River conditions, fisheries and fish history drive variation in upstream survival and fallback for Upper Columbia River spring and Snake River spring/summer Chinook salmon

Lisa Crozier, Lauren Wiesebron, Elene Dorfmeier and Brian Burke

Report of research by

Fish Ecology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
2725 Montlake Blvd. East
Seattle, WA 98112

May 2017

Executive Summary

To identify what factors drove variation in survival during upstream migration, we analyzed a large database of spring/summer Chinook salmon from both the Upper Columbia River spring run and Snake River spring/summer run evolutionarily significant units (ESUs). We analyzed how individual fish characteristics and environmental conditions were related to adult migration survival from 2004-2015 for 5,062 Upper Columbia and 11,496 Snake River Chinook salmon.

We examined survival over two reaches within the hydrosystem: one in the Columbia River (Bonneville to McNary Dam, both ESUs) and one in the Snake River (Ice Harbor to Lower Granite Dam, Snake River populations only). Based on a bimodal distribution of migration times described in Crozier et al. (2016), we separated Snake River populations into early- and late-migrating sets, differentiated as "spring" and "summer" run fish in this report.

To identify the best predictors of survival and fallback over dams, we used a generalized linear modelling approach. For the Snake River ESU, we initially tested whether run was a significant factor. If it was, we analyzed spring and summer populations separately. If not, we analyzed the Snake River ESU populations together. We used the term stock to differentiate between 1) upper Columbia spring, 2) Snake River spring, and 3) Snake River summer populations.

Temperature had the most consistent influence on survival across all stocks through both reaches. Temperature generally showed a quadratic relationship with survival in both Columbia and Snake River reaches. Thus when the two reaches were combined for the Snake River ESU, survival from Bonneville to Lower Granite Dam varied from a low of 20% at temperatures over 20°C to a high of 80% at optimal temperatures (13-16°C). The year of lowest annual survival for all stocks, 2015, was also the warmest year, with a mean temperature of 17.9°C during the summer run (65% survival from Bonneville to Lower Granite).

Survival from Bonneville to McNary also responded negatively to high spill. The year of second lowest survival was 2011, when flows were 50% above normal. These high flows likely reduced adult survival through the Columbia River reach.

Annual and seasonal variation in harvest significantly affected the survival of all stocks. The year of third lowest survival was 2014, which had normal temperature and flow, but especially high catch during the Snake River summer Chinook migration (21% of the run at large). An even higher catch rate (25%) exacerbated the impacts from temperature in 2015. We found a significant interaction between catch and run, such that summer-run populations appeared to suffer more indirect effects of catch as well as higher catch rates in some years.

Fish characteristics important in some of the analyses were hatchery/wild origin, fish age, and a history of juvenile transportation. However, impacts of these factors were less consistent than those from the primary factors of temperature, spill, and catch.

Survival through the Snake River reach from Ice Harbor to Lower Granite Dam was closely related to temperature and previous travel time in the hydrosystem (Bonneville to Ice Harbor Dam).

Fallback rates were highest and most variable at Lower Granite Dam, followed by McNary and Bonneville Dam. Temperature was important at all dams, although the shape of the relationship varied. Cumulative temperature, which is a combination of travel time and temperature, consistently had a positive correlation with fallback. Cumulative temperature was a better predictor of fallback rate than travel time alone at three dams. Flow, spill and prior travel time were also important at several dams.

Managing natural variation in temperature and flow across the enormous Columbia River Basin while accommodating economic and social needs is extremely complex. Logistical constraints and trade-offs make simplistic solutions impractical. However, to the extent that climate change will increase the frequency of years like 2015, lower survival in warm years could be a growing management concern.

Some engineering solutions are already being implemented to prevent the extreme temperatures that fish experienced in 2015. But additional mitigations might entail tradeoffs between juvenile and adult migration survival. The results of this analysis clarify the sensitivity of this crucial life stage. Net costs and benefits of catch and spill regimes over the entire salmon life cycle need to be analyzed comprehensively under alternative management scenarios to plot a successful course toward long-term recovery of these threatened species.

Contents

Introduction

Adult salmon migration through the Columbia and Snake Rivers involves passage through a major fishery and a series of hydroelectric dams. Over the 19th and 20th centuries, harvest and dams contributed to salmon declines that led to listing of numerous Columbia River salmon under the Endangered Species Act (NMFS 1992). To ensure that these anthropogenic factors do not currently endanger protected Evolutionarily Significant Units (ESU) of salmon, the National Marine Fisheries Service recommended monitoring survival through the adult migration and evaluating the causes of differential mortality among populations over time (RPA Action 52, NOAA Fisheries 2008).

Previous work analyzing upstream survival of spring/summer-run Chinook salmon migrating through the Columbia River hydrosystem found that total escapement from Bonneville to Lower Granite Dam in 2000-2002 for Snake River fish was 78-97%, of which radiotags returned from mainstem harvest accounted for 0-17% mortality, depending on the subgroup of fish (Table 4, Keefer et al. 2005). Escapement was negatively correlated with river discharge. They further reported that a history of transportation as juveniles lowered survival about 10% from Bonneville to Lower Granite Dam. Additionally, fish that fell back over dams were less likely to complete the migration. However, no negative effects of temperature were observed in these years.

In more recent years, high temperatures in the Columbia and Snake rivers have been associated with mortality in salmonids that migrate later in the summer, particularly sockeye (Keefer et al. 2008c; Naughton et al. 2005; NOAA Fisheries 2016). Better understanding of how environmental factors influence survival of Chinook salmon is especially important in the context of climate change. As temperatures rise globally, the need to anticipate impacts on listed species has become a management priority (Link et al. 2015; McClure et al. 2013).

Fisheries in the Columbia River are managed to meet treaty obligations with tribal nations and agreements between federal and state agencies. Catch is monitored in various ways. Following a management agreement in 2008, harvest targets follow a sliding scale based on the aggregate run size of upriver-migrating Chinook salmon (United States v. Oregon 2008). Harvest quotas at the beginning of the spring/summer Chinook run are based on predicted returns of upper Columbia spring and Snake River spring/summer Chinook salmon. Run size is updated mid-season in early May, at which time quotas are re-evaluated. The harvest schedule changes on June 15, when the run size of unlisted Columbia River summer Chinook is used to set the harvest target.

Most previous analyses relied on radio-tagged salmon of unknown origin to characterize survival (e.g., Caudill et al. 2007; Caudill et al. 2013; Jepson et al. 2010; Keefer et al. 2005). Because population origin was generally unknown prior to extensive use of genetic analysis and juvenile-tagged fish, small sample sizes limited the ability to compare survival of different biological populations of fish. Increasing effort in juvenile tagging and adult detection over the past decade has greatly improved our statistical power. Taking advantage of this growing dataset, we evaluated the extent to which variation in environmental conditions, reported catch, and certain fish attributes could explain variation in survival in two Evolutionarily Significant Units (ESU) from 2004 to 2015.

We investigated upstream migration in adult upper Columbia spring-run and Snake River spring/summer-run Chinook salmon from 2004 to 2015. Our analysis was based on fish tagged with passive integrated transponder (PIT) tags. Release and detection information from tagged fish are recorded and stored in a database with which we could identify population of origin and other factors associated with individual fish history.

We first modeled the interannual variability of upstream survival in relation to major factors known to influence survival in Pacific salmon. Next, we analyzed factors that affected the probability that a fish would fall back and reascend a dam. Fallback can occur for many reasons and is not always detrimental for fish (Keefer and Caudill 2014; Keefer et al. 2008a). Nonetheless, higher fallback rates are associated with a lower probability of successful migration through the hydrosystem to spawning tributaries (Keefer et al. 2005).

This report supplements the work of Crozier et al. (2016), who described population-specific annual variation in migration timing at Bonneville and McNary Dam, calculated annual estimates of fallback at all mainstem dams with PIT detection, and used mark-recapture statistical methods to estimate annual survival rates between mainstem dams. They showed that for both upper Columbia and Snake River fish, survival was most variable through the Zone 6 fishery, in the 236-km reach from Bonneville to McNary Dam. For Snake River fish, survival was next most variable in the 167-km reach from Ice Harbor to Lower Granite Dam (Crozier et al. 2016).

Here we focus on identifying factors that drove the majority of interannual variation in survival and fallback. For both analyses, we considered three categories of potential covariates: juvenile history, migrating fish characteristics (e.g., travel time, age, fallback, concurrent catch), and environmental conditions. This approach was similar to that used by Crozier et al. (2014): we used the same survival data summarized in the previous report, but added some new years of data to the fallback analysis. Summary statistics for the complete fallback analysis are shown in Appendix Table 1.

Results from this analysis will inform the Adaptive Management Implementation Plan for the Federal Columbia Power System Biological Opinion (NOAA Fisheries 2014). The Biological Opinion summarized historical factors known to limit survival through the hydrosystem. This report presents new information for future decisions regarding protection of these ESA-listed fish.

Methods

Fish Data and Run Identification

Our analysis used data collected from monitoring systems in fish ladders at dams. Fish had been implanted with unique PIT-tags as juveniles, and these tags were detected in the ladders on their return migration as adults. A full description of PIT-tag data processing procedures was described by Crozier et al. (2016).

Briefly, the PTAGIS database was queried for Chinook salmon that were tagged and released and then detected again within the Columbia River Basin. Only release sites that were within a single major population group (MPG, Ford et al. 2016) were included. Therefore, fish tagged at mainstem dams were excluded from this analysis.

We used a maximum size criterion of 300 mm at tagging to ensure fish had been tagged as juveniles with two additional criteria to verify that our observations reflected adult return migration: 1) at least 2 years had passed between the juvenile migration and detection, and 2) the first detection of the year occurred in an adult fish ladder. To be included in the covariate analysis, fish had to be detected in one of the adult fish ladders at Bonneville Dam.

Based on a previous analysis of run timing (Crozier et al. 2016), we defined "spring run" as fish from the Lower Snake MPG, Grande Ronde MPG excluding Imnaha, Middle Fork Salmon MPG, and upper salmon MPG excluding Pahsimeroi. Our "summer run" category included fish from the Imnaha and Pahsimeroi River and the entire South Fork Salmon MPG.

The upper Columbia River spring-run Chinook ESU consists of a single MPG which is comprised of the Entiat, Wenatchee, and Methow River populations. The Tucannon River confluence with the Snake River lies downstream of Lower Granite Dam, so Tucannon River fish are not expected to pass Lower Granite. We therefore excluded the Lower Snake MPG from the analysis of survival from Ice Harbor to Lower Granite Dam.

Covariate Factors

We selected variables for analysis that covered three broad categories of influential factors: juvenile fish covariates, adult migration characteristics, and environmental conditions. Two additional covariates were included for analyses in the reach from Ice Harbor to Lower Granite Dam: travel time and cumulative temperature exposure from Bonneville Dam to reach entry.

Juvenile Covariates and Adult Migration Characteristics

Juvenile fish covariates included whether the fish was of wild or hatchery origin and whether it migrated downstream in the river as opposed to being barged. Adult migration characteristics included the number of years a fish spent in the ocean, the first day it was detected at the furthest downstream dam in the study reach, and an index of catch during its time in the Zone 6 fishery. We also included whether a fish fell back and reascended dams during migration.

Records from the PTAGIS database specified whether fish were of hatchery or wild origin. Fish were defined as having been transported downstream as juveniles if their last juvenile detection site was at the entrance to a raceway destined for barging. Barge departures were confirmed through personal communication with personnel involved in transportation efforts. The number of years between the juvenile migration year and observation year are described as ocean years.

We analyzed fallback at Bonneville, McNary, Ice Harbor and Lower Granite Dam for Snake River spring/summer-run Chinook salmon. For upper Columbia River Chinook salmon, we analyzed fallback at Bonneville, McNary, Priest Rapids and Rock Island Dam. To determine when a fish fell back over a dam and reascended, we followed the methods described by Crozier et al. (2016).

Briefly, we classified a fish as having fallen back if it was detected moving upstream in an adult ladder and then detected again in that same ladder after a lag of more than 6 h. A fish was also identified as having fallen back if it was detected in a different ladder at the same dam or in a ladder at a downstream dam (Burke et al. 2004). We used a program developed specifically to infer fallbacks from detections of PIT-tagged fish (Tiffani Marsh, NOAA Fisheries, personal communication).

