# Passage and Survival of Adult Snake River Sockeye Salmon within and Upstream from the Federal Columbia River Power System 

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Report of research to

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## Executive Summary

Snake River sockeye salmon Oncorhynchus nerka is among the most endangered of all evolutionarily significant units (ESUs) of Pacific salmon, with production sourced primarily from captive broodstock since 1990. The adult migration presents an especially significant challenge to recovery of this population because adults must migrate through various fisheries, pass 8 hydroelectric dams, and travel over 1,500 km to reach native spawning areas. Since 2008, survival for adult Snake River sockeye salmon from Bonneville Dam to the Sawtooth Weir has ranged from $60 \%$ in 2010 to $13 \%$ in 2013.

To increase the number of spawners for natural production and hatchery broodstock, one potential management strategy under consideration is adult transportation from Lower Granite Dam. When conditions in the river are unfavorable for in-river migrant survival, fish would be collected at the dam and transported to the Sawtooth Valley. As a first step in assessing this option, we analyzed existing data from 920 fish marked with passive integrated transponder (PIT) tags and detected at Bonneville Dam from 2008 through 2013. The goal of our analysis was to determine whether we could identify the river conditions most unfavorable for migration success and to explore the implications of potential triggers for transportation.

Specifically, we evaluated the extent to which migration success varied with juvenile characteristics such as origin and downstream migration history, adult migration characteristics such as timing and fallback, and river conditions in reaches from Bonneville Dam to the Sawtooth Valley. We then explored potential "triggers" to initiate transportation by comparing the survival rates of various proportions of the population with expected survival from transportation scenarios based on different types of triggers (date and temperature). Scenarios were constructed for different locations of potential transport (Bonneville, Ice Harbor, or Lower Granite Dam) and for different threshold values on transportation triggers. Below we summarize major findings from these analyses.

During 2008-2013, fallback affected a relatively small percentage of fish at McNary Dam ( $\sim 3-6 \%$ of fish fell back at least once) but increasingly larger percentages at Bonneville (4-15\%), Ice Harbor (7-18\%) and Lower Granite Dam (6-38\%). Because some sockeye salmon fell back multiple times, the fallback rate (total number of fallback events divided by unique fish passing the dam) was quite high compared to that reported for spring/summer Chinook salmon and steelhead, particularly at Lower Granite Dam. Fallback rate peaked at Lower Granite Dam in 2012 (49.2\%) and 2013 (48.4\%). In 2013, fish that had been transported as juveniles fell back at Bonneville, The Dalles, and McNary Dam at higher rates than fish that had not been transported.

After summing the 2013 fallbacks at these three dams during 2013, we found that fish transported as juveniles exhibited 50 fallbacks per 100 fish, whereas those that migrated in-river as juveniles exhibited 12 fallbacks per 100 fish. However, this effect was weak or absent in other years, so further investigation is needed to determine whether this factor was confounded with something else. Temperature and/or flow correlated strongly with the probability of falling back, but dissolved gas and fish history also influenced fallback risk.

Based on magnitude of effect, the most important predictors of survival across reaches and years were thermal exposure and fish travel time. Dramatically higher temperature exposure in the lower Snake River contributed to both high fallback rates and lower survival rates observed in 2013. In the Columbia River, juvenile transportation and fishery catch also strongly influenced adult survival. In comparison to upper Columbia River sockeye, Snake River sockeye had lower conversion rates from Bonneville Dam to McNary Dam. Snake River sockeye migrated 3-5 d later than upper Columbia River sockeye but had similar travel times.

Adult migration survival varied strongly as a function of temperature and dropped below $50 \%$ when river temperatures surpassed $18^{\circ} \mathrm{C}$. In most years, no particular trigger or threshold produced a dramatic or strongly non-linear advantage over others, but a threshold temperature of $18^{\circ} \mathrm{C}$ or higher at Bonneville, Ice Harbor or Lower Granite Dam noticeably improved in-river survival to the Sawtooth Valley in our scenarios. Across years, 23 to $92 \%$ of the run experienced temperatures over $18^{\circ} \mathrm{C}$ at Lower Granite Dam.

An early onset of warm temperatures in 2013 likely exacerbated cumulative thermal stress, and this cumulative stress, rather than maximum temperature per se, may be primarily responsible for the reduced survival observed in 2013. If so, a useful strategy might include combining temperature and day information in any decision to transport.

Additional data nearly always improve the predictive ability of models, but this is especially true when few data are available for model fit. We had just 3-4 years of data. Moreover, the observed range in predictive factors was relatively narrow compared to the likely future conditions over which we are trying to project. Our analysis also suffered from unbalanced representation of observations for the various options across years, particularly for the juvenile history traits. We demonstrated challenges for forecasting by trying to predict survival in 2013 based on data from prior years. Although temperature emerged as a key driving factor in these forecasts, the magnitude of negative effects from higher temperatures was underestimated, especially for survival in reaches from Ice Harbor Dam to the Sawtooth Valley.

We identified the following five areas of outstanding need for data important to the management of adult Snake River sockeye:

1) Refine understanding of how thermal experience affects survival, especially to determine the relative roles of acute vs. cumulative thermal stress for both survival and fallback
2) Explore factors that affect migration timing both between years and within a year, and the extent to which run timing affects losses in the Bonneville to McNary Dam reach, and tolerance of warm years
3) Better discriminate among the influences of flow, spill, and gas, especially for fallback at Columbia River dams and survival through the Snake River
4) Obtain more accurate estimates of fallback rates
5) Pursue a more conclusive evaluation of whether juvenile transportation truly influences fallback and adult survival

To resolve these questions, finer-scale resolution of fish behavior and the river environment is needed, along with experimental manipulations and further data analysis.

To obtain data at this resolution, we recommend studies using radio telemetry with data-intensive tags (i.e., depth and temperature sensors) to help clarify the thermal habitats selected by adult sockeye during migration. This approach would provide information on both acute and cumulative thermal effects and would provide the data needed to improve estimates of the factors that affect fallback. Experimental thermal exposures followed by intensive monitoring of condition and survival (e.g., Crossin et al. 2008b) would help to identify delayed effects of thermal exposure in the hydrosystem that affect fish upstream in the Snake and Salmon Rivers. In addition, it would help to determine thresholds of exposure tolerance and to separate cross-correlated environmental factors. Minimally, additional years of PIT-tag data collection and analysis are needed to broaden our predictive power

It is important to note that the practicality of transporting fish when conditions are already stressful (e.g., over $18^{\circ} \mathrm{C}$ ) needs to be evaluated. High temperatures during collection may substantially reduce the survival of transported fish. If this is the case, an alternative option would be to collect fish earlier in the migration season, perhaps at Bonneville Dam. However, this option would require some means of identifying and collecting Snake River sockeye, which are a small proportion of the run at Bonneville Dam compared to the proportion from unlisted upper Columbia sockeye populations.

These data can provide the unique combinations of information on environmental and biological conditions that will allow refinement of the models to better inform management decisions.

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## Introduction

Of the 27 populations of Pacific salmon Oncorhynchus spp. listed as threatened or endangered under the U.S. Endangered Species Act, Snake River sockeye salmon O. nerka have the most dramatic history. This population migrates further than any other salmonid-over 1500 km inland-and climbs 2000 m to the highest spawning habitat (Waples et al. 1991, Figure 1). It is also the southernmost sockeye population; the species range extends north through British Columbia, Canada, and Alaska, and along the coast of Asia.


Figure 1. Map showing location of Snake River, Wenatchee, and Okanogan Sockeye Salmon ESUs and PIT-tag detection sites on the Columbia, Snake and Salmon Rivers used for this study. Detection at Eleven Mile or Iron Creek constituted survival to the Salmon River. Detection at either Valley Creek or Sawtooth Hatchery qualified as survival to Sawtooth Valley. The monitoring station at Anatone, Idaho, is also shown (USGS 2014).

Over the past century, the population of Snake River sockeye salmon has plummeted. From 1989 to 1999, a total of 75 adults were observed at Lower Granite Dam on the Snake River, and only 24 adults reached trapping areas in the Sawtooth Valley, approximately 750 km upstream (Dan Baker, Idaho Department of Fish and Game, personal communication). The entire population, which represents an evolutionarily significant unit (ESU) was collected for captive broodstock starting in 1991 and has been maintained through hatchery propagation and supplementation for two decades. Restoring the wild population would represent a major accomplishment.

In recent years, annual releases of $150,000-200,000$ smolts from captive broodstock supported by favorable ocean conditions have increased the number of adult returns to Lower Granite Dam (~470-2,200 from 2008 to 2013). Many of these fish were tagged as juveniles with passive integrated transponder (PIT) tags, allowing us to track their return migration. Detection facilities at multiple projects within and upstream of the hydrosystem allow individual migration histories of each fish to be determined and analyzed.

Here we describe estimated detection efficiency, conversion rates, migration characteristics, and correlates of survival for 920 PIT-tagged sockeye that originated in the Sawtooth Valley and were detected at Bonneville Dam between 2008 and 2013 (Table 1). Note that 927 fish were included in detection efficiency and conversion-rate analyses, but the seven that were not detected at Bonneville Dam lacked data on important covariates tested in the other analyses.

Table 1. Count of adult PIT-tagged sockeye salmon tagged as juveniles and released in the Sawtooth Valley.

|  |  |  |  | Lower <br> Granite | Sawtooth | Total unique <br> fish |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 2008 | 14 | 0 | 10 | 10 | 10 | 3 | 14 |
| 2009 | 23 | 0 | 16 | 17 | 17 | 11 | 23 |
| 2010 | 40 | 0 | 34 | 30 | 31 | 25 | 41 |
| 2011 | 516 | 0 | 343 | 315 | 332 | 253 | 520 |
| 2012 | 122 | 0 | 70 | 67 | 64 | 40 | 123 |
| 2013 | 205 | 170 | 138 | 121 | 91 | 27 | 206 |
| Total | 920 | 170 | 611 | 560 | 545 | 359 | 927 |

The adult migration presents a significant challenge to recovery of this population. Survival from Bonneville Dam to the weir at Sawtooth Hatchery ranged from 60 to $13 \%$ between 2008 and 2013. As mentioned above, the adult migration is
long and strenuous; furthermore, unlike most Chinook salmon that follow the same route, these sockeye migrate in July and August - the hottest time of year. Historically, weekly mean water temperature in these months nearly always exceeded $20^{\circ} \mathrm{C}$ and frequently surpassed $23^{\circ} \mathrm{C}$ at the U.S. Geological Survey monitoring station located 225 km upstream from Lower Granite Dam at Anatone, Idaho (USGS 2014; Figure 1). These conditions approach the lethal thermal maximum for sockeye salmon, although some local adaptation is possible (Crossin et al. 2008; Eliason et al. 2011). Previous studies of fish tagged as adults with radio transmitters found that late migrants returning to both the upper Columbia (Okanogan and Lake Wenatchee ESUs; (Naughton et al. 2005) and Snake River (Keefer et al. 2008b) encounter higher temperatures en route and have very low survival. Here we examine the larger dataset of PIT-tagged fish to explore both individual fish characteristics and environmental factors that correlate with survival patterns.

