	51.6
2016	157	28	56	17.8	35.7
2017	58	1	1	1.7	1.7
McNary Dam					
2008	10	0	0	0.0	0.0
2009	16	1	1	6.3	6.3
2010	34	1	1	2.9	2.9
2011	343	17	19	5.0	5.5
2012	70	3	3	4.3	4.3
2013	138	7	15	5.1	10.9
2014	214	0	0	0.0	0.0
2015	100	4	5	4.0	5.0
2016	132	2	2	1.5	1.5
2017	46	0	0	0.0	0.0
Ice Harbor Dam					
2008	10	0	0	0.0	0.0
2009	17	3	3	17.6	17.6
2010	30	4	4	13.3	13.3
2011	316	23	26	7.3	8.2
2012	67	7	8	10.4	11.9
2013	121	14	21	11.6	17.4
2014	204	24	26	11.8	12.7
2015	60	6	6	10.0	10.0
2016	126	18	23	14.3	18.3
2017	44	7	9	15.9	20.5
Lower Monumental Dam					
2014	213	18	23	8.5	10.8
2015	50	13	14	26.0	28.0
2016	126	12	15	9.5	11.9
2017	46	5	6	10.9	13.0

Appendix Table 2. Continued.

Year	Number of fish detected	Total number of fish that fell back	Total number of fallbacks	Fallback percent	Fallback rate
		Snake River (continued)			
Little Goose Dam					
2014	205	17	21	8.3	10.2
2015	32	3	3	9.4	9.4
2016	125	8	9	6.4	7.2
2017	43	4	7	9.3	16.3
Lower Granite Dam					
2008	10	1	1	10.0	10.0
2009	17	1	1	5.9	5.9
2010	31	3	13	9.7	41.9
2011	332	47	55	14.2	16.6
2012	64	17	21	26.6	32.8
2013	91	24	39	26.4	42.9
2014	199	53	70	26.6	35.2
2015	27	3	3	11.1	11.1
2016	124	12	14	9.7	11.3
2017	42	4	4	9.5	9.5
		Upper Columbia River			
Bonneville Dam					
2008	45	2	2	4.4	4.4
2009	326	12	12	3.7	3.7
2010	957	69	76	7.2	7.9
2011	651	46	51	7.1	7.8
2012	572	34	37	5.9	6.5
2013	172	1	1	0.6	0.6
2014	313	4	4	1.3	1.3
2015	413	6	6	1.5	1.5
2016	146	3	3	2.1	2.1
2017	115	5	5	4.3	4.3
The Dalles Dam					
2013	148	4	4	2.7	2.7
2014	290	7	7	2.4	2.4
2015	359	5	5	1.4	1.4
2016	133	0	0	0.0	0.0
2017	111	1	1	0.9	0.9
McNary Dam					
2008	35	1	1	2.9	2.9
2009	244	9	10	3.7	4.1
2010	752	9	9	1.2	1.2
2011	395	14	14	3.5	3.5
2012	408	8	8	2.0	2.0
2013	139	3	3	2.2	2.2
2014	262	2	2	0.8	0.8
2015	249	2	2	0.8	0.8
2016	121	0	0	0.0	0.0
2017	102	2	2	2.0	2.0

Appendix Table 2. Continued.

Year	Number of fish detected	Total number of fish that fell back	Total number of fallbacks	Fallback percent	Fallback rate
Upper Columbia River (continued)					
Priest Rapids Dam					
2008	41	1	1	2.4	2.4
2009	257	3	3	1.2	1.2
2010	770	22	23	2.9	3.0
2011	441	17	17	3.9	3.9
2012	403	6	6	1.5	1.5
2013	133	2	2	1.5	1.5
2014	259	4	4	1.5	1.5
2015	217	3	3	1.4	1.4
2016	120	3	3	2.5	2.5
2017	95	6	6	6.3	6.3
Rock Island Dam					
2008	34	0	0	0.0	0.0
2009	232	7	7	3.0	3.0
2010	713	15	16	2.1	2.2
2011	371	12	13	3.2	3.5
2012	339	5	5	1.5	1.5
2013	114	0	0	0.0	0.0
2014	84	0	0	0.0	0.0
2015	173	2	2	1.2	1.2
2016	111	0	0	0.0	0.0
2017	84	1	1	1.2	1.2
Rocky Reach Dam					
2008	22	1	1	4.5	4.5
2009	71	3	3	4.2	4.2
2010	248	8	9	3.2	3.6
2011	106	2	2	1.9	1.9
2012	128	4	4	3.1	3.1
2013	71	1	1	1.4	1.4
2014	154	0	0	0.0	0.0
2015	141	5	5	3.5	3.5
2016	70	2	2	2.9	2.9
2017	58	0	0	0.0	0.0
Wells Dam					
2008	22	1	1	4.5	4.5
2009	42	2	2	4.8	4.8
2010	140	7	7	5.0	5.0
2011	87	7	7	8.0	8.0
2012	99	3	3	3.0	3.0
2013	62	2	2	3.2	3.2
2014	148	0	0	0.0	0.0
2015	116	6	7	5.2	6.0
2016	67	0	0	0.0	0.0
2017	57	0	0	0.0	0.0

Appendix Table 3. Correlation coefficients among variables tested in reach-survival models. Values over the 0.7 cutoff are highlighted.