Fallbacks were summed to produce a cumulative fallback predictor variable for each dam, up to and including the dam at the beginning of the reach or dam of interest. This analysis required data for 2004-2015, so dams with no PIT detectors or with detectors only recently installed were not included. Therefore, for survival analyses from

Ice Harbor to Lower Granite Dam, cumulative fallback was the sum of fallbacks detected at Bonneville, McNary, and Ice Harbor, but not at The Dalles or John Day Dam. In the fallback model, the cumulative fallback covariate was the sum of all fallbacks at dams up to but not including the analyzed dam.

Our index of catch was derived from estimates of combined tribal and non-tribal catch within Zone 6 (roughly from Bonneville to McNary Dam) summarized by NOAA-Fisheries staff (Jeromy Jording, personal communication, Figure 1). These estimates were not spatially explicit within Zone 6. The estimates summarized catch spanning various time periods, from days to months. When the Ceremonial and Subsistence catch estimate exceeded one month, we disaggregated the total catch into days in proportion to the relative size of the Bonneville Dam Chinook count during that period. For example, if a total of 1000 fish passed Bonneville within a given catch period and 100 fish passed on day 1, 10% of the catch would be attributed to day 1. We had nearly identical model results when the catch was distributed uniformly across the time span, so the general results in terms of the significant covariates of survival are not sensitive to the exact index calculation. Nonetheless, this representation appeared more realistic than the assumption of uniform catch across the time period.

We compared three metrics of catch. First, we examined weekly catch estimated for the statistical week during which a fish passed Bonneville Dam. If the fish was detected at Bonneville Dam on multiple days, we used the last detection date. Second, we weighted weekly catch by weekly sum of Chinook window counts at Bonneville Dam (“weighted catch”). This metric assumed that the impact of catch on a tagged fish was proportional to the size of the run at large at that time.

Third, we calculated a “time-adjusted catch” to account for variation in fish travel time. Time-adjusted catch assumes that travel time affects exposure to fisheries, and hence risk of capture. This metric was calculated by disaggregating weekly catch estimates into daily estimates, assuming all days in a statistical week had equal catch.

We summed the daily catch for each day the fish was in Zone 6, which we defined as the interval between the last day of detection at Bonneville and first day of detection at McNary. This interval was based on actual day of passage at McNary Dam for fish that survived this reach. For fish not detected at McNary Dam, we estimated a stock-specific catch exposure interval, which was defined as median passage time by year for upper Columbia, Snake River spring, and Snake River summer stocks. We then estimated an expected passage day at McNary based on the last day of detection at Bonneville plus the expected catch exposure interval.

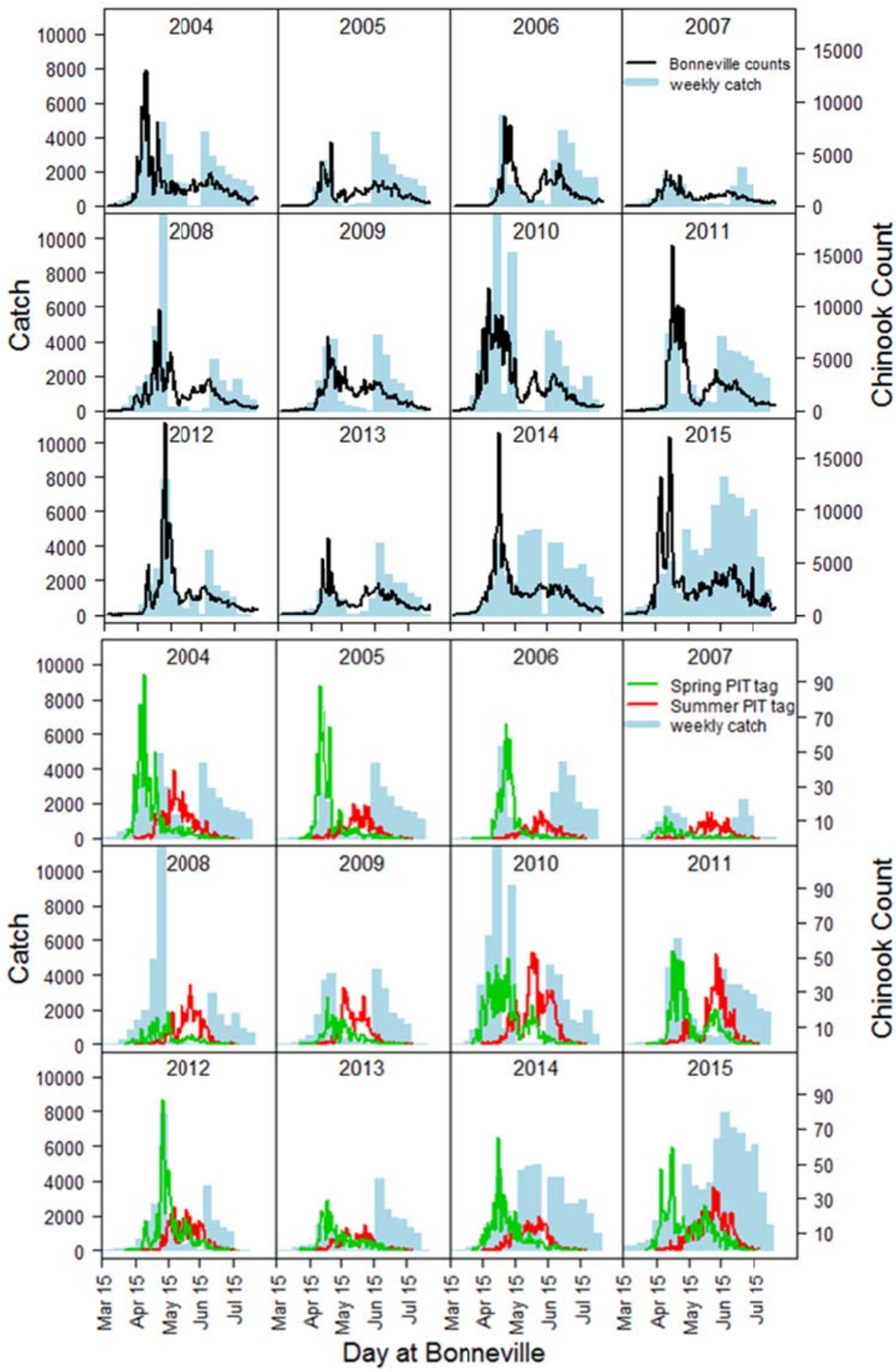

Figure 1. Frequency distribution of fish passage dates at Bonneville Dam vs. weekly catch in Zone 6, 2004-2015. Fish passage dates are garnered from Bonneville fish count window (upper panel), and PIT-tag detection data (lower panel). Note that estimated weekly catch is the same in upper and lower panels.

Environmental Data

Environmental data came from two sources. Daily averages of temperature, flow, spill, and percentage of dissolved gas were collected by the U.S. Army Corps of Engineers and distributed by the Columbia River *Data Access in Real Time* project (CBR 2016). We included both daily mean and daily maximum spill in the analysis. We also included a quadratic temperature term for both survival and fallback models.

For each fish, we used values measured at each project on the day of first detection at that project. We prioritized data from the tailrace of each project (CBR project codes CCIW, TDDO, MCPW, IDSW, and LGNW). In cases where data was not available from the tailrace, we used data reported for the forebay (CBR project codes: BON, TDA, MCN, IHR, LWG, PRD, RIS). Percent dissolved gas in the forebay was included for all dams.

We excluded individual temperature readings that were highly anomalous for the season and recorded at only one dam. To do this, 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 corrected these data by interpolation.

Environmental covariates vary systematically over the course of each season (Figure 2), with the strongest linear seasonal correlation between temperature and day. Flow and spill were also highly correlated. To avoid problems with collinearity, we excluded from the same model one of any two covariates with a correlation coefficient greater than 0.7.

Travel Time and Cumulative Temperature Exposure

For analyses of survival from Ice Harbor to Lower Granite Dam and for analyses of fallback at all dams other than Bonneville, the additional covariates of travel time and cumulative temperature exposure were considered. Travel time consisted of the interval between first detection at Bonneville and last detection at the upstream dam of each study reach. Cumulative temperature exposure was the product of temperature and travel time, summed across all relevant reaches. For example, cumulative temperature for a fish entering the Ice Harbor to Lower Granite reach would be the sum of exposure from Bonneville to McNary and McNary to Ice Harbor.

We calculated cumulative temperature for a given reach as the average of 1) daily mean temperature at Bonneville Dam, measured on the day of passage and 2) daily mean temperature at the upstream dam on last day of detection at the dam multiplied by the travel time interval, or number of days the fish was in the reach. For travel time intervals that included passage at McNary, Ice Harbor, or Lower Granite Dam, temperatures used in this calculation came from hourly measurements reported by the U.S. Army Corps of Engineers (USACE 2015). These measurements covered a vertical line (string) near the navigation lock at a series of depths from 0.5 to 32 m at McNary, Ice Harbor and Lower Granite Dam.

We used daily mean temperature measured at the 0.5-m depth to estimate reservoir surface temperature. Missing data for a single daily mean or series of two daily means were filled through interpolation. For longer series of missing data (30 consecutive days or less), means were filled by regressing the string temperatures of that year against the string temperatures of the adjacent dam for the same year. Temperatures above 28°C were considered errors and interpolated. We filled stretches of missing data greater than 30 consecutive days with temperature measured at the dams. Cumulative temperatures for Upper Columbia dams in the fallback analysis were calculated using temperatures recorded at dam tailraces.

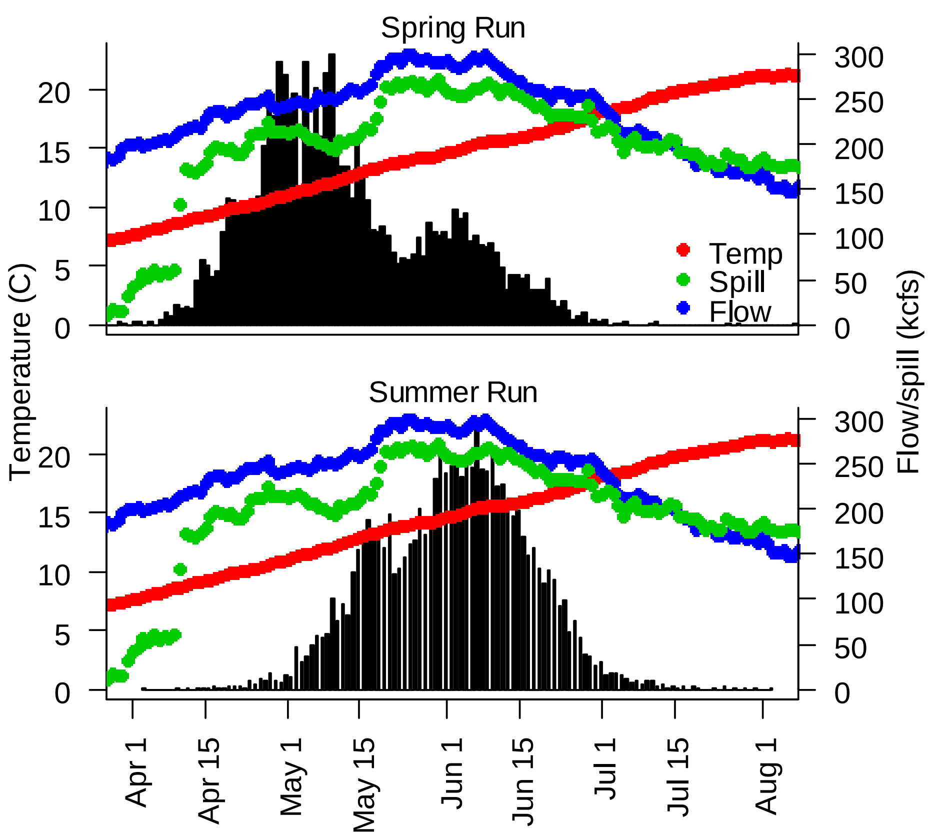

Figure 2. Bars show density distribution and run timing of adult Snake River spring/summer-run Chinook salmon based on PIT-tagged fish returning 2004-2015. Lines show mean daily temperature, flow, and spill (doubled for plotting purposes) at Bonneville Dam overlaid on spring (upper panel) and summer run timing (lower panel).

Data Analysis

We modelled covariate predictors of survival and fallback for each ESU independently in the reach from Bonneville to McNary Dam. For the Snake ESU, we modeled covariate predictors in the reach from Ice Harbor to Lower Granite Dam. For Snake River spring vs. summer runs, we re-fit the models separately by run only if run was a significant factor.