A primary focus of recovery efforts for depressed stocks of Pacific salmon Oncorhynchus spp. has been assessing and improving passage conditions at mainstem dams on the Columbia and Snake Rivers. Results of this study provide a first step in informing management options for adult transportation of sockeye salmon. This study addresses research needs outlined in the 2008 Biological Opinion for the Federal Columbia River Power System (Reasonable and Prudent Alternative Actions 28, 42, and 55). Information from this work is required to implement the 2009 Adaptive Management Implementation Plan (BPA et al. 2009) incorporated into the 2010 Supplemental Biological Opinion (NOAA Fisheries 2010).

Both the 2008 and 2010 Supplemental Biological Opinions recommended studying the feasibility of transporting adult sockeye salmon. Therefore, one potential management strategy under consideration is to collect adult sockeye at Lower Granite Dam and transport them to the Sawtooth Valley to increase the number of spawners for natural production and hatchery broodstock. A pilot study was completed in 2010, with 11 female and 8 male adult sockeye successfully transported (i.e., fish survived until they were spawned at Eagle Fish Hatchery, Dan Baker, Idaho Department of Fish and Game, personal communication). Transportation occurred between 1 and 15 July at Lower Granite Dam, when mean daily temperature was $17.4^{\circ} \mathrm{C}$ in the tailrace and $18.9^{\circ} \mathrm{C}$ at the $0.5-\mathrm{m}$ depth in the forebay.

If shown to be effective, transport could be used when river conditions reach levels likely to impair migration success. We analyzed existing PIT-tag data to determine whether we could identify strong explanatory factors of migration mortality, and we examined support for potential transportation "triggers." Our goal was to identify what conditions affect migration success to inform managers attempting to determine when transportation would produce a net benefit to this population. Specifically, we evaluated
the relationship between timing, river environment, and migration success in individual reaches from Bonneville Dam to the Sawtooth Valley.

Our analysis involved the following four major steps.

1. Estimate annual detection efficiency at each detector along the migration route to calculate conversion rates (survival) by individual reach from 2008 to 2013.
2. Describe migration characteristics for the population over this period: overall migration timing, travel time within each reach, and fallback rate.
3. Analyze conversion rates and fallback as a function of covariates; covariates included some aspects of juvenile history, adult migration characteristics, and environmental factors during the adult migration.
4. Explore the utility of environmental and seasonal "triggers" for transportation, and based on these triggers, develop scenarios to compare the survival of fish left in river with those that would have been transported.

Each of these steps is detailed in the following four sections.

# Detection Efficiency and Conversion Rates 

## Methods

For both annual and total (all years combined) cohorts of adult sockeye salmon detected at Bonneville Dam, we constructed a five-digit detection history for each fish. Each detection history denoted detection or not at Bonneville Dam, McNary Dam, Ice Harbor Dam, Lower Granite Dam, and the Sawtooth Valley. The final grouping (Sawtooth Valley) included detection at any site within the ESU boundary, e.g., Valley Creek or the Sawtooth Hatchery Trap.

We then conducted a mark-recapture analysis using these detection histories to estimate detection efficiency at Bonneville, McNary, Ice Harbor, and Lower Granite Dam using the Cormack-Jolly-Seber model with the software program SURPH, Survival Under Proportional Hazards (Lady et al. 2001). Survival estimates produced by this model were the conversion rates for each reach between these detection sites. We used the term survival interchangeably with conversion rate in describing our analyses.

In 2013, PIT detectors were installed at The Dalles Dam and at two sites near Salmon, Idaho: Eleven Mile Creek (rkm 437) and Iron Creek (rkm 460). Thus, for 2013 we produced an 8 -digit detection history and calculated detection efficiency and conversion rates for these locations. The two in-stream sites near Salmon, Idaho, were pooled because of their proximity to one another and because in-stream detectors are expected to have lower detection rates. Detection at either of these sites is referred to as detection at Salmon, Idaho. We present conversion rates from Lower Granite Dam and Salmon, Idaho, to the Sawtooth Valley assuming detection rates of $100 \%$ at the headwaters.

We also estimated cumulative survival in the following individual reaches: from Bonneville to Lower Granite, Bonneville to the Sawtooth Valley, McNary to Lower Granite, McNary to the Sawtooth Valley, and Lower Granite to the Sawtooth Valley. We described cumulative survival from both McNary and Bonneville Dam to eliminate harvest in the Zone 6 fishery (i.e., between Bonneville and McNary Dams) as a confounding factor.

Sockeye salmon juveniles have also been PIT-tagged in the upper Columbia River Basin, and have exhibited substantial adult returns during 2008-2012. We constructed models similar to those described above, but for estimates of survival we used detections
at Priest Rapids and Rock Island Dam in addition to those at Bonneville, The Dalles (in 2013), and McNary Dam.

Finally, in some years, adult sockeye salmon were PIT-tagged at Bonneville and released below the dam (Fryer 2009; Fryer et al. 2011; Fryer et al. 2012). Because Snake River sockeye represent a very small fraction of the sockeye run as a whole, the vast majority of these tagged adults were from upper Columbia River ESUs (Okanogan and Lake Wenatchee). We constructed Cormack-Jolly-Seber models as described above to assess detection efficiency and conversion rates for these fish at The Dalles (in 2013) and McNary Dams.

## Results

Estimated detection efficiency was over $97 \%$ at Bonneville and Lower Granite Dam in all 6 study years and at The Dalles Dam in 2013 (Table 2). Detection efficiency improved at McNary Dam from 90.9 and $94.1 \%$ in 2008-2009 to over $97 \%$ from 2010 to 2013. Ice Harbor Dam had the lowest adult detection efficiency of the mainstem dams, averaging 93.4\%. In the Upper Salmon River, the in-stream PIT detection system installed for 2013 had an average detection efficiency of $85.2 \%$, based on fish that survived to the weir at Sawtooth Hatchery. Detection efficiencies for Snake River sockeye were similar to or higher than those for upper Columbia River sockeye salmon (Table 3).

Table 2. Estimated detection probabilities (mean and SE) for adult sockeye salmon PIT-tagged as juveniles and released in the Sawtooth Valley.

|  | Mean estimated detection probability for adult Snake River sockeye salmon (SE) |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | :---: |
| Year | Bonneville | The Dalles | McNary | Ice Harbor | Lower Granite | Salmon, ID |
| 2008 | $100.0(0.0)$ | -- | $90.9(8.7)$ | $90.0(9.5)$ | $100.0(0.0)$ | -- |
| 2009 | $100.0(0.0)$ | -- | $94.1(5.7)$ | $100.0(0.0)$ | $100.0(0.0)$ | -- |
| 2010 | $97.1(2.8)$ | -- | $100.0(0.0)$ | $90.3(5.3)$ | $100.0(0.0)$ | -- |
| 2011 | $98.9(0.6)$ | -- | $97.1(0.9)$ | $90.4(1.6)$ | $97.2(1.0)$ | -- |
| 2012 | $98.6(1.4)$ | -- | $97.1(2.0)$ | $95.3(2.6)$ | $97.4(2.5)$ | -- |
| 2013 | $99.4(0.6)$ | $98.6(1.0)$ | $98.4(1.1)$ | $94.5(2.4)$ | $100.0(0.0)$ | $85.2(6.8)$ |
| Average | $99.0(0.9)$ | $98.6(1.0)$ | $96.3(3.1)$ | $93.4(3.6)$ | $99.1(0.6)$ | $85.2(6.8)$ |

Table 3. Estimated detection probability for upper Columbia River sockeye salmon (mean and SE) PIT-tagged as juveniles and as adults at the Bonneville Dam adult fish facility.

|  | Mean estimated detection probability for adult Columbia River sockeye salmon (SE) |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Fish tagged as adults |  |
| Year | Bonneville | The Dalles | McNary | The Dalles |  |
| 2008 | $93.0(3.9)$ | -- | $85.0(5.7)$ | - | McNary |
| 2009 | $98.9(0.7)$ | - | $99.4(1.1)$ |  |  |
| 2010 | $98.7(0.4)$ | -- | $95.9(1.6)$ | - | $94.6(0.9)$ |
| 2011 | $98.0(0.7)$ | -- | $87.0(1.6)$ | - | $96.1(0.7)$ |
| 2012 | $99.3(0.4)$ | -- | $96.8(0.9)$ | - | $86.0(1.5)$ |
| 2013 | $95.3(1.7)$ | $97.7(1.3)$ | $97.6(1.4)$ | $98.7(0.4)$ | $97.9(0.5)$ |
| Average | $97.2(1.3)$ | $97.7(1.3)$ | $92.5(2.0)$ | $98.7(0.4)$ | $93.7(0.8)$ |

Conversion rates through the entire hydrosystem (Bonneville to Lower Granite Dam) exceeded 70\% from 2008 to 2010 (albeit low sample sizes), but then declined progressively to a low of $44 \%$ in 2013 (Tables $4-5$; Figure 2). The bulk of this loss occurred in the reach from Bonneville to McNary Dam, where fish experienced a minimum conversion rate of only $58.2 \%$ in 2012. During the weeks fish were passing, catch was 2.5 to 6 times higher in 2012 than in other years of the study. Similar to the cumulative pattern from Bonneville to Lower Granite Dam, survival from Lower Granite Dam to Sawtooth peaked in 2010 and 2011, declined in 2012 and then dropped by half in 2013 (Figure 3).