Bonneville to McNary

	Survival	Day	Fallback	Gas	Flow	Temp	Catch	Spill
Day	-0.14							
Fallback	-0.15	-0.04						
Gas	0.33	-0.14	-0.07					
Flow	0.34	-0.02	-0.08	0.88				
Temp	-0.45	0.32	0.04	-0.80	-0.87			
Catch	-0.08	-0.27	0.10	0.09	-0.05	0.01		
Spill	0.21	-0.04	-0.09	0.75	0.88	-0.68	-0.05	

McNary to Ice Harbor

	Survival	Day	Fallback	Gas	Flow	Temp	CumTemp	Spill	Travel time
Day	-0.07								
Fallback	-0.13	0.20							
Gas	0.12	0.04	-0.06						
Flow	0.12	0.02	-0.04	0.81					
Temp	-0.18	0.11	0.04	-0.47	-0.73				
CumTemp	-0.26	0.37	0.43	-0.25	-0.26	0.33			
Spill	0.10	0.04	-0.03	0.78	0.98	-0.67	-0.23		
Travel time	-0.22	0.36	0.45	-0.14	-0.11	0.16	0.98	-0.09	

Ice Harbor to Lower Granite

	Survival	Day	Fallback	Gas	Flow	Temp	CumTemp	Spill	Travel time
Day	-0.08								
Fallback	-0.16	0.23							
Gas	0.12	-0.20	-0.07						
Flow	0.21	-0.04	-0.07	0.58					
Temp	-0.33	0.10	0.09	-0.38	-0.87				
CumTemp	-0.30	0.41	0.42	-0.21	-0.22	0.31			
Spill	0.21	0.16	-0.04	0.44	0.88	-0.78	-0.16		
Travel time	-0.22	0.40	0.42	-0.14	-0.05	0.10	0.97	0.00	
Day^2	-0.13	0.23	0.35	-0.25	-0.15	0.12	0.49	-0.07	0.49
Temp^2	-0.30	-0.20	-0.01	0.21	0.25	0.05	0.17	0.16	0.14

Lower Granite to Sawtooth

	Survival	Day	Fallback	Gas	Flow	Temp	CumTemp	Spill	Travel time
Day	-0.25								
Fallback	-0.15	0.18							
Gas	0.23	-0.20	-0.10						
Flow	0.31	-0.14	-0.15	0.64					
Temp	-0.26	0.10	0.14	-0.40	-0.87				
CumTemp	-0.32	0.59	0.13	-0.26	-0.37	0.33			
Spill	0.18	-0.20	0.04	0.37	0.48	-0.36	-0.29		
Travel time	-0.27	0.58	0.11	-0.17	-0.19	0.15	0.97	-0.18	
LTD	-0.22	-0.04	0.08	-0.31	-0.71	0.87	0.33	-0.32	0.17

Appendix Table 4 Top five individual models in covariate analysis for survival. T^2 = quadratic effect of temperature, d^2 = quadratic effect of day, cumT = cumulative temperature, tt = travel time, hw = hatchery vs. wild origin.

Model rank	Model	df	dAICc
Bonneville to McNary			
1	$S \sim T^2$ + transport + fallback + age + catch + d^2	9	0.00
2	$S \sim T^2$ + transport + fallback + age + catch + d	8	0.21
3	$S \sim T^2$ + transport + fallback + age + catch	7	0.54
4	$S \sim T^2$ + transport + fallback + age + catch + d^2 + spill	10	0.89
5	$S \sim T^2$ + transport + fallback + age + catch + d^2 + hw	10	1.17
McNary to Ice Harbor			
1	$S \sim T^2$ + cumT + age + tt + spill	7	0.00
2	$S \sim T^2$ + cumT + age + tt + spill + transport	8	0.13
3	$S \sim T^2$ + cumT + age + tt + transport	7	0.22
4	$S \sim T^2$ + cumT + age + tt	6	0.63
5	$S \sim T^2$ + cumT + age + tt + spill + transport + hw	9	0.88
Ice Harbor to Lower Granite			
1	$S \sim T^2$ + cumT + fallback	5	0.00
2	$S \sim T^2$ + cumT + fallback + age	6	0.18
3	$S \sim T^2$ + cumT + fallback + age + transport	7	0.68
4	$S \sim T^2$ + cumT + fallback + transport	6	0.84
5	$S \sim T^2$ + cumT + fallback + d^2	7	1.07
Lower Granite to Sawtooth			
1	S~flow + spill + fallback + d^2 + cumT + age	8	0.00
2	S~flow + spill + fallback + d^2 + cumT + age + gas	9	0.53
3	S~flow + spill + fallback + d^2 + age	8	0.54
4	S~flow + spill + fallback + d^2 + cumT	7	1.21
5	S~flow + spill + fallback + d^2 + age + gas	9	1.49