To determine the factors associated with survival and fallback rate, we compared covariates using generalized linear models. These models were selected because they are robust to many assumptions, flexible, and widely understood (McCullagh and Nelder 1989). An alternative approach would have added covariates to mark-recapture models. However, detection rates were extremely high at upstream dams in both reaches (98.8 100%; Crozier et al. 2016). Therefore, there was little benefit to this approach, as undetected survivors would be too few to change the relative importance of covariates.

We scaled all predictor variables in the analysis so that model coefficients for different covariates reflected the relative effect size of the covariate. All possible subsets of covariates were fitted using the dredge function from the *R* package *MuMIn*, and models were ranked based on Akaike information criterion. A quadratic temperature term and an interaction between run and catch were included. We did not test whether there was a significant interaction between temperature and catch because of complication that resulted from using this interaction term in the quadratic form.

We excluded variable combinations that had a Pearson correlation coefficient over 0.7. Multiple indices derived from the same raw data, such as daily mean and maximum spill, were not used in the same model or in final model averages. For these variables, we first evaluated the relative importance of each member of a pair (e.g., daily mean spill and daily maximum spill). We then eliminated the variable with lower importance and re-calculated the model average coefficients. The model average included all ranked models with cumulative weight capped at 0.95.

Variable importance and model average coefficients were derived from the *model.avg* function in the *MuMIn* package. We also report whether the variable had a coefficient that was significantly different from zero in the conditional model average, which averages only over models that include that covariate. All analyses were conducted using R (R Core Team 2013).

We applied the same modelling approach and performance metrics for survival as for fallback with the following exceptions: 1) Survival was treated as a binomially distributed variable with a logit-link function, whereas a log link was used for fallback with a Poisson distribution. 2) Catch was included as a covariate for survival but not for fallback.

Results

Survival Covariates

Environmental factors had more consistent effects on survival than on fallback. Temperature had very strong effects for all stocks in both the Columbia River and the Snake River reaches. Catch and spill also had strong effects on survival in the Columbia River for all stocks. Other covariates were more stock- or reach-specific in importance.

Survival from Bonneville to McNary Dam

For both ESUs, survival through the reach from Bonneville to McNary Dam was very sensitive to temperature. The quadratic temperature effect was highly significant, with fitted survival over 80% between 10 and 16°C (all other factors at their mean, Figure 3, Table 1). Spill also had an importance of 1 for all stocks (Figure 4, Table 1).

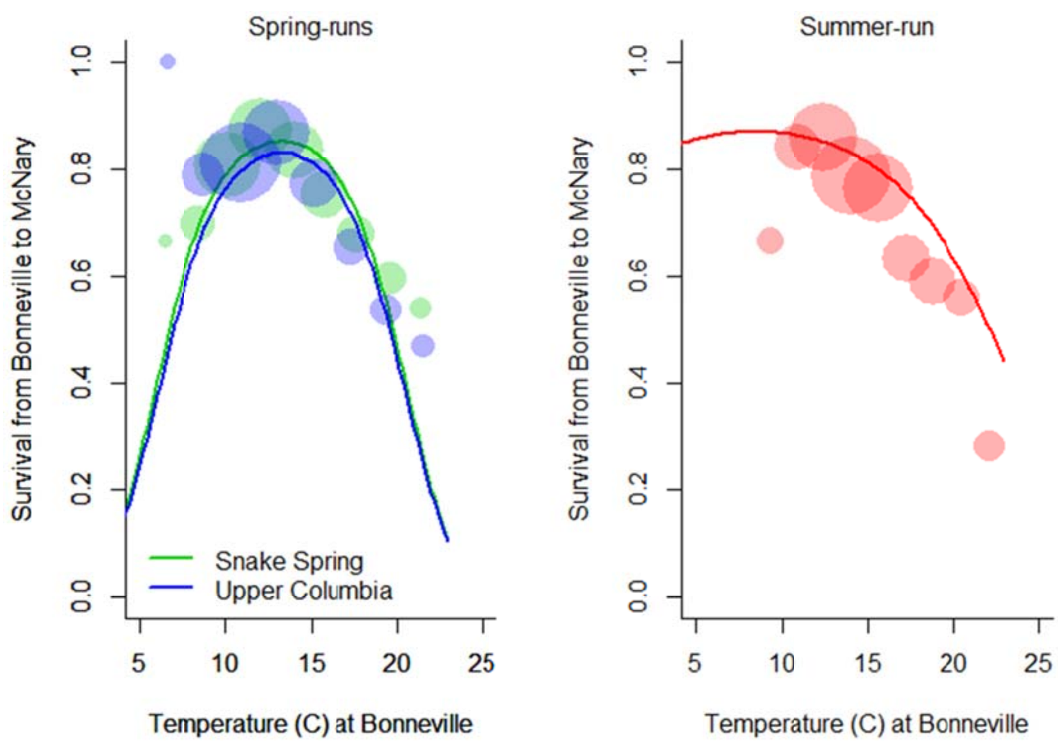

Figure 3. Survival of the two spring-run stocks (left) and summer-run (right) Chinook salmon from Bonneville to McNary Dam as a function of temperature at Bonneville Dam. Fish were grouped by temperature experienced. Circle size is proportional to the number of grouped fish. Lines show modeled survival as a function of temperature, with other covariates at their mean.

Table 1. Model results for survival from Bonneville to McNary Dam. Model average coefficients and variable importance are shown. Coefficients that were statistically significant (*P* <0.001) in the conditional model are indicated with an asterisk.

Snake River

	Coefficient	Importance
Intercept	1.61*	
Temp (quadratic)	-0.14*	1.00
Temperature	-0.05	1.00
Weighted catch	-0.35*	1.00
Weighted catch × run	-0.06*	0.96
Run	-0.004	0.96
Spill	-0.25*	1.00
Gas	-0.07*	0.87
Hatchery/Wild	0.10*	1.00
Ocean years	-0.02	0.54
Transport	-0.02	0.59
Fallback	-0.002	0.26

Upper Columbia River spring-run

	Coefficient	Importance
Intercept	1.62*	
Temp (quadratic)	-0.21*	1.00
Temperature	0.04	1.00
Weighted catch	-0.27*	1.00
Spill	-0.35*	1.00
Gas	0.002	0.25
Hatchery/wild	0.15*	0.99
Ocean years	0.10*	0.94
Transport	-0.10*	0.76
Fallback	-0.03	0.51

Snake River spring run

	Coefficient	Importance
Intercept	1.78*	
Temp (quadratic)	-0.24*	1.00
Temperature	0.02	1.00
Weighted catch	-0.28*	1.00
Spill	-0.21*	0.99
Gas	-0.15*	0.98
Hatchery/Wild	0.04	0.59
Ocean years	0.02	0.39
Transport	-0.08*	0.83
Fallback	0.01	0.29

Snake River summer-run

	Coefficient	Importance
Intercept	1.37*	
Temp (quadratic)	-0.03*	0.76
Temperature	-0.27*	1.00
Weighted catch	-0.48*	1.00
Spill	-0.34*	1.00
Hatchery/Wild	0.13*	1.00
Ocean years	-0.08*	0.96
Transport	0.00	0.26
Fallback	-0.007	0.32

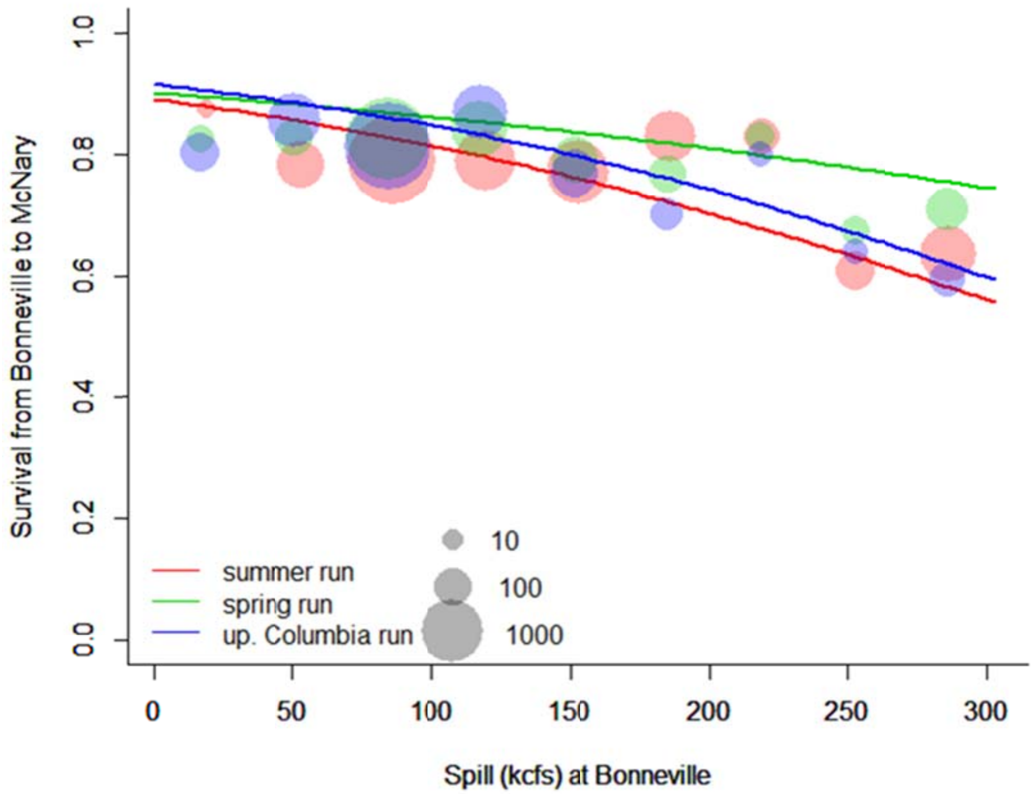

Figure 4. Survival of the summer-run Chinook salmon from Bonneville to McNary Dam as a function of spill at Bonneville Dam. Fish were grouped by spill levels experienced. Circle size is proportional to the number of grouped fish. Lines show modeled survival with all other variables at their mean.

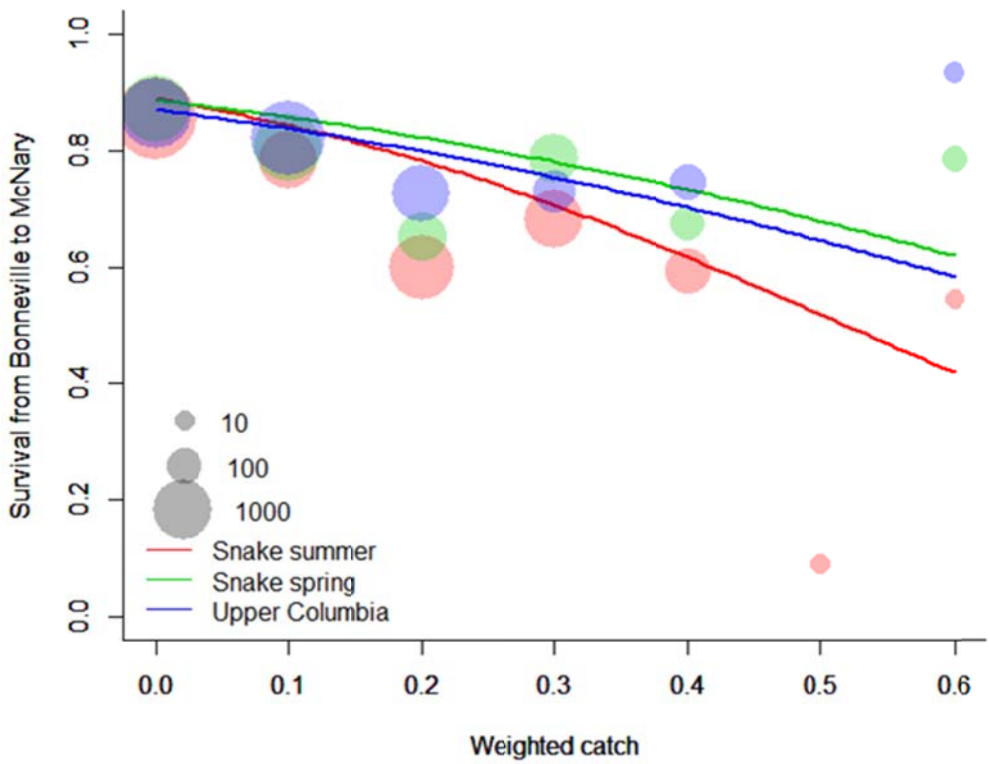

Figure 5. Survival as a function of Bonneville Chinook count-weighted catch for spring and summer runs and upper Columbia ESU (modeled separately).