Table 4. Conversion rates (mean and SE) of PIT-tagged Snake River sockeye salmon.

| Year | Mean conversion rate (SE) |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Bonneville to The Dalles | Bonneville to McNary | Bonneville to Lower Granite | The Dalles to McNary | McNary to Ice Harbor | McNary to Lower Granite |
| 2008 |  | 78.6 (11.0) | 71.4 (12.1) |  | 101.0 (1.4) | 90.9 (9.7) |
| 2009 |  | 73.9 (9.2) | 73.9 (9.2) |  | 100.0 (0.0) | 100.0 (0.0) |
| 2010 |  | 85.0 (5.7) | 77.5 (6.6) |  | 97.7 (3.0) | 91.2 (4.9) |
| 2011 |  | 67.9 (2.1) | 65.4 (2.1) |  | 98.8 (0.7) | 96.3 (1.1) |
| 2012 |  | 58.2 (4.5) | 53.0 (4.6) |  | 97.4 (2.0) | 91.0 (3.8) |
| 2013 | 83.6 (2.6) | 67.9 (3.3) | 44.4 (3.5) | 81.2 (3) | 91.2 (2.7) | 65.4 (4.1) |
| Average |  | 71.9 (5.9) | 64.3 (6.3) |  | 97.7 (1.6) | 89.1 (3.9) |
|  | Ice Harbor to Lower Granite | Lower Granite to Sawtooth | Lower Granite to Salmon | Salmon to Sawtooth | Bonneville to Sawtooth |  |
| 2008 | 90.0 (9.5) | 30.0 (14.5) |  |  | 21.4 (11.0) |  |
| 2009 | 100.0 (0.0) | 64.7 (11.6) |  |  | 47.8 (10.4) |  |
| 2010 | 93.3 (4.6) | 77.4 (7.5) |  |  | 60.0 (7.7) |  |
| 2011 | 97.5 (1.0) | 74.1 (2.4) |  |  | 48.5 (2.2) |  |
| 2012 | 93.4 (3.4) | 60.3 (6.2) |  |  | 32.0 (4.2) |  |
| 2013 | 71.7 (4.1) | 29.7 (4.8) | 49 (5.8) | 60.5 (7.9) | 13.2 (2.4) |  |
| Average | 91.0 (3.8) | 56.0 (7.8) |  |  | 37.1 (6.3) |  |

Table 5. Conversion rates of upper Columbia River sockeye salmon PIT-tagged as juveniles.

|  | Mean conversion rate (SE) |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
| Year | Bonneville to <br> McNary | McNary to Priest <br> Rapids | Bonneville to The <br> Dalles | The Dalles to <br> McNary |
| 2008 | $88.9(4.7)$ | $100.0(0.0)$ |  |  |
| 2009 | $79.9(2.2)$ | $97.5(1.0)$ |  |  |
| 2010 | $81.5(1.3)$ | $98.3(0.5)$ |  |  |
| 2011 | $68.8(1.8)$ | $98.0(0.7)$ |  |  |
| 2012 | $73.1(1.9)$ | $97.6(0.8)$ | $84.1(2.8)$ | $93.6(2.1)$ |
| 2013 | $78.6(3.2)$ | $96.1(1.7)$ | $84.1(2.8)$ | $93.6(2.1)$ |
| Average | $78.6(3.2)$ | $97.9(0.8)$ |  |  |



Figure 2. Conversion rates by reach from Bonneville Dam to Lower Granite Dam for Sawtooth Valley sockeye salmon.


Figure 3. Conversion rates from Lower Granite Dam to the Sawtooth Valley for Sawtooth Valley sockeye salmon.

In 2013, survival from Bonneville Dam to the Sawtooth Valley was very low in all reaches, producing the lowest cumulative migration success of the study period (Figure 4). There was often a strong seasonal effect, such that later fish had lower survival than early fish, but even early fish had very low survival in 2013 (Figure 5). Comparing each first quartile of the annual run from 2010 to 2013, survival dropped from $83 \%$ in 2010 to $52 \%$ in 2011-2012 to $35 \%$ in 2013. Survival during 2013 continued to drop after the first quartile, falling from 35 to $12 \%$ during the second quartile and to only $4 \%$ during the third; no fish in the last quartile survived to Sawtooth.

In comparison to upper Columbia River sockeye, Snake River fish had substantially lower survival through the reach from Bonneville to McNary Dam (compare Tables 4 and 5) except in 2010, when survival was high for both groups. Average survival across all years was $71.9 \%$ for Snake River sockeye, and $78.6 \%$ for fish tagged as juveniles in the upper Columbia River. In 2013, the only year for which data were available for estimates, survival between Bonneville and The Dalles Dam was similar for Snake vs. Columbia River sockeye salmon. However, between The Dalles and McNary Dam, survival was considerably lower for Snake than for Columbia River fish ( 81.2 vs. 93.6\%).


Figure 4. Cumulative conversion rates from Bonneville to Sawtooth Valley.


Figure 5. Observed survival from Bonneville and Lower Granite Dams to the Sawtooth Valley as a function of seasonal progression of the run by quartile (i.e., first $25 \%$ of the run, then $26-50 \%$ of the run, etc.). The years 2008 and 2009 are not shown because sample sizes were too small to adequately represent quartiles of the run.

# Migration Timing and Rates of Fallback 

## Methods

We calculated a variety of passage time and fallback metrics for PIT-tagged Snake River sockeye salmon returning as adults between 2008 and the 2013. These metrics were chosen for their ability to measure factors having the most impact on migration success for sockeye or Chinook salmon (Naughton et al. 2005; Caudill et al. 2007; Keefer et al. 2008b). We summarized migration timing based on first detections of fish at each monitoring site and then calculated travel time as time from last detection at a monitoring site to first detection at the next upstream site. We calculated fallback rates using a program developed specifically for that purpose (Tiffani Marsh, National Marine Fisheries Service, personal communication).

We developed this program because fallback events cannot be evaluated directly using PIT-tag data (Burke et al. 2004). To confirm that fallback has occurred, we must first observe a fish passing upstream through a fish ladder, followed by a second attempt at passing the ladder (thereby deducing that the fish fell back over the dam between ascensions). By comparing the physical location of two detections adjacent in time, one can determine direction of movement.

For example, if detection coils within a ladder are numbered in descending order downstream, then a series of PIT-tag detections ordered from coils 6,4 , and 2 , can be interpreted to mean that the fish was traveling upstream in the ladder. If these detections are the last detections at a dam, we can interpret this series as a successful passage event. However, if detections at coils 6,4 , and 2 are closely followed by detection at coils 4, 6, and 8 , we must conclude that the fish traveled downstream within the fishway.
Unfortunately, when salmon move downstream within a fishway, they can avoid detection by passing over the weirs, rather than through the orifices, of the ladder. This phenomenon can be species-specific and can vary with instream conditions. It also means detection of upstream movement is more consistent than that of downstream movement.

It is important to understand that because adult fish can pass over a weir without being detected, interpretation of movement data within a ladder is somewhat subjective. We used a software program created to address this ambiguity (Tiffani Marsh, National Marine Fisheries Service, personal communication). The program is similar in concept to the algorithm described by Burke et al. (2004), in that codes are assigned to PIT-tag detections to represent whether a fish was traveling upstream $(+)$, downstream (-), or remaining at the same weir (○). Placed in sequence, these codes allow more accurate
interpretation of fish movement. For example, the series $[+++-+++]$ would indicate that a fish traveled upstream through the ladder, while the series [ ++-- ] would indicate initial movement upstream followed by movement downstream through the orifices.

Unfortunately, there was not always a concrete way to distinguish a series that represented successful passage followed by reascension from one that represented upstream movement followed by downstream movement (without being detected) followed by further movement upstream (Burke et al. 2004). We therefore used a time-based cutoff to separate records into distinct blocks. Specifically, if a series of detections was followed by a lack of detections for 6 h or more, it was classified as a block and considered separately from any following detections. If a block suggested upstream movement and ladder passage, we labeled the block as a successful passage event: any subsequent detections, regardless of position in the ladder, were interpreted as a separate ascension event (reascension).

For example, in examining blocks within an individual ladder, blocks [+++] and $[+++++++]$ would represent two passage events (which implies a fallback between passage events). A similar set of detections is represented by the blocks [++-] and $[+++++++]$, with one noticeable difference: the first block ends with an indication of downstream movement. This second pair of blocks does not imply two passage events, but rather an unsuccessful attempt followed by a successful attempt. We used this method for analyses of detections from all PIT-tagged sockeye salmon at Bonneville, The Dalles (in 2013), McNary, Ice Harbor, and Lower Granite Dam.

## Results

## Migration Timing

Median arrival dates at Bonneville Dam varied by one week, from 29 June in 2009 and 2010 to 5 July in 2011 and 2012 (Table 6; Figures 6-7). The year 2009 was very warm (Figure 8), and it is interesting to note that the early start to the migration probably helped fish to avoid the warm temperatures experienced by fish arriving at the average time (e.g., 2013, Figure 7). Upper Columbia River sockeye consistently arrived about one week earlier than Snake River fish (Table 7, Figure 6).

Table 6. Dam arrival dates (median and 25-75\% range) for Snake River sockeye.

| Year | Bonneville | The Dalles | McNary | Ice Harbor | Lower Granite |
| :---: | :---: | :---: | :---: | :---: | :--- |
| 2008 | 30 Jun (28 Jun-2 Jul) |  | 5 Jul (3-9 Jul) | 7 Jul (4-12 Jul) | 11 Jul (9-16 Jul) |
| 2009 | 29 Jun (22 Jun-1 Jul) |  | 5 Jul (29 Jun-8 Jul) | 7 Jul (2-10 Jul) | 13 Jul (11-14 Jul) |
| 2010 | 29 Jun (25 Jun-9 Jul) |  | 4 Jul (1-12 Jul) | 7 Jul (3-12 Jul) | 10 Jul (7-16 Jul) |
| 2011 | 5 Jul (1-9 Jul) | 12 Jul (8-16 Jul) | 14 Jul (10-17 Jul) | 18 Jul (15-23 Jul) |  |
| 2012 | 5 Jul (29 June-10 Jul) | 10 Jul (4-16 Jul) | 13 Jul (6-18 Jul) | 16 Jul (9-24 Jul) |  |
| 2013 | 1 Jul (27 June-6 Jul) | 2 Jul (29 Jun-7 Jul) | 6 Jul (3-11 Jul) | 8 Jul (5-12 Jul) | 13 Jul (7-27 Jul) |

Table 7. Dam arrival dates (median and 25-75\% range) for upper Columbia sockeye.

| Year | Bonneville | The Dalles | McNary |
| :--- | :--- | :---: | :---: |
| 2008 | 25 Jun (22-29 Jun) |  | 30 Jun (26 Jun-13 Jul) |
| 2009 | 26 Jun (22-29 Jun) | 2 Jul (29 Jun-6 Jul) |  |
| 2010 | 24 Jun (21-28 Jun) | 30 Jun (27 Jun-4 Jul) |  |
| 2011 | 30 Jun (26 Jun-5 Jul) | 7 Jul (2-11 Jul) |  |
| 2012 | 27 Jun (23 Jun-2 Jul) |  | 13 Jul (29 Jun-8 Jul) |
| 2013 | 25 Jun (20 Jun-1 Jul) | 27 Jun (22 Jun-3 Jul) | 1 Jul (25 Jun 5-Jul) |



Figure 6. Arrival timing at Bonneville Dam (left) and McNary Dam (right) for Snake River and upper Columbia River sockeye PIT-tagged as juveniles. Lines show the median arrival date by year, boxes show the interquartile range, and whiskers show $\pm 1.5$ the interquartile range.

Figure 7.
Run timing, shown as cumulative passage, of adult PIT-tagged Snake River sockeye at Bonneville Dam each year from 2008 to 2013.



Figure 8. Temperatures at Ice Harbor Dam by calendar date for each year (top), and in proportion to arrival time by the fish (bottom). Horizontal line shows the median, boxes show the first and third quartiles.