All three indices of catch produced very similar results in relation to the other covariates. Raw and weighted catch were highly correlated (r = 0.78), but models with weighted catch had lower AIC (dAIC at least 7) for both ESUs and both runs within the Snake River ESU. There was a significant interaction between catch and run for the Snake River ESU, such that at a given catch, the impact on summer run was higher than the impact on spring run (Table 1). We therefore modeled spring and summer runs separately, and the relationship with catch is shown in Figure 5.

Upper Columbia River spring Chinook—For the upper Columbia ESU, survival from Bonneville to McNary Dam was also associated with hatchery vs. wild origin, fish age, and transportation history (Table 1). Along with temperature, catch, and spill, these factors were included in nearly all models in the 95% confidence interval set (importance 0.77-1). None of the other covariates had coefficients significantly different from 0 in the conditional model set. The range of annual survival observed was 77-85%, and that predicted by the model was 77-85%. The 95% confidence intervals of the observation and model prediction overlapped in all years (Figure 6).

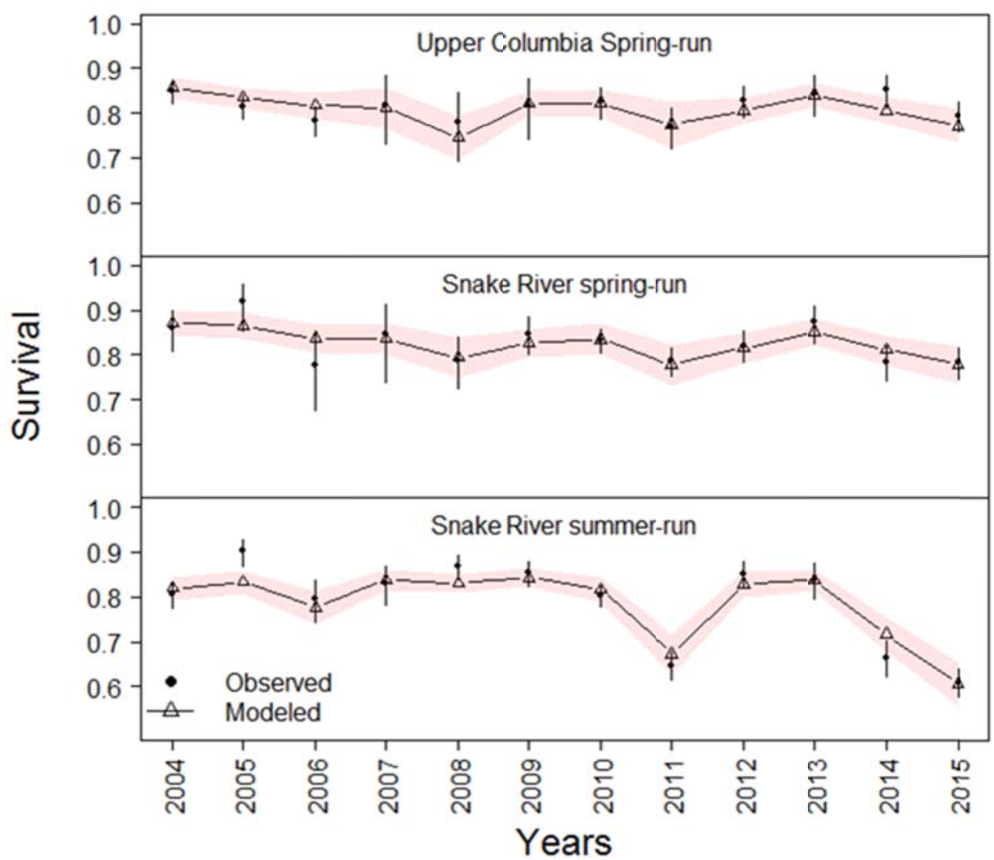

Figure 6. Observed and predicted survival from Bonneville to McNary Dam for upper Columbia ESU (top) and Snake River ESU spring- (middle) and summer-run (bottom). Solid circles are observed rates with 95% confidence interval assuming binomial variance. The open circles are model estimates, with the shaded area showing the 95% confidence interval for the prediction.

Snake River spring Chinook**—**For Snake River spring-run fish, survival from Bonneville to McNary Dam was also predicted by transportation history and gas (importance 0.82 and 0.99, respectively), in addition to temperature, catch, and spill. However, age and hatchery origin were not important in this analysis. The range of annual survival observed was 78-92%, and that predicted by the model was 78-87%. Model predictions were within the 95% confidence interval of observations in all years (Figure 6).

Snake River summer Chinook**—**Snake River summer-run Chinook was the only stock for which survival varied widely from Bonneville to McNary Dam (60-90%). In addition to temperature, catch and spill, hatchery origin and fish age were significant. The magnitude of the hatchery effect was similar to that seen for the upper Columbia ESU. However, fish age had the opposite sign, such that older fish had lower survival. Model predictions and observed confidence intervals overlapped in all years except 2005.

Environmental conditions were least favorable in 2011 and 2015 (Figure 7). In 2011, flow and spill were very high, whereas in 2015, temperature was high, causing low predicted survival. For the summer run, mean catch rate was 21% in 2014 and 25% in 2015. These catch rates were much higher than those seen previous years (Figure 7), and they caused predicted survival to be relatively low in both years. For the summer run, both temperature and catch levels reached a peak in 2015, causing the lowest predicted and observed rates of survival (both 61%) over the 2004-2015 study period.

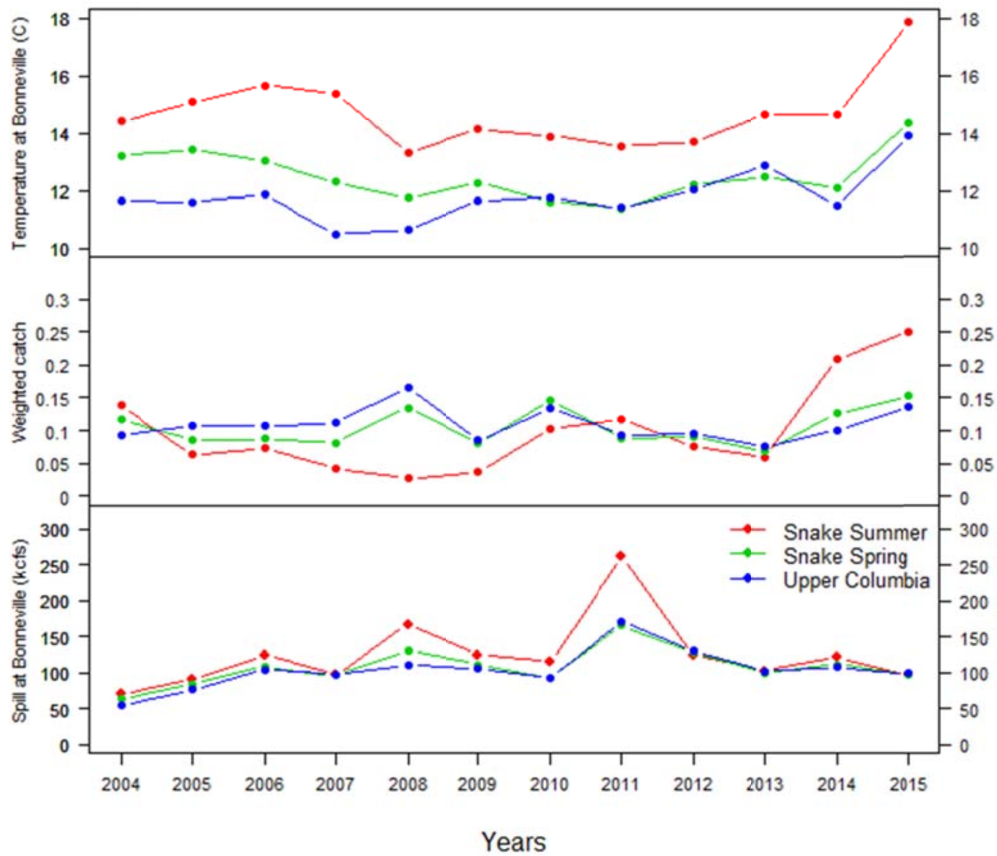

Figure 7. Annual mean value for each run (i.e., weighted by fish timing) for temperature at Bonneville Dam on the day of passage (top), weighted catch in Zone 6 (middle), and spill at Bonneville Dam on the day of passage (bottom).

Survival from Ice Harbor to Lower Granite Dam

In the reach from Ice Harbor to Lower Granite Dam, temperature had a very strong, consistent effect on survival across runs, similar to the temperature effects seen in the reach from Bonneville to McNary Dam (Figure 8 left, Table 2). Travel time was also included in all models for both runs. Temperature effects were compounded by the negative effects of longer transit times through the hydrosystem prior to entering this reach (Figure 8, right). Longer transit times tended to produce later arrival at Ice Harbor Dam and hence exposure to higher seasonal mean temperatures.

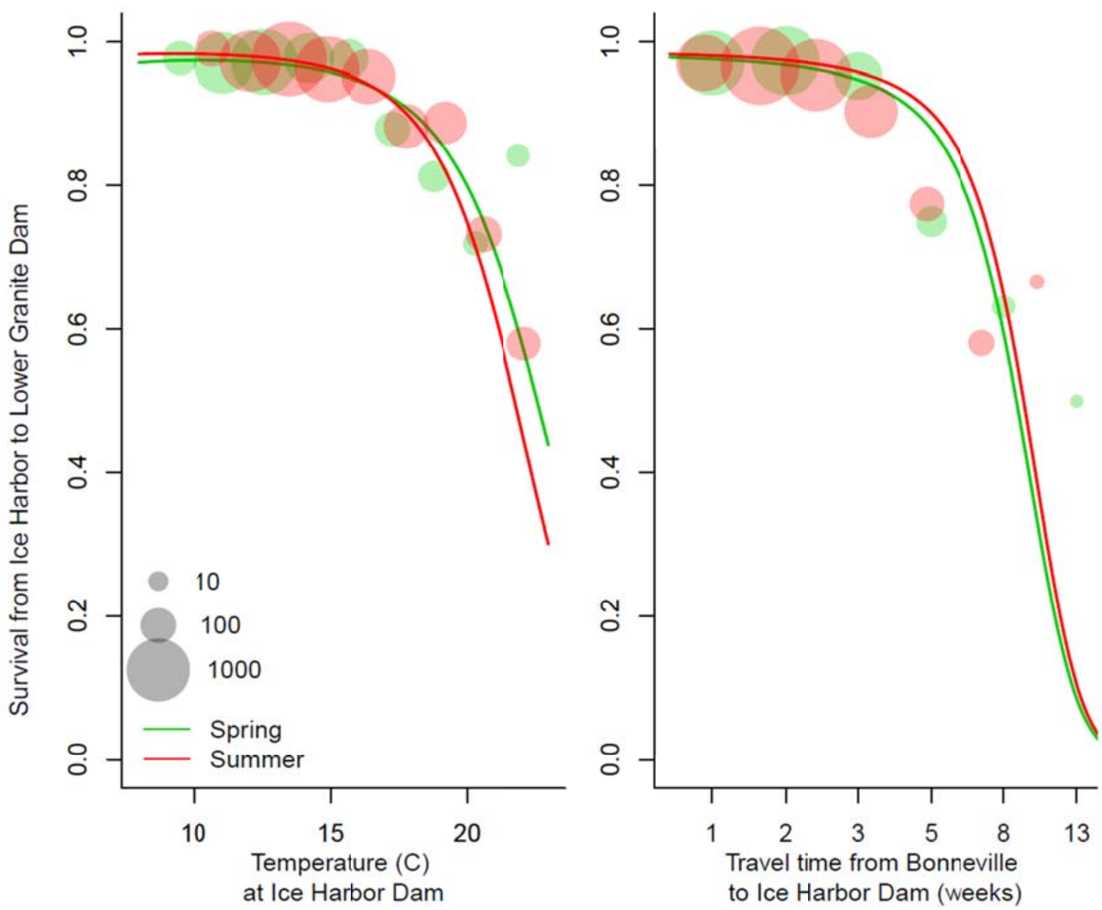

Figure 8. Survival of all Snake River spring/summer-run Chinook from Ice Harbor to Lower Granite Dam as a function of temperature at Ice Harbor Dam on the day of passage (left) or travel time from Bonneville to Ice Harbor Dam (right). Fish are grouped by temperature or travel time. Circle size is proportional to the number of fish in each group.