## Travel Time

Travel time from Bonneville to McNary Dam averaged 5-6 d for Snake and upper Columbia River sockeye tagged as juveniles and for upper Columbia River sockeye tagged as adults (Table 8). Over all study years, median travel time was about 12 d through the whole hydrosystem (Bonneville to Lower Granite Dam) and ranged 47-57 d from Bonneville Dam to Sawtooth Hatchery (Table 9). Sockeye travel time was shortest in 2010 and longest in 2009 (but note the very small sample size in 2009). Travel time in 2013 was average in the first quartile and median, but slower in the third quartile than in any other year ( 80 d , compared with the second slowest 62 d in 2011).

Table 8. Median and $25-75 \%$ range of travel time in days from Bonneville to McNary Dam for fish PIT-tagged in the Sawtooth Valley, upper Columbia River, and at Bonneville Dam.

|  | Travel time (d) between Bonneville and McNary Dam |  |  |  |
| :--- | :--- | :---: | :---: | :---: |
|  | Sockeye tagged as juveniles |  |  | Sockeye tagged as adults |
| Year | Sawtooth Valley | Upper Columbia River |  | Bonneville Dam adult facility |
| 2008 | $5.05(4.77-5.45)$ | $5.15(4.48-7.63)$ |  | $5.43(4.89-6.79)$ |
| 2009 | $5.96(4.85-7.41)$ | $5.41(4.93-6.39)$ |  | $5.16(4.84-6.03)$ |
| 2010 | $5.22(4.53-5.95)$ | $5.24(4.68-6.12)$ |  | $5.11(4.77-6.09)$ |
| 2011 | $5.96(5.24-6.76)$ | $5.94(5.24-6.81)$ |  | $5.83(5.15-6.79)$ |
| 2012 | $5.69(5.28-6.48)$ | $5.75(5.1-6.51)$ |  | $5.44(5.03-6.27)$ |
| 2013 | $5.3(4.86-6.42)$ | $5.01(4.58-5.67)$ |  | $5.07(4.72-5.86)$ |

Table 9. Median travel time through the hydrosystem and above for Snake River sockeye salmon (in days). New PIT-tag monitoring systems were installed at The Dalles Dam and in the Salmon River prior to the 2013 adult migration (Figure 1).

|  | Sockeye salmon median travel time (d) |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | ---: | ---: |
|  | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 |
| Bonneville to The Dalles | -- | -- | -- | -- | -- | 1.84 |
| Bonneville to McNary | 5.05 | 5.96 | 5.22 | 5.96 | 5.69 | 5.30 |
| Bonneville to Ice Harbor | 6.61 | 7.94 | 7.24 | 7.88 | 7.72 | 7.09 |
| Bonneville to Lower Granite | 11.43 | 13.13 | 11.52 | 12.57 | 12.21 | 12.54 |
| Bonneville to Salmon, ID | -- | -- | -- | -- | -- | 33.51 |
| Bonneville to Sawtooth Hatchery | 50.59 | 56.63 | 47.06 | 53.19 | 48.96 | 52.76 |
| The Dalles to McNary | -- | -- | -- | -- | -- | 3.65 |
| The Dalles to Ice Harbor | -- | -- | -- | -- | -- | 5.29 |
| The Dalles to Lower Granite | -- | -- | -- | -- | -- | 10.96 |
| The Dalles to Salmon, ID | -- | -- | -- | -- | -- | 31.62 |
| The Dalles to Sawtooth Hatchery | -- | -- | -- | -- | -- | 30.01 |
| McNary to Ice Harbor | 1.44 | 1.85 | 1.84 | 1.85 | 1.81 | 1.67 |
| McNary to Lower Granite | 6.07 | 6.81 | 5.88 | 6.64 | 6.73 | 7.06 |
| McNary to Salmon, ID |  |  |  |  |  | 27.85 |
| McNary to Sawtooth Hatchery | 46.76 | 47.47 | 41.52 | 46.61 | 42.97 | 47.01 |
| Ice Harbor to Lower Granite | 4.02 | 4.84 | 4.04 | 4.7 | 4.27 | 5.27 |
| Ice Harbor to Salmon, ID |  |  |  |  |  | 25.41 |
| Ice Harbor to Sawtooth Hatchery | 45.31 | 48.51 | 39.28 | 44.89 | 40.72 | 45.47 |
| Lower Granite to Sawtooth Hatchery | 41.31 | 42.74 | 35.41 | 39.28 | 37.22 | 41.09 |
| Lower Granite to Salmon, ID | -- | -- | -- | -- | -- | 21.47 |
| Salmon, ID to Sawtooth Hatchery | -- | -- | -- | -- | -- | 21.07 |

## Fallback

The probability of fallback varied enormously across years and dams (Table 10, Figure 9). Fallback rates were relatively low at McNary ( $\sim 3-6 \%$ of fish fell back) but increasingly larger percentages at Bonneville (4-15\%), Ice Harbor (7-18\%) and Lower Granite Dam (6-38\%). Lower Granite Dam had especially high fallback rates in 2012 (38\%) and 2013 (33\%).

Table 10. Fallback percentage (unique fish falling back/unique fish passing $\times 100$ ) and rate (total fallback events/unique fish passing $\times 100$ ) at each dam.

| Fallback statistics for adult Snake River sockeye salmon |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Year and dam | Number of fish passing | Number of fish that fell back | Total number of fallbacks | Fallback percent | Fallback rate |
| Bonneville Dam |  |  |  |  |  |
| 2008 | 14 | 0 | 0 | 0 | 0 |
| 2009 | 23 | 2 | 2 | 8.7 | 8.7 |
| 2010 | 40 | 3 | 3 | 7.5 | 7.5 |
| 2011 | 516 | 39 | 49 | 7.6 | 9.5 |
| 2012 | 122 | 5 | 7 | 4.1 | 5.7 |
| 2013 | 205 | 31 | 67 | 15.1 | 32.7 |
| The Dalles Dam |  |  |  |  |  |
| 2013 | 169 | 31 | 52 | 18.3 | 30.8 |
| McNary Dam |  |  |  |  |  |
| 2008 | 10 | 0 | 0 | 0 | 0 |
| 2009 | 16 | 1 | 1 | 6.2 | 6.2 |
| 2010 | 34 | 1 | 1 | 2.9 | 2.9 |
| 2011 | 340 | 17 | 19 | 5 | 5.6 |
| 2012 | 69 | 2 | 2 | 2.9 | 2.9 |
| 2013 | 137 | 7 | 15 | 5.1 | 10.9 |
| Ice Harbor Dam |  |  |  |  |  |
| 2008 | 10 | 0 | 0 | 0 | 0 |
| 2009 | 17 | 3 | 3 | 17.6 | 17.6 |
| 2010 | 30 | 4 | 4 | 13.3 | 13.3 |
| 2011 | 313 | 23 | 26 | 7.3 | 8.3 |
| 2012 | 66 | 7 | 8 | 10.6 | 12.1 |
| 2013 | 120 | 12 | 17 | 10 | 14.2 |
| Lower Granite Dam |  |  |  |  |  |
| 2008 | 10 | 2 | 2 | 20 | 20 |
| 2009 | 17 | 1 | 2 | 5.9 | 11.8 |
| 2010 | 31 | 4 | 14 | 12.9 | 45.2 |
| 2011 | 328 | 82 | 94 | 25 | 28.7 |
| 2012 | 63 | 24 | 31 | 38.1 | 49.2 |
| 2013 | 91 | 30 | 44 | 33 | 48.4 |

Individual fish fell back 1-9 times. Because some fish fell back multiple times, the absolute number of fallbacks, and thus the total fallback rate, was high relative to that reported by Boggs et al. (2004) for spring summer Chinook salmon and Naughton et al. (2006) for sockeye in the cool year 1997. The fallback rate for sockeye at The Dalles and Bonneville Dams in 2013 was 31-33; fallback rates ranged 45-49 at Lower Granite Dam in 2010, 2012 and 2013 (Table 10). Although our method of detecting fallbacks was less precise than methods based on radiotelemetry data, it was interesting to note that Keefer et al. (2008a) documented fallback patterns very similar to those we observed. At each of the dams monitored, the number of fallbacks in 2013 was among the highest of all years.


Figure 9. Fallback rates by dam as either a percentage of all unique fish passing that fell back, regardless of the number of fallbacks per fish (top) or as the total fallback rate, or number of fallback events at each dam per unique fish passing (bottom).

# Covariate Analysis of Survival and Fallback 

## Methods

For this analysis we first classified each fish by migration fate based on detection history. Fates included detection at the upstream end of a reach, straying away from the primary migration route in the Sawtooth Valley, or loss within a reach from unknown sources, which could include harvest. We denote "survival" as successful passage upstream. We then explored three categories of covariates: juvenile factors, adult migration characteristics, and environmental factors.

## Potential Covariates

Juvenile Factors-Juvenile factors included 1) the hatchery of origin, 2) release location, 3) juvenile migration history, meaning whether the fish was transported and from which location, 4) juvenile detection history, meaning whether the fish was detected (other than on transport collection raceways) during its downstream migration, and 5) fish length at tagging. All juvenile factor data were retrieved from the PTAGIS database, but in some cases missing data were filled in by research personnel (Mike Peterson, Idaho Department of Fish and Game, personal communication).

Adult Migration Characteristics-Adult migration characteristics included the 1) age of return, 2) day of arrival at reach entry, 3) travel time from Bonneville to reach entry for reaches above Bonneville, 4) sum of fallbacks detected for an individual prior to and including the dam at the beginning of a reach, and 5) estimated sockeye catch in the Zone 6 fishery immediately after the fish passed Bonneville Dam. Age at return was calculated as the difference in the year of adult detection minus the juvenile migration year, assuming all fish migrated as yearling smolts. Day of arrival was the day of first detection at dam.

Weekly sockeye catch is estimated by Columbia River Inter-Tribal Fish Commission, and was shared by Stuart Ellis (CRITFC, personal communication). This weekly estimate include both specified days of gillnet opening and weekly (or longer) averages for platform and hook-and-line fishing. We combined these estimates into a daily catch by assuming catch was equally distributed within each of these periods. For example, if the gill net catch was open for 3 d , the total gill net catch would be divided by three. For individual fish, we associated exposure to the fishery by summing daily catch over the interval when the fish was known to be between Bonneville and McNary Dam (i.e., between last detection at Bonneville and first detection at McNary). For fish not detected at McNary Dam, exposure to the fishery was associated with daily catch over the 6 days following detection at Bonneville (i.e., the overall median migration time).

Some fishing occurred upstream of McNary Dam, but we did not have sufficient quantitative information to include this in our analysis.

The vast majority of sockeye caught in the Zone 6 fishery are of upper Columbia rather than Snake River origin, so the risk faced by an individual fish might be proportional to the size of the total run rather than the catch alone. We therefore calculated a second index of catch, in which daily catch was divided by daily total sockeye count at Bonneville Dam on the same day (data from DART 2014), ignoring the lag time between passing the dam and exposure to the fishery.

Environmental Factors-Environmental factors were derived from two sources. The primary source was daily average temperature (TempC), flow (Outflow), spill (Spill), and the percentage of dissolved gas (GasP) measured at each project (DART (2014). We prioritized data from the tailrace of each project (project codes: CCIW, TDDO, MCPW, IDSW, and LGNW). However, in some cases data was not available from the tailrace but it was reported for the forebay, so missing data for temperature, flow and spill was filled in with data from project codes: BON, TDA, MCN, IHR, LWG, respectively.

Our secondary source for temperature was the string temperature data reported by the U.S. Army Corps of Engineers (USACE 2014). Water temperature was measured hourly along 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 calculated daily mean and maximum temperatures at the $0.5-$ and $15-\mathrm{m}$ depth. For both temperature datasets, we matched the day the fish arrived at a dam with the daily temperature measured at that dam. For fish that were not detected at the upstream dam, we used the conditions at the upstream dam on the day the fish would have reached that dam, had it been traveling at the median migration rate for that reach.

The final environmental covariate tested was cumulative temperature exposure (CumT). This was an interaction term between temperature and travel time, wherein temperature exposure is progressively accumulated from Bonneville Dam upstream. We calculated cumulative temperature for every reach using temperatures measured at the lower and upper ends of the reaches:

$$
\text { CumT }=\frac{\left(T_{0.5, \text { Lower }, t}+T_{0.5, \text { Upper }, t+x}\right)}{2} * D
$$

where $T_{0.5, \text { Lower,t },}$ is temperature at the $0.5-\mathrm{m}$ depth on the day a fish passed the lower dam, $T_{0.5, \text { Upper, } t^{+x}}$ is temperature at the $0.5-\mathrm{m}$ depth on the day a fish passed (or was expected to pass) the upper dam, and $D$ is the number of days it took to travel between upper and lower dams.

For example, from Bonneville to McNary Dam, we averaged 1) daily mean temperature at the $0.5-\mathrm{m}$ depth on passage day at Bonneville Dam and 2) daily mean temperature at the $0.5-\mathrm{m}$ depth on passage (or expected passage) day at McNary Dam. We then multiplied this average by the number of days a fish remained between the two dams. Cumulative temperature exposure was then summed across reaches. For example, when analyzing survival from Lower Granite Dam to Sawtooth, cumulative thermal stress would be the sum of thermal exposures from Bonneville to McNary Dam, McNary to Ice Harbor Dam, and Ice Harbor to Lower Granite Dam, based on the individual passage history of that fish.

## General Modeling Approach and Variable Reduction

We began this analysis with a very large number of potentially collinear covariates for each reach. The most highly correlated variables ( $r>0.95$ ) were string temperature at different depths and string temperature and tailrace temperatures for the same day. We eliminated daily mean and maximum temperatures at the $15-\mathrm{m}$ depth, and daily maximum temperature at the $0.5-\mathrm{m}$ depth for Ice Harbor and Lower Granite Dam because they had more missing data than collinear temperature metrics.

Correlation coefficients were still high among certain combinations of temperature, flow, spill, and gas within and between projects. To solve this problem, we compared models of reach survival as a function of all the environmental variables but did not allow variables with correlation coefficients greater than 0.8 to occur in the same model. When a pair of factors was strongly correlated ( $r>0.90$ ), we eliminated the factor with lower importance in the model average. These specific situations are identified in our results.

The next step in our analysis involved model comparison that included juvenile, migration and environmental covariates. All analyses were conducted using R software ( R Core Team 2013) Our basic model structure was the generalized linear model. The number of fallbacks per fish was modeled as a Poisson distribution and a log link function; survival was modeled as a binomial variable using a logit link function. We conducted model comparison by generating all possible combinations of variables and testing up to four variables per model using the function "dredge" in the MuMIn package of R. Models were ranked using Akaike's information criterion (AIC, Akaike 1973). We then computed the model average (function model.avg) for the set of models that contributed up to $95 \%$ of model weight (following Burnham and Anderson 2002).

We report two statistics from this analysis. The first, "variable importance," captured how frequently a given variable appeared in highly ranked models by summing the weights of all models that include the variable. This metric clarified the consistency
of a predictor in improving model fit, but not necessarily its biological importance in terms of the magnitude by which this variable influenced outcomes.

Our second metric, "variable effect," shows standardized regression coefficients for all variables in the model average. This statistic captures the relative magnitude of a variable's effect on outcomes. Note that we standardized all numeric variables and reduced most categorical variables, such as hatchery origin and transportation history, to dichotomous factors. This latter procedure avoided skewed significance of the factor due to very few fish in certain categories (e.g., "wild" origin).

When comparing models in this manner, it is essential to use the same fish in all models, i.e., build all models from a common database. Therefore, if a given fish is missing data for a single variable, that fish was eliminated from the entire analysis, even for models that did not include that variable. Thus, factors with a lot of missing data can change the outcome of the analysis even if they are not biological important.

We therefore focused attention on variables with substantial missing data to ascertain whether they could be removed from our analysis. We first included all possible covariates as factors, and calculated the importance of all variables in the model average. If the variable of interest had low importance (less than 0.1 ), we eliminated it from the set of variables, and repeated the analysis. Fish length at tagging had the most missing data (43 fish) but was not significant in any initial analysis and was therefore removed from the final model at all projects. For this same reason, we eliminated mean daily temperature at the $0.5-\mathrm{m}$ depth at McNary Dam.

A second concern was that, in some cases, factor levels were not represented evenly enough to make statistically valid comparisons. For example, the vast majority of fish in our dataset came from either Sawtooth or Oxbow Hatchery ( 906 out of 920 fish). Eleven fish were identified as wild because they were collected in the stream as smolts and lacked a fin clip. These 11 fish had higher survival than the average for hatchery fish. However, the sample size for wild fish was so small it was not reliable. Thus, we recommend a separate analysis to assess the relative performance of hatchery and wild smolts.

For our analysis, we reduced the dataset to include only fish from the two major hatcheries. We then computed the importance of hatchery in the model average for each reach. If the importance was low (i.e., less that 0.1 ), we eliminated it from further analysis. Similar issues arose with juvenile release site and certain juvenile transportation sites. Although they appeared significant in the initial analyses, they were highly influenced by a very small number of fish. Release site was eliminated from all
models, and transportation was reduced to a binomial variable (either the fish was transported or it was not).

We assessed the assumption of the relationship between the mean and the variance inherent in the Poisson distribution in our analysis of fallback by examining the ratio between Pearson residual deviance and degrees of freedom for the Poisson model. For survival, we examined the dispersion estimate for a negative binomial model (from package MASS, glm.nb), and compared the coefficients from the negative binomial fit with our binomial model results. We examined the fit of 1) models that included all variables significant at the $95 \%$ confidence level in the model average, and 2) models that included only significant factors out of the set defined by the model average.

Nearly all models were either underdispersed (fallback models for Bonneville, McNary, and Ice Harbor Dam) or close to $1(<1.1)$. The Dalles Dam, on the other hand, included only one year of data and was overdispersed. However, because it had extremely high standard error, the negative binomial was not significantly better based on an ANOVA comparison. For this project, additional data is definitely necessary to draw any conclusions. We also compared the coefficient estimates from either the Poisson or binomial model with the negative binomial and got very similar results. Although not all diagnostics were perfectly normal, no major patterns of nonlinear relationships or remaining trend was observed for the modeled variables.

## Model Calibration and Validation

Our analysis is a pilot study to determine whether additional data is needed to evaluate transportation as a management tool for Snake River sockeye salmon. Therefore, we considered it important to test our models against data that were not used to fit the models. We did this by fitting our models to the data from 2008 to 2012 and testing model predictions against observations in 2013. We then re-fit the models to all data (2008-2013), and assessed how much model fit changed with an additional year of data and which factors had not been sufficiently represented in earlier years to predict the migration failure in 2013.

## Covariates Summary

We analyzed covariates of fallback in the same manner as those for migration fate. At each project, we modeled the number of fallbacks for an individual fish as a function of all three categories of predictors:

1) Juvenile history (origin, release site, length at tagging, detection history on juvenile bypass routes, and migration history (whether/from where it was transported as a juvenile);
2) Migration history (age of adult return, day of first arrival at the dam, travel time from Bonneville Dam to the project of interest (for projects upstream from Bonneville Dam), the number of previous detected fallbacks (excluding The Dalles Dam as a predictor for upstream dams, because that could only be detected in 2013), and exposure to the fishery);
3) Environmental conditions (temperature, flow, spill and gas levels at the project of interest at the time of first arrival at the project, and cumulative thermal exposure from Bonneville Dam to the project as described above).

## Results

## Factors Influencing Fallback

Our results pointed to different factors being important for the Columbia versus the Snake River dams. The most important predictor of fallback at Columbia River dams was a history of juvenile transportation (Tables $11 \& 12$, Figure 10). Substantial numbers of returning adults had been previously transported in 2 years of our analysis: $41 \%$ in 2011, and $29 \%$ in 2013. The positive correlation with fallback occurred in 2013 but not in 2011, so some other variable might have influenced our result. The next most consistent predictor was flow (which is difficult to separate statistically from spill and gas). We observed a negative correlation between flow and fallbacks at all dams except The Dalles.

At Ice Harbor and Lower Granite Dam, temperature was a more important predictor of fallback than flow (i.e., in comparing models that included temperature with models that included flow, the temperature models had higher explanatory value). Because flow and temperature are negatively correlated themselves, it seems likely that the significant results for flow and gas at Lower Granite Dam were secondary to a more direct effect of temperature.

A history of falling back at Bonneville Dam increased the likelihood of additional fallbacks at both The Dalles and McNary Dams (Table 11). We also found that fish that spent more years in the ocean tended to fall back more than younger fish, particularly at Lower Granite Dam, but we had relatively few older fish, so this result needs further study.