Table 2. Model results for survival from Ice Harbor to Lower Granite Dam. Model average coefficients and variable importance are shown. Coefficients that were statistically significant (*P* <0.001) in the conditional model are indicated with an asterisk. Factors with importance below 0.25 are not shown.

Snake River spring run			**Snake River summer run**		
	Coefficient	Importance		Coefficient	Importance
(Intercept)	3.35*		(Intercept)	3.66*	
Temp (quadratic)	-0.07	0.68	Temp (quadratic)	-0.12*	0.99
Temperature	-0.36*	1.00	Temperature	-0.46*	1.00
Travel time (BO_IH)	-0.37*	1.00	Travel time (BO_IH)	-0.37*	1.00
Transport	-0.14	0.71	Ocean yrs	-0.15*	0.93
Gas	-0.16	0.68	Fallback (BO_IH)	0.00	0.26
Fallback (BO_IH)	-0.03	0.33	Gas	-0.08	0.58
			Hatchery/Wild	0.03	0.37
			Max spill	-0.03	0.30
			Transport	-0.01	0.28

For spring-run fish, only the linear temperature component and travel time were included in all models. Transportation history was included in the top three models, with transported fish experiencing lower survival. Gas and the quadratic temperature component were also included in the top models. Flow and spill had a combined importance of less than 0.5, indicating that discharge was not very important for survival through this reach.

For summer-run fish, the quadratic temperature term and travel time were significant and very important, but none of the discharge-related variables was important. The remaining significant factor for summer-run fish was age, with older fish surviving at lower rates than younger fish.

Survival was over 93% for spring Chinook in all years (Figure 9). Interannual variability was higher for summer-run compared with spring-run through this reach, as it was for the Bonneville to McNary reach. The lowest survival observed was 87% for Snake River summer-run fish in 2015. Confidence intervals for model predictions and observations overlapped in all years (Figure 9).

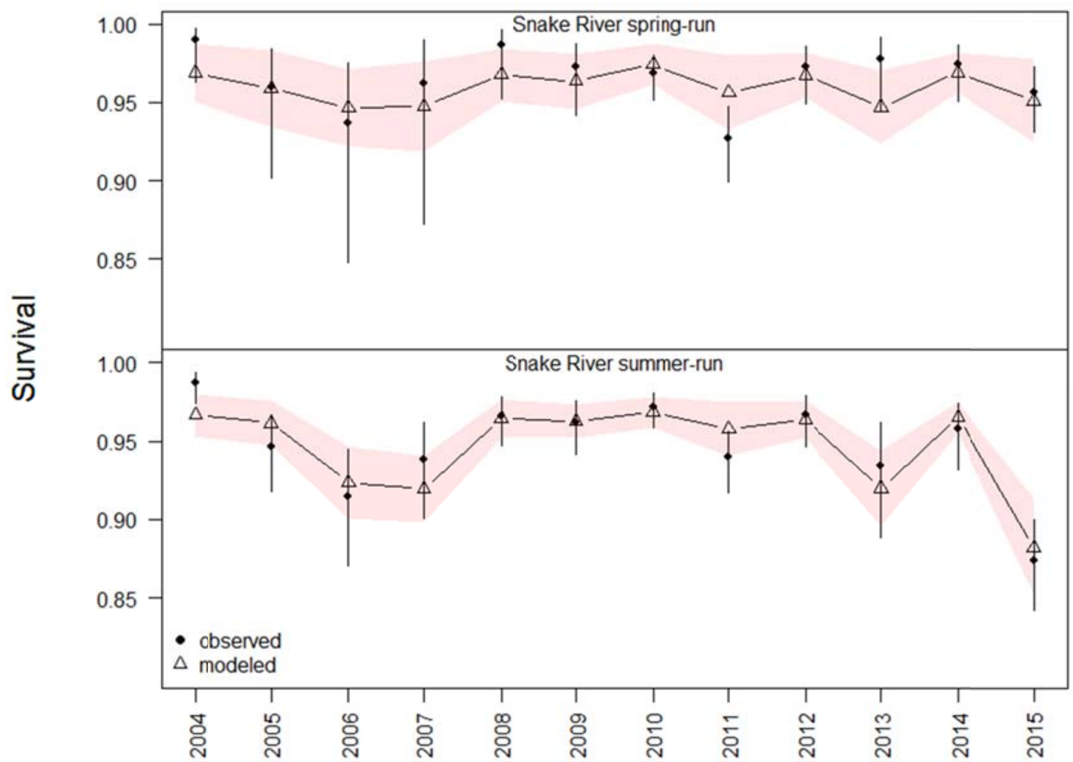

Figure 9. Observed and predicted survival from Ice Harbor to Lower Granite Dam for Snake River spring-run (top) and summer-run (bottom). Solid circles are observed rates with 95% confidence interval assuming binomial variance. The open circles are model predictions, with the shaded area showing the 95% confidence interval for the prediction.

Fallback Covariates

The influence of environmental factors on the number of fallbacks differed in direction and magnitude across dams, but was often similar for upper Columbia and Snake River fish (Table 3). For Snake River fish, run was not a significant predictor of fallback, so we analyzed both runs together.

Table 3. Covariate effects on fallback rate (number of fallbacks per fish) by dam for upper Columbia and Snake River ESUs. Variables with importance over 0.75 and that were significant in the conditional models are in bold.

	Upper Columbia Chinook fallback rate summary							
	Bonneville		McNary		Priest Rapids		Rock Island	
	Coefficient	Importance	Coefficient	Importance	Coefficient	Importance	Coefficient	Importance
Transport	**0.11**	**0.75**	-0.03	0.34	-0.11	0.37	-0.06	0.36
Flow	**0.46**	**1.00**	0.00	0.21	-0.06	0.22	0.01	0.18
Spill	---	---	-0.01	0.23	-0.06	0.34	0.00	0.17
Temperature2	**0.16**	**1.00**	0.017	0.40	**-0.59**	**1.00**	**0.01**	0.26
Temperature	-0.10	**1.00**	**0.16**	**0.99**	0.00	**1.00**	**-0.82**	**1.00**
Travel time	---	---	**0.25**	**1.00**	**0.09**	0.19	---	---
Cum Temp	---	---	---	---	**0.54**	**0.81**	**0.53**	**1.00**
Fallback	---	---	0.03	0.30	**0.26**	**0.88**	0.03	0.35
Age	-0.05	0.58	0.00	0.26	-0.01	0.36	0.05	0.47
Hatchery/wild	-0.01	0.26	0.01	0.26	-0.03	0.30	-0.01	0.27
Gas	-0.08	0.61	-0.03	0.39	-0.03	0.25	-0.01	0.18
	Snake River Chinook fallback rate summary							
	Bonneville		McNary		Ice Harbor		Lower Granite	
	Coefficient	Importance	Coefficient	Importance	Coefficient	Importance	Coefficient	Importance
Transport	**0.09**	**1.00**	**-0.09**	**1.00**	0.00	0.25	0.00	0.26
Flow	**0.02**	0.10	**-0.19**	**0.98**	0.00	0.21	---	---
Spill	**0.16**	**0.90**	**0.00**	0.02	-0.01	0.28	**0.20**	**1.00**
Temperature2	0.00	0.14	**-0.12**	**1.00**	0.00	0.26	**0.06**	**0.93**
Temperature	-0.03	0.55	**0.24**	**1.00**	-0.09	**0.84**	**-0.33**	**1.00**
Travel time	---	---	**0.21**	**1.00**	**0.34**	**1.00**	---	---
Cum Temp	---	---	---	---	---	---	**0.34**	**1.00**
Fallback	---	---	0.03	0.36	0.01	0.28	0.00	0.25
Age	0.00	---	-0.015	0.40	-0.01	0.29	-0.01	0.40
Hatchery/wild	-0.02	0.50	0.00	0.30	-0.06	0.65	-0.02	0.51
Run	0.01	0.30	0.00	0.27	-0.01	0.31	0.01	0.32
Gas	0	0.24	-0.01	0.3	0.03	0.45	0	0.26

Flow/Spill

At Bonneville Dam, flow or spill had the largest covariate effect and was positively correlated with fallback. At McNary Dam, flow was negatively correlated with fallback for Snake River fish but had no effect for upper Columbia fish. Neither flow nor spill was significant at Priest Rapids, Rock Island, or Ice Harbor Dam. Spill had a significant positive effect on fallback at Lower Granite Dam. Thus, higher flow or spill increased fallback at Bonneville and Lower Granite but decreased fallback at McNary and had no effect at other dams.

Temperature

Temperature was a significant predictor of fallback for all upper Columbia fish, and for Snake River fish at McNary and Lower Granite. However the modeled direction of the temperature effect was inconsistent across dams and stocks. For upper Columbia fish, fallback rate increased monotonically with temperature at McNary but decreased monotonically at Rock Island. For Snake River fish, the model predicted higher fallback rates at both low and high temperatures at Bonneville and Lower Granite, but the inverse at McNary. Because relatively few fish were sampled at low and high temperatures, confidence in these quadratic forms was limited.

Travel Time, Cumulative Temperature, Fallback History and Transportation

More consistent effects emerged for travel time, cumulative temperature, transportation, and fallback history. Longer travel times in the hydrosystem prior to reaching a given dam were associated with higher fallback rates for both ESUs at all dams that had travel time variable inputs (i.e. all dams except Bonneville). There was stronger support for cumulative temperature over travel time in Rock Island and Lower Granite models, indicating that an interaction between river temperatures and time in the hydrosystem might be connected with higher fallback rates over longer distances.

A previous history of falling back increased the probability of additional fallback at all dams, but the increase was significant only at Priest Rapid Dam. Transported fish from both ESUs had increased fallback rates at Bonneville, and transported Snake River fish had increased fallback at McNary, but migration history was not significant elsewhere. Hatchery vs. wild origin, fish age, and gas effects were not significant.

Model Fit

Confidence intervals for model predictions and observations in upper Columbia fish overlapped in all years at all dams with one exception (Figure 8). In 2004, observed fallbacks at McNary Dam were extremely low relative to other years and relative to model predictions. Confidence intervals were relatively wide in other years with higher point estimates of fallback rate.

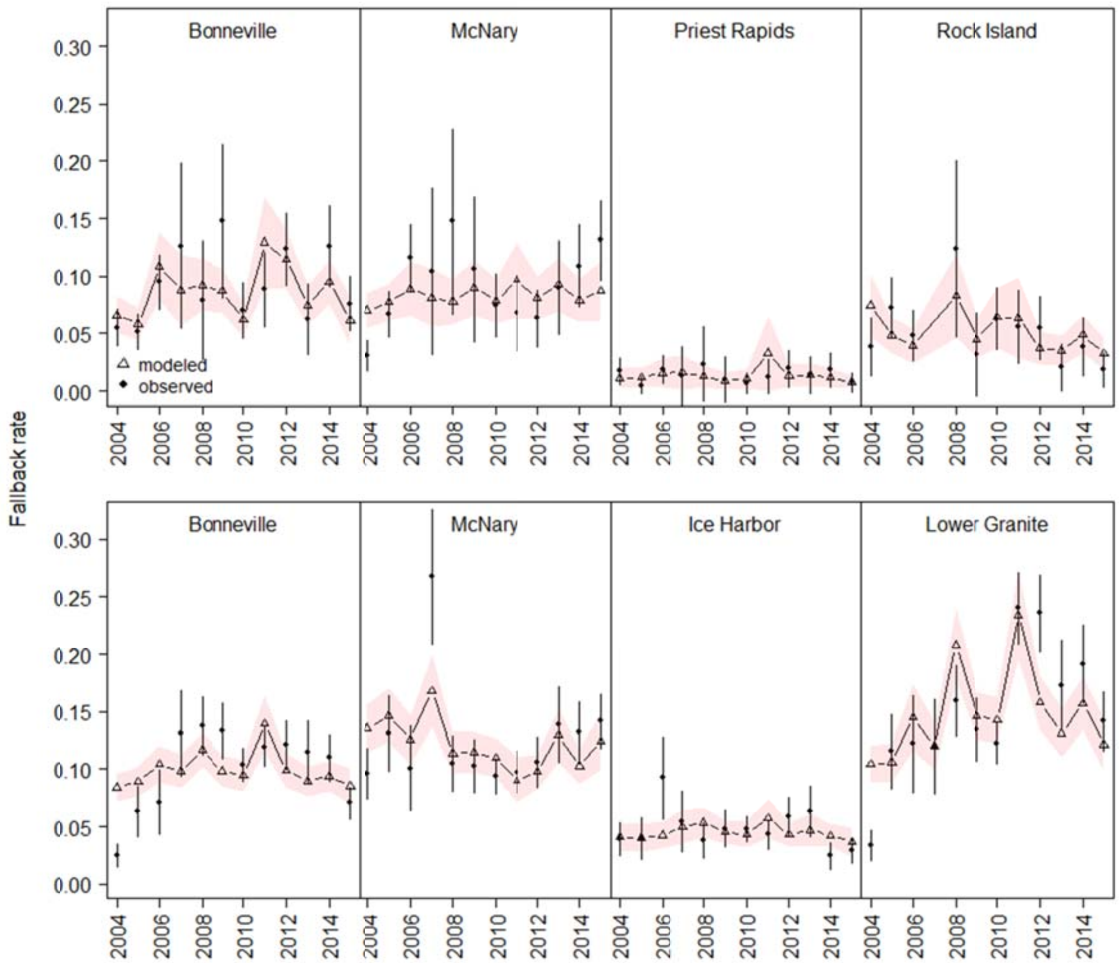

Figure 8. Fallback rates for upper Columbia (upper panel) and Snake River (lower panel) ESUs. Solid circles are observed rates, with 95% confidence interval assuming Poisson variance. Open circles are model predictions, with shaded areas showing the 95% confidence interval for the model prediction.

For Snake River fish, every dam had at least one year in which confidence intervals from model predictions and observations did not overlap, but different years diverged at different dams. Relative to model predictions, observed fallbacks were low in 2004 at both Bonneville and Lower Granite Dam. Observed fallbacks were higher than predicted in 2007 at McNary, in 2006 at Ice Harbor, and in 2011 at Lower Granite.

Upper Columbia fish fell back most frequently at McNary Dam (mean 8.9%, SD ±3.2) and least frequently at Priest Rapids Dam (1.4 ±0.5). Snake River fish fell back most frequently at Lower Granite (13.3% ±4.8) and least frequently at Ice Harbor (4.7 ±1.7, Appendix Table 1).

Discussion

Spring/summer-run Chinook salmon migrate through the Columbia and Snake rivers in early summer. Previous analyses of upstream migration survival have shown that migration was inhibited by flow, but not temperature (Keefer et al. 2005). Historically, spring/summer run Chinook have rarely encountered stressful temperatures. Quantitatively, from 2004 to 2014, only 3% of the summer run passed Bonneville Dam at temperatures above 16°C. However, in recent years that picture has changed.

In 2015, summer-run Chinook salmon experienced the warmest river conditions of all study years, with fish experiencing a mean temperature of 17.9°C at Bonneville Dam and 18°C at Ice Harbor. The second warmest year was 2006, when mean temperature at Bonneville was 15.7°C (Figure 7). Of fish that passed Bonneville while temperatures were above 16°C (71% of the run), only 41% survived to Lower Granite Dam (Figure 9). In comparison, of fish that passed Bonneville at temperatures of 16°C or lower, 76% survived.

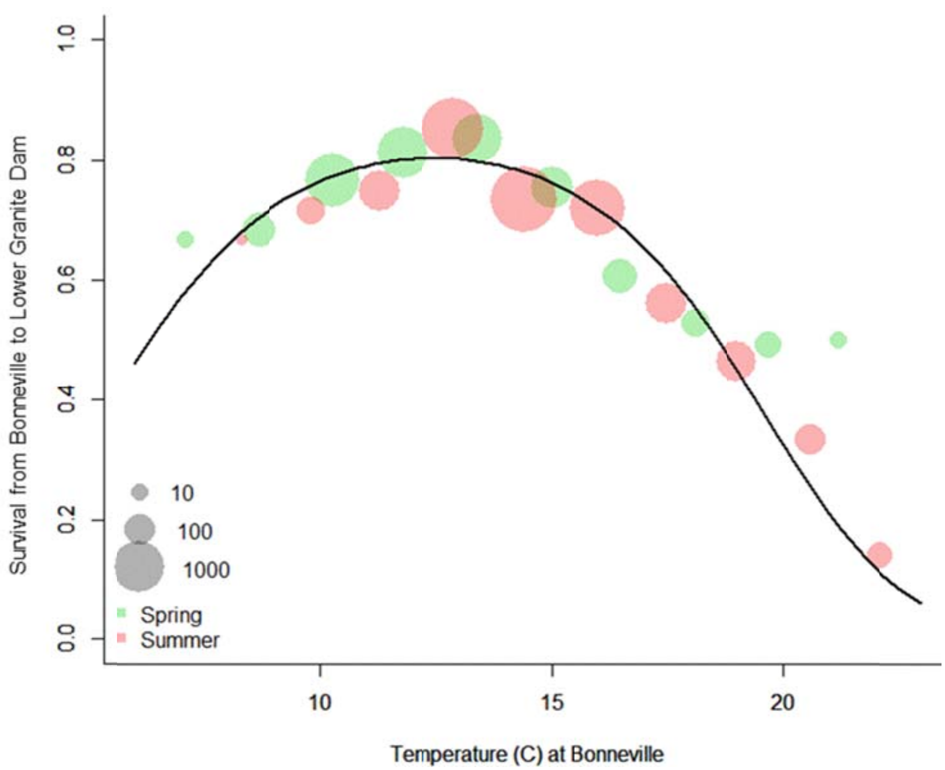

Figure 9. Survival of Snake River spring- and summer-run Chinook salmon from Bonneville to Lower Granite Dam as a function of temperature at Bonneville Dam on the day of passage. Fish are grouped by temperature or travel time. Circle size is proportional to the number of fish in each group.

Temperature demonstrated strong effects in both reaches, from Bonneville to McNary (Figure 3) and from Ice Harbor to Lower Granite (Figure 8). The negative impact of high temperature could have been caused by a variety of proximate mechanisms. Temperatures over 25°C are directly lethal (Richter and Kolmes 2005), but lower temperatures often increase vulnerability to disease such that in the wild, temperatures over 20°C are typically considered extremely stressful for salmon (McCullough 1999).

High temperature differentials from the tailrace to the top of fish ladders has been shown to inhibit dam passage (Caudill et al. 2013). More subtly, bioenergetic costs increase exponentially as temperatures increase. However, fish tend to travel faster at higher temperatures up to a point, thus potentially compensating for a higher daily metabolic cost by reducing total travel time.

Above some temperature, fish stop migrating altogether. Goniea et al. (2006) described slowed migration and use of thermal refugia in Columbia River fall Chinook at temperatures over 20°C. Hyatt et al. (2003) observed that Okanogan River sockeye salmon stop migrating at 21°C, and Strange (2010) reported that although Klamath River Chinook migrated at temperatures up to 24°C, higher temperatures inhibited migration.

Population-specific responses to warm migration temperatures indicate adaptation is possible over time (Strange 2012). Klamath River Chinook appeared to anticipate brief windows of cooler temperatures and sprint upstream (Strange 2010). In general, summer Chinook migrate faster than other runs and do not spend much time in thermal refugia (Keefer et al. 2004). Regardless of whether adaptation is possible, present rates of low survival during high temperatures suggest populations could decline if such temperatures occur consistently.

Fish that enter the river at the end of the run nearly always experienced higher temperatures and lower survival than earlier migrants. Consistent selection for earlier migration will eventually shift timing of these populations, as occurred in sockeye over the 20th century (Crozier et al. 2011; Quinn and Adams 1996). A similar shift in timing for spring/summer Chinook will probably depend on the rate of temperature rise and non-genetic factors that affect migration timing.

Broadly speaking, spring/summer Chinook salmon begin the adult migration earlier in warmer years (Keefer et al. 2008b), which reduces exposure to high temperature. However, in our data, median migration date of summer populations was not correlated with monthly temperature. Additional analysis is needed to determine existing plasticity in this trait, which might be obscured by the wide migration window within populations. Nonetheless, plasticity in migration timing may not be sufficient to prevent selection against late migrants.

The second environmental factor that was consistently important in affecting survival was spill. Previous work has also shown that high discharge rates lower survival (Keefer et al. 2005). Spill had high importance for all stocks in the reach from Bonneville to McNary. However, the biological impact was greater on summer-run than on Snake River spring-run fish, as shown by the difference in survival predictions in 2011 (Figures 4 & 6). The only run/year combination in which mean spill was over 225 kcfs was for summer-run fish in 2011. At lower spill levels, the influence of spill on survival was relatively subtle. Nonetheless, summer-run Chinook typically migrate through the lower Columbia River during peak spill and flow periods (Figure 2), which makes them more vulnerable to discharge extremes.

Mechanisms driving the negative relationship between survival and spill likely include the difficulty of finding fishways in highly turbulent tailraces and the increased bioenergetic cost of swimming upstream against a stronger current. Previous work also indicated that higher fallback rates are associated with high discharge (Boggs et al. 2004). Our analysis did not indicate spill had a strong effect on fallback at most dams, but spill was a significant factor influencing fallback at Bonneville and Lower Granite (Table 3). We caution that our ability to detect the impact of spill was limited by the location of PIT-tag monitoring systems, which are located in fishways. Consequently, altered behavior in the tailrace was not necessarily captured by PIT-tag data.

Our index of harvest (weighted catch) was a highly significant predictor of fish survival in all populations, which is to be expected. However, our ability to differentiate the impact of harvest on spring vs. summer populations is a direct result of improvements in pit-tag data. Although mean catch across all years was the same for all stocks (10%), the variability in mean catch by year in spring runs was much narrower than in the summer run (Snake River spring: 7-15%, Upper Columbia spring: 8-16%, Snake River summer: 3-25%).

Higher variability of catch on summer run likely reflects harvest policy, which shifts over the course of the season. Precautionary principles prevent the highest harvest rates at the beginning of the season, when the total number of fish that might become available for harvest is not known. However, mid-season updates can lead to a reduction or increase in catch rates through June 15. Figure 10 shows that usually catch rate drops in late May and early June, then goes up after June 15. However, the highest weekly catches have also occurred in that middle period, such that the widest range of weighted catches happen in late May and early June. Figure 1 shows the yearly variation in catch timing and magnitude as well.

In some years summer-run overlaps extensively with the unlisted upper Columbia summer-run (Fig. 1), which has a higher proscribed harvest rate. Figure 10 shows the step up in weighted catch for later migrants.

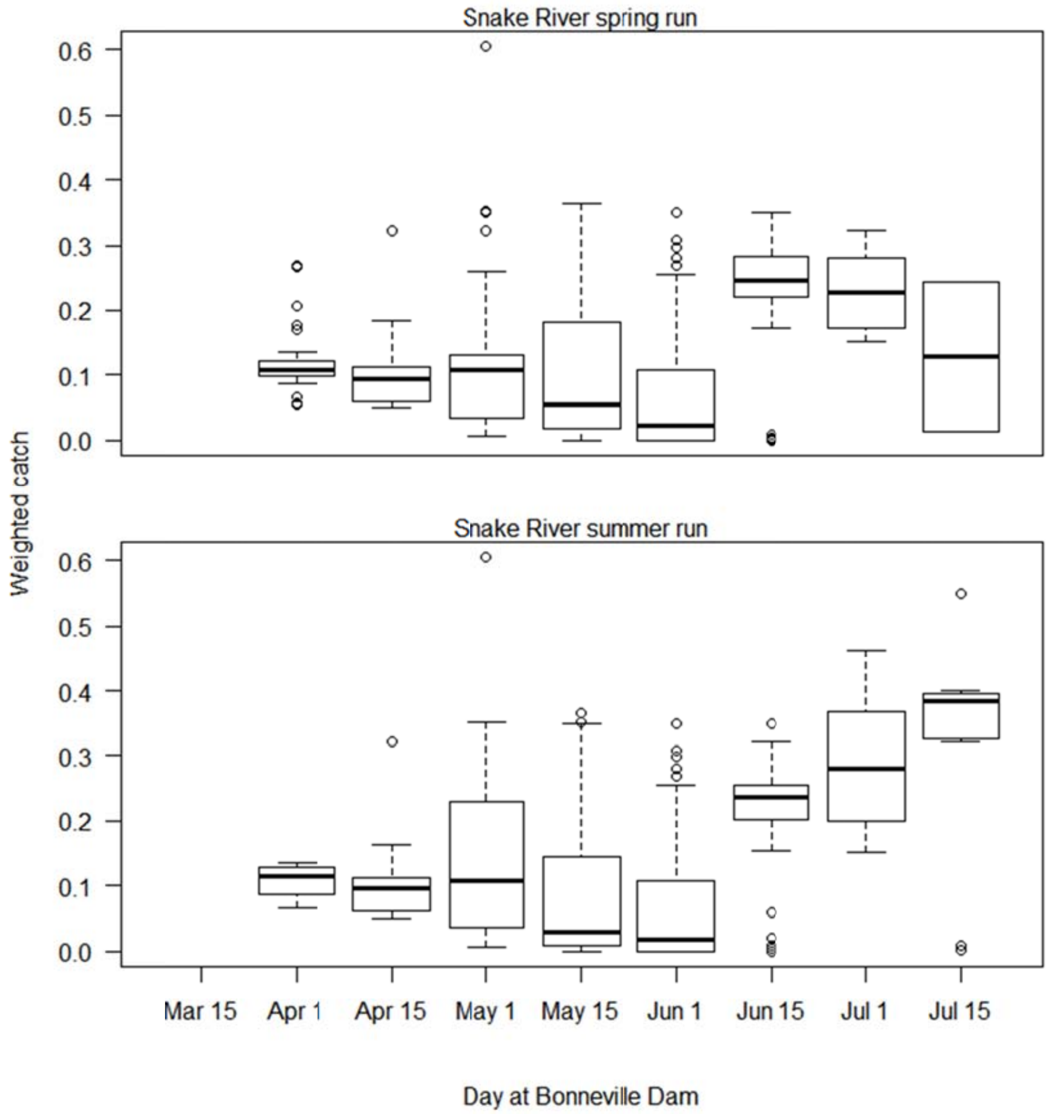

Figure 10. Weighted catch for Snake River spring (top) and summer (bottom) populations, by migration timing. Fish were grouped by either the first half or second half of each month. The beginning of each time period is shown on the x-axis.