Table 11. Relative magnitude of covariate effect on fallback frequency (mean and SE). Shaded cells with asterisk (*) indicate estimates where zero was not included in the $95 \%$ CI.

| Factor | Bonneville | The Dalles | McNary | Ice Harbor | Lower Granite |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Juvenile history |  |  |  |  |  |
| Transport history | 1.33 (0.20)* | 2.55 (0.42)* | 1.59 (0.40)* | 0.58 (0.31) | 0.05 (0.19) |
| Bypass detection history | -0.23 (0.28) |  | -0.69 (0.59) | -0.37 (0.32) | 0.17 (0.16) |
| Hatchery origin (Sawtooth) |  |  |  | 0.61 (0.33) | -0.06 (0.20) |
| Migration history |  |  |  |  |  |
| Age at adult return | 0.11 (0.08) |  | 0.22 (0.17) | 0.05 (0.15) | 0.17 (0.08)* |
| Travel time from Bonneville |  | -0.45 (0.14)* | 0.47 (1.15) | -0.02 (0.25) | -0.23 (0.36) |
| Passage day of year | -0.13 (0.09) |  | -0.01 (0.19) | 0.07 (0.23) | -0.05 (0.09) |
| Fallback history |  | 0.27 (0.04)* | 0.31 (0.09)* | 0.18 (0.12) | -0.07 (0.12) |
| Zone 6 catch rate during passage |  |  | 0.06 (0.26) | 0.05 (0.14) | -0.03 (0.08) |
| Environmental conditions |  |  |  |  |  |
| Temperature, mean daily | -0.25 (0.13) |  | 0.52 (0.33) | 0.57 (0.20)* | 0.33 (0.11)* |
| Flow, mean daily | -0.84 (0.15)* | 0.49 (0.17)* | -0.73 (0.21)* | -0.53 (0.37) | -0.30 (0.13)* |
| Spill, mean daily |  | 0.49 (0.20)* | -0.72 (0.23)* | 0.05 (0.30) | 0.12 (0.12) |
| Dissolved gas, mean daily | 0.11 (0.10) | 0.45 (0.16) | -0.24 (0.26) | -0.22 (0.34) | 0.21 (0.10)* |
| Cumulative temperature |  |  | -0.36 (0.98) | 0.01 (0.37) | 0.04 (0.47) |
| (Intercept) | -2.84 (0.18) | -3.2 (0.41) | -3.8(0.36) | -2.72 (0.34) | -1.09 (0.10) |

Table 12. Importance of covariates on fallback frequency. The most important variables for each dam are shaded. An importance of zero means the factor was eliminated from the analysis prior to the final model being run.

| Factor | Bonneville | The <br> Dalles | McNary | Ice <br> Harbor | Lower <br> Granite |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Juvenile history |  |  |  |  |  |
| $\quad$ Transport history | 1.00 | 1.00 | 1.00 | 0.47 | 0.10 |
| Bypass detection history | 0.12 | 0.00 | 0.15 | 0.25 | 0.17 |
| Hatchery origin (Sawtooth) | 0.00 | 0.00 | 0.00 | 0.54 | 0.12 |
|  |  |  |  |  |  |
| Migration history |  |  |  |  |  |
| $\quad$ Age at adult return | 0.29 | 0.00 | 0.19 | 0.14 | 0.67 |
| $\quad$ Travel time from Bonneville | 0.00 | 1.00 | 0.11 | 0.12 | 0.26 |
| $\quad$ Passage day of year | 0.35 | 0.00 | 0.07 | 0.17 | 0.12 |
| Fallback history | 0.00 | 1.00 | 0.88 | 0.28 | 0.11 |
| $\quad$ Zone 6 catch rate during | 0.00 | 0.00 | 0.07 | 0.13 | 0.10 |
| passage |  |  |  |  |  |
|  |  |  |  |  |  |
| Environmental conditions | 0.57 | 0.00 | 0.24 | 0.73 | 0.75 |
| Temperature, mean daily | 1.00 | 0.50 | 0.56 | 0.32 | 0.20 |
| Flow, mean daily | 0.00 | 0.26 | 0.28 | 0.12 | 0.25 |
| Spill, mean daily | 0.25 | 0.24 | 0.13 | 0.12 | 0.55 |
| Dissolved gas, mean daily | 0.00 | 0.00 | 0.10 | 0.13 | 0.22 |
| Cumulative temperature |  |  |  |  |  |

Columbia River Dams


Figure 10. Factors that were significant predictors of fallback (at the $95 \%$ CI level) at Columbia (left) and Snake River dams (right). Values are the factor coefficient in the model average for each dam. Abbreviations: Temp, daily mean temperature at the dam on day of passage; TT, travel time from
Bonneville Dam; Fallbacks, history of fallback at Bonneville Dam (for The Dalles and McNary Dam).

## Factors Influencing Conversion Rates

Models of survival from Bonneville to McNary Dam fit the data well in all years except 2010, when observed survival was lower than predicted by the model (Figures 11-12). Prior to 2013, the significant predictors of survival were sockeye catch in Zone 6 the week following passage at Bonneville Dam and fish age (Tables 13-14). Including data from 2013, temperature and flow had larger effects (both negative) on the probability of reaching McNary Dam (Table 15). Nonetheless, observed survival in 2013 was within the confidence interval of the prediction made with the 2012 model (Figure 11).

## 2012 Models



Figure 11. Predicted reach survival as a function of covariates compared with observed survival based on data from 2008 to 2012. The 1:1 line shows a perfect prediction. Points above the line show the model predicted survival would be higher than observed, and points under the line were predicted lower survival than observed. Predictions were based on the model average shown in Table 13. Vertical lines show the $95 \%$ confidence interval on the prediction.

Survival from McNary Dam to Ice Harbor Dam was fairly constant across years (over $97 \%$ from 2008-2012, Table 4) and always high due to the short length of this reach (Figure 1). It is important to note that in general, lower detection efficiency leads to a greater difference between the conversion rates shown in Table 4, which were estimated by the Cormack-Jolly-Seber method, and the raw detection data for individual fish histories used in the covariate modeling exercise.

## 2013 Models



Figure 12. Predicted reach survival as a function of covariates compared with observed survival, as in Figure 11, except that model predictions are based on data from 2008 to 2013. The $1: 1$ line shows a perfect prediction. Points above the line show the model predicted survival would be higher than observed, and points under the line were predicted lower survival than observed. Predictions were based on the model average shown in Table 15. Vertical lines show 95\% CI on the prediction.

Table 13. Relative magnitude of covariate effect on reach survival, estimated from data from 2008-2012 (model average coefficient and SE). Zeros indicate covariates not sufficiently significant to appear in model average. Shaded cells with asterisk $\left(^{*}\right)$ indicate estimates with zero not included in the $95 \%$ CI. Downstream and upstream refer to respective lower and upper ends of each reach except Lower Granite to Sawtooth, where downstream refers to Ice Harbor Dam, and upstream refers to Anatone, Idaho.

| Factor | Bonneville to McNary | McNary to Ice Harbor | Ice Harbor to Lower Granite | Lower Granite to Sawtooth NFH |
| :---: | :---: | :---: | :---: | :---: |
| Temp $\begin{array}{ll}\text { downstream } \\ & \text { upstream }\end{array}$ | 0.18 (0.20) | 0.25 (0.45) | 0.04 (0.40) | -0.64 (0.22)* |
|  | -0.12 (0.22) | -0.22 (0.38) | 0.35 (0.30) | -0.51 (0.27) |
| Flow downstream | -0.15 (0.15) | -0.15 (0.26) | 0.00 (0.00) | 0.44 (0.28) |
| upstream | -0.15 (0.11) | 0.00 (0.00) | -0.55 (0.32) | 0.00 (0.00) |
| Spill downstream | 0.00 (0.00) | 0.00 (0.00) | -0.22 (0.37) | 0.31 (0.20) |
| upstream | 0.00 (0.00) | -0.52 (0.28) | 0.00 (0.44) | 0.00 (0.00) |
| Gas downstream | 0.00 (0.00) | -0.10 (0.29) | 0.00 (0.00) | 0.19 (0.17) |
| upstream | -0.10 (0.14) | 0.00 (0.00) | -0.66 (0.23)* | 0.00 (0.00) |
| Cumulative temp | -0.02 (0.11) | 0.13 (0.48) | -3.84 (3.14) | -1.06 (1.01) |
| Travel time | 0.00 (0.00) | 0.05 (0.54) | 2.60 (2.09) | -0.53 (0.97) |
| Catch | -0.16 (0.08)* | 0.21 (0.22) | 0.15 (0.24) | 0.04 (0.14) |
| Fallback | 0.07 (0.14) | -0.28 (0.20) | -0.19 (0.33) | -0.26 (0.15) |
| Age | -0.20 (0.10)* | 0.17 (0.17) | 0.28 (0.21) | 0.14 (0.13) |
| Hatchery | 0.07 (0.14) | 1.17 (0.35)* | 0.00 (0.00) | 0.00 (0.00) |
| Bypass | -0.11 (0.17) | -0.22 (0.36) | -0.21 (0.45) | -0.34 (0.24) |
| Day | -0.11 (0.15) | -0.24 (0.28) | 0.08 (0.45) | -0.37 (0.24) |
| Transport | -0.11 (0.17) | -0.25 (0.38) | 0.00 (0.47) | 0.07 (0.29) |
| Intercept | 0.71 (0.11) | 1.72 (0.27) | 2.63 (0.36) | 0.69 (0.18) |

The lowest detection efficiencies estimated in this study occurred at Ice Harbor Dam, so the observed survival shown in Figures 11 and 12 is substantially lower than the probable true survival (Table 4). Nonetheless, assuming that detection probability is not related to covariates in the model, the relative support for various factors affecting survival is likely valid. Prior to 2013, hatchery source was the only significant predictor of survival (Table 13). Updating the model with 2013 data introduced more juvenile-transported fish, and this factor became significant (Table 15). However, it was not significant for any other reach, so the caveats mentioned previously should be kept in mind.

Table 14. Variable importance in reach survival model based on data from 2008-2012.

| Factor | Bonneville to <br> McNary | McNary to Ice <br> Harbor | Ice Harbor to <br> Lower Granite | Lower Granite to <br> Sawtooth NFH |
| :--- | :---: | :---: | :---: | :---: |
| Temp downstream | 0.18 | 0.15 | 0.09 | 0.59 |
| $\quad$ upstream | 0.13 | 0.19 | 0.13 | 0.33 |
| Flow downstream | 0.22 | 0.16 | 0.00 | 0.10 |
| $\quad$ upstream | 0.24 | 0.00 | 0.29 | 0.00 |
| Spill downstream | 0.00 | 0.00 | 0.09 | 0.29 |
| $\quad$ upstream | 0.00 | 0.62 | 0.12 | 0.00 |
| Gas $\quad$ downstream | 0.00 | 0.12 | 0.00 | 0.16 |
| $\quad$ upstream | 0.20 | 0.00 | 0.94 | 0.00 |
| Cumulative temp | 0.15 | 0.12 | 0.85 | 0.56 |
| Travel time | 0.00 | 0.12 | 0.70 | 0.50 |
| Catch | 0.67 | 0.21 | 0.09 | 0.09 |
| Fallback | 0.17 | 0.24 | 0.08 | 0.33 |
| Age | 0.73 | 0.18 | 0.15 | 0.13 |
| Hatchery | 0.00 | 1.00 | 0.00 | 0.00 |
| Bypass | 0.19 | 0.13 | 0.07 | 0.19 |
| Day | 0.22 | 0.18 | 0.10 | 0.26 |
| Transport | 0.26 | 0.14 | 0.07 | 0.08 |

The reach from Ice Harbor to Lower Granite Dam also exhibited quite high sockeye salmon survival from 2008 to $2012(>90 \%$, Table 4), but survival dropped dramatically in 2013. The only significant predictor up to 2012 was dissolved gas at Lower Granite Dam (Table 13). This model overestimated survival in 2013 (Figure 11).