Day at Bonneville Dam

The significant interaction between catch and run shown in Figure 5 is not explained by harvest policy. The interaction indicates that higher catch rates had a greater impact on summer run than spring run, even when the weighted catch rate was the same (Figure 5). Thus in addition to the direct effect of catch, there may be indirect effects that differ by run.

Larger indirect effects of the fishery could reflect effects on fish that are not caught, and hence not included in the catch index. For example, some fish are injured by encounters with gillnets despite having escaped capture. Gillnet scars have been documented on fish that survive to Lower Granite Dam, and are collected in the trap there. Injured fish might be more likely to die in summer run compared with spring run because they typically encounter more challenging environmental conditions. Injured fish are more vulnerable to other stressors, such as high temperature or flow. Thus summer-run fish might be more likely to suffer indirect and interacting effects.

Experiments in other river systems after catch-and-release consistently show higher mortality at higher temperature (see review in Gale et al. 2013). We did not directly test for an interaction between catch and temperature because of the quadratic form of the temperature effect, which complicated interpretation of an interaction term. The two factors were also somewhat confounded because the highest rates for both temperature and catch occurred in the same year. However, analyses using additional data, along with analyses of injury rates from trap data, could help tease apart these possible mechanisms. An analysis of the ratio of gillnet injuries at Lower Granite Dam as a function of weighted catch and temperature might shed light on this type of indirect effect.

Alternative explanations for the interaction term are also possible. For example, the index of weighted catch might underestimate the actual harvest rate on summer run. We assumed here that tagged fish were equally likely to be caught as co-migrating untagged fish in the run at large. The majority of Chinook migrating in June and July belong to a different ESU (unlisted upper Columbia River summer run). Because they are from a different ESU, they might differ from Snake River fish in behavior (e.g., migrate along a different river bank or at a different rate), which could affect the probability of encountering fishing gear. They could also be more likely to be caught in a given type of fishery due to some other characteristic, such as fish age and size.

However, this type of error would presumably have caused the impact of catch to be higher at lower catch rates as well and caused a significant run effect, not just a significant interaction with catch. Moreover, Snake River summer run typically return at younger ages than Columbia River summer run, and hence seem unlikely to be favored by the fishery.

A final possibility is that the interaction term could have been an artefact of from our procedure for disaggregating catch into daily estimates. This procedure was only conducted for the spring management period, and could have misrepresented the actual timing in some way that produced this result. This explanation seems unlikely because the interaction was also significant when we assumed catch was uniform across the reporting period, suggesting there was not a systematic bias due to this procedure.

Other differences between fisheries could also explain this result, and warrant further study. Our index has numerous caveats that could be avoided using more detailed catch data. For example, variation in the fishery over time and space that were not captured in our dataset (e.g., individual gillnet openings and closings and different types of fishing gear) could refine the estimate of exposure to the fishery. Furthermore, the window counts at Bonneville might not represent the run at large precisely. For example, fallbacks might be counted multiple times. Also, the count is a sample of the true run at large, and has sampling error that was not accounted for. Nonetheless, using the weighted catch, which was estimated by dividing actual catch by Bonneville window count, greatly improved the model fit for all runs. This suggests window count is a valuable indicator of the fishery impact on tagged fish.

In most years and for most stocks, models explained the vast majority of variation observed in the data. For example, the low survival observed in summer-run fish was explained largely by high spill in 2011, high catch in 2014 and 2015, and high temperature in 2015. The model slightly over-predicted survival in 2014 (predicted: 71%, observed: 66%), although confidence limits on the two estimates overlapped. One idiosyncrasy in 2014 was that survival among the three summer-run populations differed more from one another than they did in other years.

More specifically, in 2014, survival of South Fork Salmon and Imnaha River fish was lower than expected (67 and 63%, respectively), whereas survival of Pahsimeroi River fish was higher than predicted by the model (78%, Table 13 in Crozier et al. 2016). This difference among populations did not occur in 2011 or 2015, when all three populations had very similar survival rates (within 2 percentage points). Observation error due to low sample size was unlikely (n = 549, Table 13 in Crozier et al. 2016). Therefore, population-specific factors that were not represented in the model could be important in certain years.

Alternatively, there could be non-additive effects between catch and temperature, and high temperature in 2015 might have obscured the potential effect of catch in that year. A fish can only die once, so one factor can reduce the importance of another, especially when the population of interest composes a small percentage of the actual catch.

Longer travel times from Bonneville to Ice Harbor Dam were associated with lower survival to Lower Granite Dam, particularly when transit times exceed three weeks. Transported fish that survived to McNary had significantly longer travel times than fish that had not been transported (mean difference = 0.74 d, P <0.001, $F_{1,8969} = 46$), and the difference was larger for summer- than spring-run fish. Thus, a history of transportation was not a significant predictor of survival from Ice Harbor to Lower Granite in itself, but a negative effect of transportation might have been captured by the larger travel time effect.

Travel times exceeding three weeks might entail undetected fallbacks, extensive "reverse migrations" (Keefer et al. 2006), straying, as well as injury and other unknown factors. Such lengthy migration times can also entail greater cumulative temperature loads, which are not captured by temperature on the day of dam passage (Figure 2).

After temperature, spill, catch, and travel time, the factors that most often predicted survival were hatchery vs. wild origin and fish age for upper Columbia and Snake River summer-run fish and transportation history for Snake River spring-run fish. Wild fish had 2-5% higher survival than hatchery fish. Although the sport fishery is mark-selective, and hence might have greater impact on hatchery fish, the much larger commercial fishery does not select for hatchery fish, so catch is probably not the reason for the hatchery/wild differential. Hatchery fish also show an increased propensity to stray, which could affect both estimated and observed rates of survival (Keefer et al. 2008a). Higher survival of wild fish has been observed at other life stages as well, and might represent less vigor in a variety of ways (Christie et al. 2014; Holsman et al. 2012).

Fish age had inconsistent effects across populations and reaches. Fish that spent 3 years in the ocean had higher survival from Bonneville to McNary than either 2- or 4-ocean fish in all runs. The different coefficients probably reflect different proportions of fish in the older age classes in samples from each population.

Snake River spring-run fish that had been transported downriver as juveniles had significantly lower survival in the Columbia River (raw difference of 3%), but transportation did not have significant effects for other stocks or in the Snake River reach.

Fallback rates were not statistically significant predictors of survival in any of the reaches we examined. However, cumulative fallback was underestimated in our analysis because of the lack of PIT-monitoring systems at some dams in most or all years. This underestimation might have hindered our ability to detect the full impact of fallback on survival.

Higher fallback rates in general for Snake vs. Columbia River ESU fish were partly explained by juvenile transportation, which largely affects only Snake River fish. However, additional factors at Lower Granite Dam contributed to higher mean fallback. Travel time, transport, and a previous history of fallback were relatively consistent in sign and magnitude of their effects on fallback across ESUs and dams, although they were not always significant. Nevertheless, all of these factors were associated with higher levels of fallback.

Environmental predictors were not consistent in their effects on fallback across stocks and dams. Flow and spill were important factors increasing fallback at Bonneville and Lower Granite Dam, but were both negatively related to fallback at McNary Dam. Temperature showed the full range of possible effects, monotonically increasing, monotonically decreasing, intermediate temperature minimum, and intermediate temperature maximum. These differences in environmental influences could reflect 1) structural differences among dams, such as the position of fish ladder exits in relation to the spillway, 2) management at different dams, such as diurnal variation in spill protocols, as well as 3) differences in the reservoir environments such as increased stratification upstream.

Conclusions

We found that Snake River summer-run populations experienced higher maximum rates of spill, temperature, and a wider range of catch rates, which caused larger fluctuations in the annual survival of these three populations (Imnaha, Pahsimeroi, and South Fork Salmon River) compared with spring-run populations.

Harvest on Snake River summer-run populations was especially high in 2014 and 2015 (21% and 25%, respectively) compared with the target harvest rates for these ESA-listed fish (approximately 11-16%, Joint Columbia River Management Staff et al. 2016). Harvest quotas apply to the spring/summer run as a whole based on the aggregate run-size estimate. In cases where harvest quotas are substantially revised mid-season, the differential largely affects summer run. Thus summer-run is exposed to higher variability overall between years than spring run, and this variability is not necessarily linked to the abundance of these populations.

Harvest rates on the portion of the summer-run that is in Zone 6 after June 15 (up to 59% of the run, based on the distribution of passage dates at McNary, Crozier 2016) are determined by the size of the unlisted upper Columbia summer run. Thus, Snake River summer run face higher harvest rates when the upper Columbia summer run is relatively large, or Snake River fish migrate later than usual. In 2014 and 2015, both early and late components of the Snake River summer run faced relatively high harvest rates.

In addition to travel during periods of higher harvest rates, summer-run showed a greater indirect effect of weighted catch on survival than spring-run. Indirect effects of the fishery might be reflect an interaction with higher temperature that is characteristic of later migration timing.

Two environmental factors also played a major role in driving variation in summer-run survival. High temperatures observed in early summer 2015 were unusual, but are likely to become more frequent (Di Lorenzo and Mantua 2016; Mantua et al. 2010; Wade et al. 2013). The extent to which those observations offered a preview of future challenges remains to be seen.

Regardless of future trends, the impact of high temperatures on listed fish is a concern in the existing climate. Negative effects of high air temperatures can be exacerbated by certain management actions, such as surface spill (NOAA Fisheries 2016), and possibly catch.

High temperatures exacerbate stress caused by other factors, such as non-lethal encounters with fishing gear (Gale et al. 2013). At a minimum, high catch rates in years of environmentally driven low survival should be expected to depress survival below management targets, especially for summer-run populations.

Managing natural variation in temperature and flow across the enormous Columbia River Basin, as well as economic and social needs is extremely complex. Logistical constraints and trade-offs make simplistic solutions impractical. However, to the extent that climate change will increase the frequency of years like 2015, these results suggest that all possible management levers should be considered to improve survival to spawning grounds.

Some engineering solutions are already being implemented to prevent the extreme temperatures that fish experienced in 2015. For example, new pumps have been installed at some dams to cool the fish ladders with deep water from reservoirs and reduce temperature differentials within fish ladders. However, additional mitigations that affect spill operations could involve tradeoffs between juvenile and adult migration survival, making net benefits less clear.

Results of this analysis clarify the sensitivity of the crucial migration stage to several drivers. Net costs and benefits over the entire salmon life cycle will need to be analyzed comprehensively under alternative management scenarios to plot a successful course toward long-term recovery of these threatened species.

Literature Cited

Boggs, C. T., M. L. Keefer, C. A. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. Transactions of the American Fisheries Society 133(4):932-949.