The two factors that most improved model predictions in this reach in 2013 were 1) the inter-correlated factor pair of cumulative thermal exposure and travel time from Bonneville to Ice Harbor Dam (i.e., prior to entering the reach), and 2) temperature at Lower Granite Dam (Table 16). Cumulative thermal exposure had high weight in the model before 2013 (Table 14), but the thermal exposure itself increased (Figure 13), and the coefficient on this factor doubled in 2013 (Table 15).

It is interesting that of all years, survival was highest in 2009, which was the second warmest year during the study (after 2013) and the hottest year in the first week of August based on raw temperatures (Figure 8 top). However, movement was early and quick in 2009 (Figure 7), leading to lower cumulative thermal exposure than expected from Ice Harbor Dam temperatures alone (Figure 8 bottom).


Figure 13. Distribution of cumulative thermal exposure (in degree days: mean temperature/day $\times$ days) from Bonneville Dam to Lower Granite Dam. Boxes show interquartile ranges, lines show medians. Some outliers were cutoff from the plot. Note $\log$ scale.

Table 15. Relative magnitude of covariate effect on reach survival, estimated from data from 2008-2013 (model average coefficient and SE). Zeros indicate covariates not sufficiently significant to appear in model average. Shaded cells with asterisk $(*)$ indicate estimates with zero not included in $95 \% \mathrm{CI}$; daggers $(\ddagger)$ indicate that covariates were significant for 2008-2013 data but not for 2008-2012. Downstream and upstream refer to respective lower and upper ends of each reach except Lower Granite to Sawtooth, where downstream refers to Ice Harbor Dam, and upstream refers to Anatone, Idaho.

| Factor | Bonneville to McNary | McNary to Ice Harbor | Ice Harbor to Lower Granite | Lower Granite to Sawtooth NFH |
| :---: | :---: | :---: | :---: | :---: |
| Temp downstream upstream | -0.08 (0.12) | $\begin{aligned} & -0.10(0.24) \\ & -0.45(0.31) \end{aligned}$ | 0.39 (0.28) | -0.77 (0.20)* |
|  | -0.43 (0.17)* |  | $0.44(0.22)^{*}+$ | -0.40 (0.27) |
| Flow downstream | -0.34 (0.13)* | $\begin{array}{r} -0.06(0.19) \\ 0.00(0.00) \end{array}$ | 0.00 (0.00) | 0.75 (0.21)*+ |
|  | -0.02 (0.08) |  | $-0.54(0.23) *$ * | 0.00 (0.00) |
| Spill downstrea | 0.00 (0.00) | 0.00 (0.00) | -0.13 (0.22) | 0.43 (0.20)* $\ddagger$ |
|  | 0.00 (0.00) | -0.45 (0.31) | 0.00 (0.00) | 0.00 (0.00) |
| Gas $\begin{array}{ll}\text { downstream } \\ & \text { upstream }\end{array}$ | 0.00 (0.00) | $\begin{aligned} & 0.09(0.16) \\ & 0.00(0.00) \end{aligned}$ | 0.00 (0.00) | -0.08 (0.22) |
|  | 0.10 (0.10) |  | -0.82 (0.17)* | 0.00 (0.00) |
| Cumulative temp | 0.07 (0.08) | -0.26 (0.30) | -8.10 (2.12)** | -1.23 (0.91) |
| Travel time | 0.00 (0.00) | -0.14 (0.46) | 4.98 (1.39)* $\ddagger$ | -0.27 (1.21) |
| Catch | -0.25 (0.09)* | 0.18 (0.18) | 0.00 (0.00) | 0.15 (0.12) |
| Fallback | -0.17 (0.09) | -0.26 (0.17) | -0.16 (0.29) | -0.23 (0.13) |
| Age | -0.16 (0.08)* | 0.12 (0.14) | 0.07 (0.13) | 0.13 (0.11) |
| Hatchery | 0.00 (0.00) | 1.21 (0.30)* | 0.00 (0.00) | 0.00 (0.00) |
| Bypass | 0.03 (0.15) | -0.27 (0.42) | -0.33 (0.31) | -0.35 (0.22) |
| Day | -0.08 (0.10) | -0.15 (0.18) | 0.36 (0.20) | -0.12 (0.21) |
| Transport | -0.11 (0.16) | -0.82 (0.31)** | 0.00 (0.00) | 0.01 (0.27) |
| Intercept | 0.68 (0.07) | 1.78 (0.26) | 2.12 (0.25) | 0.50 (0.15) |

The strongest predictors of survival from Lower Granite Dam to Sawtooth in both models was temperature experienced at Ice Harbor Dam and cumulative thermal exposure from Bonneville Dam to Lower Granite Dam, based on both variable importance (Figure 14) and coefficient magnitude (Tables 13-16). However, uncertainty on cumulative exposure was high, which caused the confidence intervals to bracket zero.

In 2013, flow and spill levels at Ice Harbor Dam had significant effects, although the importance of flow was still low (Table 16). Observed survival in 2013 was slightly lower than predicted, but within $95 \%$ confidence intervals even from data prior to 2013 (Figures 11-12). Observed survival was much lower in 2008 than predicted by the model, but the sample size in this year was extremely small $(\mathrm{N}=10)$.

Table 16. Variable importance in reach survival model based on data from 2008-2013.

| Factor | Bonneville to McNary | McNary to Ice <br> Harbor | Ice Harbor to <br> Lower Granite | Lower Granite to <br> Sawtooth NFH |
| :--- | :---: | :---: | :---: | :---: |
| Temp downstream | 0.03 | 0.07 | 0.07 | 0.67 |
| $\quad$ upstream | 0.81 | 0.21 | 0.19 | 0.16 |
| Flow downstream | 0.69 | 0.07 | 0.00 | 0.25 |
| $\quad$ upstream | 0.02 | 0.00 | 0.41 | 0.00 |
| Spill downstream | 0.00 | 0.00 | 0.03 | 0.64 |
| $\quad$ upstream | 0.00 | 0.33 | 0.00 | 0.00 |
| Gas downstream | 0.00 | 0.07 | 0.00 | 0.09 |
| $\quad$ upstream | 0.11 | 0.00 | 1.00 | 0.00 |
| Cumulative temp | 0.09 | 0.40 | 1.00 | 0.69 |
| Travel time | 0.00 | 0.30 | 1.00 | 0.39 |
| Catch | 0.94 | 0.11 | 0.00 | 0.13 |
| Fallback | 0.43 | 0.17 | 0.03 | 0.30 |
| Age | 0.45 | 0.09 | 0.03 | 0.10 |
| Hatchery | 0.00 | 1.00 | 0.00 | 0.00 |
| Bypass | 0.06 | 0.09 | 0.04 | 0.19 |
| Day | 0.11 | 0.09 | 0.13 | 0.10 |
| Transport | 0.08 | 0.79 | 0.00 | 0.05 |

2012


2013


Figure 14. Variable importance in reach survival models based on data from 2008 to 2012 (top) and 2013 (bottom). Tables 14 and 16 show values.

## Discussion

## Conversion Rates

Importance of temperature-Temperature was the most important factor overall because it was a significant predictor of survival in all reaches except for the short McNary-to-Ice Harbor Dam reach (Table 15). It was also the most important factor in each of those reaches, except for catch in the Bonneville to McNary Dam reach (Table 16).

Temperature at Ice Harbor Dam in particular was a strong predictor of survival not only from Ice Harbor to Lower Granite Dam, but also from Lower Granite to Sawtooth. The fact that Ice Harbor temperature was a better predictor of survival to the spawning grounds than Lower Granite temperature might be because it was more representative of upstream conditions. Temperature at Lower Granite Dam reflects the cooling influence of releases from Dworshak Dam, but this cooling effect has generally disappeared before water reaches Ice Harbor Dam. Cooler Lower Granite Dam temperatures also do not reflect conditions upstream above the confluence of the Snake and Clearwater River (e.g., Anatone), and hence most of the migration to Sawtooth. Thus Ice Harbor Dam temperatures might be more representative of the general conditions fish face than Lower Granite Dam temperatures.

The fact that temperature at Anatone was less predictive than that experienced earlier in the migration at Ice Harbor Dam is also consistent with the concept of delayed or cumulative effects of thermal stress. Cumulative temperature outweighed temperature on the day of passage in both reaches-from Ice Harbor to Lower Granite Dam and from Lower Granite Dam to Sawtooth.

In 2013, many fish had accumulated 500 degree days upon reaching Lower Granite Dam (Figure 13). The 500 degree day sum is a known threshold for an endemic parasitic disease in the Fraser River (Wagner et al. 2005; Mathes et al. 2010), and might have comparable disease implications in the Columbia River. However, more detailed information on spatial and temporal exposure to high temperatures and subsequent mortality might reveal more direct effects, as concluded by Keefer et al. (2008b) based on radio tracking data.

A curious point is that 2009 and 2012 exhibited arguably comparable hot summers (Figure 8 ). We had a small sample size in 2009, but the tagged fish migrated earlier than in 2013. The earliest migrators (i.e., the first quartile) experienced cooler temperatures (Figure 8 bottom), and survival overall was high (similar to the very cool 2011, Figure 4). Survival of the second half of the run in 2012 was low, but still slightly
higher than in 2013 (Figures 4 and 5). Additional data from future warm years will clarify whether 2013 was anomalous for other reasons besides early onset of warm temperatures, and how interannual variation in run-timing contributes to cumulative survival.

The second most important environmental correlate of survival was dissolved gas level at Lower Granite Dam. This was the only significant predictor of survival from Ice Harbor to Lower Granite Dam prior to 2013, although temperature already had a large effect in that dataset. In general dissolved gas level depends on spill, although these factors were not necessarily statistically correlated in our analyses. Gas level either up or downstream was included in all of our analyses, so its failure to be predictive in other reaches was not because it was eliminated due to correlation. Further tests of the importance of dissolved gas need finer resolution of fish location, because PIT detection in the ladder does not necessarily capture the full exposure to dissolved gases during residence in the tailrace.

Mortality within the hydrosystem-Most of the mortality within the hydrosystem occurs in the Bonneville to McNary Dam reach, which had only 58.2\% survival in 2012. The timing of mortality within this reach is consistent with the weekly pattern of reported sockeye catch, which was the strongest predictor of survival. Older fish were more likely to die in this reach, possibly reflecting higher vulnerability to the fishery.