Burke, B. J., T. J. Bohn, S. L. Downing, M. A. Jepson, and C. A. Peery. 2004. Dam passage and fallback by Chinook salmon and steelhead as determined by Passive Integrated Transponder tags and radio tags. NOAA Fisheries and U.S. Army Corps of Engineers, Portland and Walla Walla Districts.

Caudill, C. C., and coauthors. 2013. Indirect effects of impoundment on migrating fish: Temperature gradients in fish ladders slow dam passage by adult Chinook salmon and steelhead. Plos One 8(12).

CBR, Columbia Basin Research. 2016. Columbia River Data Access in Real Time. Database of the Columbia Basin Research Program, University of Washington School of Aquatic & Fishery Sciences, Seattle. Available at www.cbr.washington.edu/dart/dart.html (Jun 2016).

Christie, M. R., M. J. Ford, and M. S. Blouin. 2014. On the reproductive success of early-generation hatchery fish in the wild. Evol Appl 7(8):883-96.

Crozier, L., E. Dorfmeier, T. Marsh, B. Sandford, and D. Widener. 2016. Refining our understanding of early and late migration of adult Upper Columbia spring and Snake River spring/summer Chinook salmon: passage timing, travel time, fallback and survival. Report of research by Fish Ecology Division, Northwest Fisheries Science Center.

Crozier, L. G., B. J. Burke, B. Sandford, G. Axel, and B. L. Sanderson. 2014. Passage and survival of adult Snake River sockeye salmon within and upstream from the Federal Columbia River Power System. Research Report for U.S. Army Corps of Engineers, Walla Walla District.

Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: A case study of a shift toward earlier migration date in sockeye salmon. American Naturalist 178(6):755-773.

Di Lorenzo, E., and N. Mantua. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Clim. Change 6(11):1042-1047.

Ford, M. J., and coauthors. 2016. 2015 Status Review Update for Pacific Salmon and Steelhead Listed under the Endangered Species Act: Pacific Northwest. National Marine Fisheries Service, Northwest Fisheries Science Center. Available at: https://www.nwfsc.noaa.gov/publications/scipubs/display_doctrack_allinfo.cfm?doctrackmetadataid=8623.

Gale, M. K., S. G. Hinch, and M. R. Donaldson. 2013. The role of temperature in the capture and release of fish. Fish and Fisheries 14(1):1-33.

Goniea, T. M., and coauthors. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135(2):408-419.

Holsman, K. K., M. D. Scheuerell, E. Buhle, and R. Emmett. 2012. Interacting Effects of Translocation, Artificial Propagation, and Environmental Conditions on the Marine Survival of Chinook Salmon from the Columbia River, Washington, USA. Conservation Biology 26(5):912-922.

Hyatt, K. D., M. M. Stockwell, and D. P. Rankin. 2003. Impact and adaptation responses of Okanagan River sockeye salmon (*Oncorhynchus nerka*) to climate variation and change effects during freshwater migration: stock restoration and fisheries management implications. Canadian Water Resources Journal 28:689-713.

Joint Columbia River Management Staff, O. D. o. F. Wildlife, and W. D. o. F. Wildlife. 2016. 2016 Joint Staff Report: stock status and fisheries for spring Chinook, summer Chinook, sockeye, steelhead, and other species and miscellaneous regulations. http://wdfw.wa.gov/publications/01780/wdfw01780.pdf.

Keefer, M. L., and C. C. Caudill. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24(1):333-368.

Keefer, M. L., C. C. Caudill, C. A. Peery, and C. T. Boggs. 2008a. Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system. Journal of Fish Biology 72(1):27-44.

Keefer, M. L., C. A. Peery, T. C. Bjornn, M. A. Jepson, and L. C. Stuehrenberg. 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake Rivers. Transactions of the American Fisheries Society 133(6):1413-1439.

Keefer, M. L., C. A. Peery, and C. C. Caudill. 2006. Long-distance downstream movements by homing adult chinook salmon. Journal of Fish Biology 68(3):944-950.

Keefer, M. L., C. A. Peery, and C. C. Caudill. 2008b. Migration timing of Columbia River spring Chinook salmon: effects of temperature, river discharge, and ocean environment. Transactions of the American Fisheries Society 137:1120-1133.

Keefer, M. L., and coauthors. 2005. Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River - Snake River hydrosystem. Canadian Journal of Fisheries and Aquatic Sciences 62(4):930-949.

Keefer, M. L., C. A. Peery, and M. J. Heinrich. 2008c. Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. Ecology of Freshwater Fish 17(1):136-145.

Link, J. S., R. Griffis, and S. Busch, editors. 2015. NOAA Fisheries Climate Science Strategy. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-F/SPO-155, Silver Spring, MD.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102(1-2):187-223.

McClure, M. M., and coauthors. 2013. Incorporating climate science in applications of the US endangered species act for aquatic species. Conserv Biol 27(6):1222-33.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, New York.

McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. U.S. Environmental Protection Agency, Region 10, Seattle, Washington.

Naughton, G. P., and coauthors. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 62(1):30-47.

NMFS, National Marine Fisheries Service,. 1992. Endandered and threatened species: threatened status for Snake River spring/summer Chinook salmon. Federal Register 57(78):14653-14662.

NOAA Fisheries. 2008. Endangered Species Act Section 7(a)(2) Consultation Biological Opinion and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation. Consultation on the Remand for Operation of the Federal Columbia River Power System, 11 Bureau of Reclamation Projects in the Columbia Basin and ESA Section 10(a)(I)(A) Permit for Juvenile Fish Transportation Program. NOAA Fisheries Log Number: F/NWR/2010/02096.

NOAA Fisheries. 2014. Endangered Species Act Section 7(a)(2) Supplemental Biological Opinion. Dept. Commerce.

NOAA Fisheries. 2016. 2015 adult sockeye salmon passage report. Available at http://www.westcoast.fisheries.noaa.gov/publications/hydropower/fcrps/2015_adult_sockeye_salmon_passage_report.pdf.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151–1162.

R Core Team. 2013. R: A language and environmental for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. USBN 3-900051-0700, available at www.R-project.org. Version 3.0.1.

Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13(1):23-49.

Strange, J. S. 2010. Upper thermal limits to migration in adult Chinook salmon: Evidence from the Klamath River Basin. Transactions of the American Fisheries Society 139(4):1091-1108.

Strange, J. S. 2012. Migration strategies of adult Chinook salmon runs in response to diverse environmental conditions in the Klamath River Basin. Transactions of the American Fisheries Society 141(6):1622-1636.

United States v. Oregon. 2008. 2008-2017 United States v. Oregon Management Agreement, May 2008. Stipulated order in U.S. v. Oregon, Civil No. 68-513-KI (D. Or.), 1969. Available at www.westcoast.fisheries.noaa.gov/publications/fishery_management/salmon_steelhead/sr--079.2008-2017.usvor.management.agreement_042908.pdf (June 2017).

Wade, A., and coauthors. 2013. Steelhead vulnerability to climate change in the Pacific Northwest. J. Anim Ecol.

Appendix

Fallback Statistics, 2004-2015

Appendix Table 1. Fallback statistics for Snake River spring/summer-run and Columbia River spring-run adult salmon by dam and year. Shown are the total number fish detected at each dam, number of fish that fell back at least once, total number of fallbacks detected, percentage of fish that fell back at least once, and the fallback rate, which is the total number of fallback events per fish that passed.

Dam	Year	Number of fish passing	Number of fish that fell back	Total number of fallbacks	Fallback percent	Fallback rate
	Snake River Chinook salmon					
Bonneville	2004	926	22	23	2.4	2.5
	2005	522	28	33	5.4	6.3
	2006	364	25	26	6.9	7.1
	2007	359	44	47	12.3	13.1
	2008	821	99	113	12.1	13.8
	2009	871	104	116	11.9	13.3
	2010	2,012	194	209	9.6	10.4
	2011	1,573	165	189	10.5	12.0
	2012	1,035	111	125	10.7	12.1
	2013	584	62	67	10.6	11.5
	2014	984	101	108	10.3	11.0
	2015	1,445	98	103	6.8	7.1
The Dalles	2013	545	9	10	1.7	1.8
	2014	828	13	13	1.6	1.6
	2015	1244	24	28	1.9	2.3
McNary	2004	781	68	74	8.7	9.5
	2005	493	57	63	11.6	12.8
	2006	291	29	29	10.0	10.0
	2007	303	75	82	24.8	27.1
	2008	707	65	74	9.2	10.5
	2009	753	75	77	10.0	10.2
	2010	1,657	145	154	8.8	9.3
	2011	1,123	98	109	8.7	9.7
	2012	878	91	93	10.4	10.6
	2013	502	68	69	13.5	13.7
	2014	711	92	93	12.9	13.1
	2015	1,010	131	143	13.0	14.2

Appendix Table 2. Continued.

Dam	Year	Number of fish passing	Number of fish that fell back	Total number of fallbacks	Fallback percent	Fallback rate
	Snake River Chinook salmon (continued)					
Ice Harbor	2004	769	27	29	3.5	3.8
	2005	479	19	19	4.0	4.0
	2006	289	26	27	9.0	9.3
	2007	300	15	16	5.0	5.3
	2008	688	27	29	3.9	4.2
	2009	738	32	37	4.3	5.0
	2010	1,619	76	78	4.7	4.8
	2011	1,080	46	47	4.3	4.4
	2012	861	49	52	5.7	6.0
	2013	495	30	31	6.1	6.3
	2014	700	17	17	2.4	2.4
	2015	977	30	31	3.1	3.2
Lower Granite	2004	768	27	28	3.5	3.6
	2005	469	50	56	10.7	11.9
	2006	269	30	34	11.2	12.6
	2007	285	29	34	10.2	11.9
	2008	675	96	112	14.2	16.6
	2009	712	84	97	11.8	13.6
	2010	1,551	177	190	11.4	12.3
	2011	1,024	205	242	20.0	23.6
	2012	814	175	192	21.5	23.6
	2013	439	68	75	15.5	17.1
	2014	658	109	127	16.6	19.3
	2015	861	108	125	12.5	14.5
	Upper Columbia River Chinook salmon					
Bonneville	2004	812	44	45	5.4	5.5
	2005	813	41	42	5.0	5.2
	2006	652	54	62	8.3	9.5
	2007	95	12	12	12.6	12.6
	2008	114	9	9	7.9	7.9
	2009	128	17	19	13.3	14.8
	2010	457	32	32	7.0	7.0
	2011	327	27	29	8.3	8.9
	2012	478	52	59	10.9	12.3
	2013	257	15	16	5.8	6.2
	2014	389	41	49	10.5	12.6
	2015	538	40	41	7.4	7.6
The Dalles	2013	241	3	3	1.2	1.2
	2014	355	2	2	0.6	0.6
	2015	499	23	35	4.6	7.0

Appendix Table 3. Continued.

Dam	Year	Number of fish passing	Number of fish that fell back	Total number of fallbacks	Fallback percent	Fallback rate
		Upper Columbia River Chinook salmon (continued)				
McNary	2004	713	20	21	2.8	2.9
	2005	687	45	46	6.6	6.7
	2006	523	56	60	10.7	11.5
	2007	80	8	8	10.0	10.0
	2008	90	13	13	14.4	14.4
	2009	104	11	11	10.6	10.6
	2010	380	27	29	7.1	7.6
	2011	255	17	17	6.7	6.7
	2012	400	25	25	6.3	6.3
	2013	223	20	20	9.0	9.0
	2014	333	36	36	10.8	10.8
	2015	441	53	57	12.0	12.9
Priest Rapids	2004	549	9	10	1.6	1.8
	2005	575	4	4	0.7	0.7
	2006	496	9	10	1.8	2.0
	2007	79	1	1	1.3	1.3
	2008	90	2	2	2.2	2.2
	2009	102	1	1	1.0	1.0
	2010	373	3	3	0.8	0.8
	2011	253	3	4	1.2	1.6
	2012	314	6	6	1.9	1.9
	2013	223	3	3	1.3	1.3
	2014	329	6	6	1.8	1.8
	2015	419	3	3	0.7	0.7
Rock Island	2004	295	11	11	3.7	3.7
	2005	489	31	31	6.3	6.3
	2006	453	21	22	4.6	4.9
	2007	75	4	4	5.3	5.3
	2008	86	10	10	11.6	11.6
	2009	104	3	3	2.9	2.9
	2010	367	20	23	5.4	6.3
	2011	225	11	12	4.9	5.3
	2012	386	26	29	6.7	7.5
	2013	210	4	4	1.9	1.9
	2014	257	8	9	3.1	3.5
	2015	339	6	6	1.8	1.8