We observed lower survival of Snake River fish relative to upper Columbia River fish between The Dalles Dam and McNary Dam in 2012 and 2013 (Tables 4 and 5). Fishery effort is largely timed to match the earlier upper Columbia River sockeye run and avoid the Snake River run, and the median arrival times were clearly differentiated in those years (Figure 6). Thus the reason for the lower Snake River sockeye survival needs further study. Additional data is needed to clarify any explanation for this result.

Overall rates of detection efficiency were high at most projects, with Ice Harbor Dam exhibiting the lowest detection rates. Lower detection efficiencies at Ice Harbor Dam reduced our precision to some extent in the analyses of factors contributing to survival from McNary to Ice Harbor Dam.

However, the strongest predictors of survival from McNary to Ice Harbor Dam in our analysis stemmed from juvenile history (Figure 14). In particular, hatchery and juvenile transportation influenced survival through this reach. Fish from Sawtooth Hatchery survived at $93 \%$ through this reach, whereas those from Oxbow Hatchery survived at only $83 \%$. Similarly, estimated survival was $92 \%$ for fish that migrated inriver as juveniles but only $85 \%$ for fish transported as juveniles.

Both of these aspects of juvenile history could affect adult migrations in the Snake River. In principle, transport can weaken the olfactory imprint acquired during juvenile migration (Keefer and Caudill 2014), and early rearing in the Columbia River (the Oxbow Hatchery is at Bonneville Dam) could affect adult homing. However, these speculations need to be tested. This magnitude of effect of juvenile transportation mirrors that reported by Keefer et al. (2008a), who found that Snake River Chinook salmon reached Lower Granite Dam from Bonneville at a $10 \%$ higher rate if they had not been barged downstream as juveniles.

## Fallback

Either temperature or flow was highly correlated with the probability of falling back at all dams (temperature had a positive correlation and flow had a negative correlation), and both temperature and flow were significant drivers of fallback at Lower Granite Dam. Dissolved gas and fish age also influenced fallback rates (Figure 10). The Dalles Dam was monitored in one year only, which makes environmental impacts much more difficult to resolve. This project displayed a different profile from the other dams (e.g., positive correlation with flow, Table 11), possibly because of insufficient representation of the full range of environmental conditions.

Adult migrants transported downriver as juveniles were twice as likely to fall back over Bonneville, The Dalles, or McNary Dams as in-river juvenile migrants, making juvenile history a significant predictor of fallback at each of these dams (Figure 10, Table 11). This difference between transported and non-transported fish occurred specifically in 2013, and was not apparent in previous years, so these results should be interpreted cautiously. Keefer et al. (2008a) also found that barged Chinook salmon were more likely to fallback than in-river juvenile migrants, but with less difference between groups (3.7\%).

In most years, fallback percentages and rates for the population as a whole were comparable to those estimated for spring-summer and fall Chinook salmon at Bonneville, McNary and Ice Harbor Dams (Boggs et al. 2004; Burke et al. 2004), but like fall Chinook were much higher at Lower Granite Dam (45-50\%).

High fallback rates are a concern both because of their impact on fish (fallbacks early in the migration tended to be followed by additional fallbacks), and because they can affect management decisions by inflating fish counts (Boggs et al. 2004; Keefer et al. 2008a). We inferred fallbacks based on the direction of movement through the fish ladder, appearance at multiple ladders, or long breaks in ladder detections (Burke et al. 2004). However, we recommend radio telemetry as the method best suited for documenting fallbacks.

# Triggers for Adult Transportation 

## Methods

Many of the factors that best predicted migration fate were specific to individual fish, such as hatchery of origin or a history of juvenile transportation. As such, these factors would not be practical as triggers to begin an adult transportation program from Lower Granite Dam to the Sawtooth Valley. Previous work has shown that survival declines seasonally, such that the latest adult migrants have extremely low survival (Naughton et al. 2005; Keefer et al. 2008b). Thus, we expected the most successful triggers would be environmental and seasonally progressive, such as day of year, temperature, or flow. Because of the strong within-year correlation between temperature and flow, and the stronger mechanistic reasoning supporting temperature, we examined temperature and not flow.

The primary management option being considered is transportation from Lower Granite Dam. However, we also considered triggers that could be applied at Bonneville Dam (assuming that Snake and Columbia River fish could successfully be separated) and Ice Harbor Dam. Neither of these latter locations is currently feasible for adult transportation, but they are presented for comparison and for discussion of future options.

We explored transporting fish from Bonneville, Ice Harbor, and Lower Granite Dams, using day or temperature as triggers for transportation. We used the same temperature sources as for the previous analysis: daily averages recorded at water quality monitoring stations in the tailrace, with data gaps supplemented by forebay temperatures. In addition, we considered surface water daily mean temperature at the $0.5-\mathrm{m}$ depth along the navigation lock (string temperature) at Lower Granite Dam (USACE 2014).

Ideally, one would assess the total survival of the run under each scenario and determine an optimum strategy. However, at this point, we do not have enough information to calculate an optimum threshold, because we do not know either the survival of transported fish or what proportion of fish that exceed the threshold would actually be transported (i.e., the sampling rate). Furthermore, the numbers of tagged fish varied greatly from year to year, and are not necessarily representative of the run as a whole. However, we can look at characteristics of trigger metrics that might pinpoint a disproportionate benefit (or cost) for the population with a small change in the trigger.

For each threshold, we calculated the number of fish that would be transported, the number left in river, the observed survival of both groups, and the number of days
when transportation would be called for. We used these metrics to explore some hypothetical survival estimates of the run as a whole under certain assumptions regarding sampling rate and transport survival.

## Day of the Year

We explored day of year by cutting the season into 10 equal parts, and binning fish that passed the dam in each interval. This produced intervals of 5-8 d, depending on the potential transport dam (3 locations $\times 10$ thresholds per location $=30$ scenarios).

## Temperature

We tested each observed temperature at each dam (rounded to the nearest whole number) as a possible threshold to trigger transportation of adult fish (8 possible thresholds at Bonneville Dam, 9 possible thresholds at Ice Harbor Dam, and 6-11 possible thresholds at Lower Granite Dam, for a total of 34 temperature scenarios). The thresholds determine the trigger scenario for transportation or cutoff in each year such that any individual fish that experiences a day or temperature above that threshold would be designated for transport.

## Results

Survival declines seasonally in most, but not all years (Figure 5) so one option is to transport all sockeye salmon that migrate after a pre-determined date. However, because survival varies so much from year to year, the benefit of transportation based on a pre-determined date will be extremely variable. For example, in 2010 and 2011, when total run survival from Lower Granite Dam to Sawtooth was 74-77\%, the benefit of transport would be much lower than in 2013, when even the earliest fish had very low survival.

The probability of an individual fish surviving the migration was strongly correlated with temperature, with survival dropping below $50 \%$ when water temperature exceeded $18^{\circ} \mathrm{C}$ (Figure 15). Using a trigger like temperature, which is more strongly correlated with interannual variation in survival, would hopefully lead to fewer transport triggers in years with higher in-river survival. Figure 16 shows this effect, where the right panels show day triggers, wherein the curves for percent of fish transported are relatively similar in all years. However, in the left panels, which show temperature triggered scenarios, lines differ much more among years. Table 17 and Appendix A, combined with Figures 16 and 17, show cumulative run statistics for all 64 model scenarios.


Figure 15. Observed survival of fish during 2010-2013 from Ice Harbor Dam to the Sawtooth Valley as a function of the temperature they experienced at Ice Harbor Dam. Circle size is proportional to the number of fish within each $1^{\circ} \mathrm{C}$ temperature bin. Hollow circles indicate a single fish.


Figure 16. Percent of tagged fish that would be transported under 64 different model scenarios for 2010 to 2013. Model scenarios are determined by 1) dam, or location of the trigger, 2) type of trigger (temperature or day of year), and 3) threshold at which transportation would be initiated. Every point represents cumulative survival of the entire run for a given year. At the lowest thresholds for each trigger, nearly all fish are transported. At the highest threshold, none are transported. The numbers in the legend show the number of fish in the simulation (i.e., the number of fish that were detected at that location). See Appendix A for the numbers associated with each scenario. Abbreviations: BO, Bonneville; IH, Ice Harbor; LG, Lower Granite Dam.


Figure 17. Observed survival of fish that would have been left in the river under in 64 different model scenarios. Every point represents the cumulative survival of the entire run for a given year left to migrate in-river under a unique model scenario. For example, the single fish that passed Bonneville Dam when it was less than $14^{\circ} \mathrm{C}$ in 2011 survived, so the in-river survival was $100 \%$ for the scenario "Temp at BO," Threshold $=14$. On the other hand, at a threshold of $21^{\circ} \mathrm{C}$ at Bonneville Dam, all of the fish are left in the river, so the scenario survival equals the observed survival of the entire sample in that year. The raw numbers associated with each scenario are shown in Table 17 and Appendix A. Abbreviations: BO, Bonneville; IH, Ice Harbor; LG, Lower Granite Dam.

Figure 17 shows observed survival from the dam indicated to Sawtooth for fish that passed a dam below each of the thresholds tested. Flattening out of the day triggers reflects the relatively few fish that migrate late in the season in some years (see Appendix A for the numbers of fish in each category), and the variation in survival of early fish (also often few in number). Steeper temperature curves show greater sensitivity to this variable. However, it is necessary to account for the numbers of fish affected by each action to better understand population implications.

Toward this goal, we discuss the implications of a $17^{\circ} \mathrm{C}$ threshold at Lower Granite Dam (Table 17). We show this example because it produced one of the larger hypothetical benefits (an improvement of $33 \%$ in expected spawners) with marginally fewer transport days than other temperature thresholds at Lower Granite Dam. Furthermore, the pilot experiment in 2010 occurred when mean daily temperature was $17.4^{\circ} \mathrm{C}$ and had high survival of transported fish, so this threshold includes at least some conditions where handling stress has been tested.

In this scenario, 48.5-94.4\% of fish passed the dam each year when the threshold was exceeded, and thus would be candidates for transport, spread over 14-28 days per year. Because the natural run survival from Lower Granite Dam to Sawtooth was near the hypothesized transport survival in 2010 and 2011, and not much lower in 2012 ( $60.3 \%$ vs $80 \%$ ), there was little proportional increase in spawners in these years ( $0-5 \%$, assuming a $20 \%$ sampling rate). In 2013, 85 out of 90 fish exceeded the threshold, so their survival would have improved from 30 to $40 \%$.

Table 17. Results of trigger analysis in which transportation would be initiated from Lower Granite Dam when the temperature reached $17^{\circ} \mathrm{C}$ at the water quality monitoring station in the tailrace. We assume $80 \%$ survival of transported fish, and that the $20 \%$ that are transported are randomly selected, with the remainder surviving at the observed in-river survival rate.

| Theoretical temperature trigger for transport with threshold at $17^{\circ} \mathrm{C}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Passage condition (n) |  |  | $\begin{gathered} \text { Transported } \\ 20 \% \\ \text { sample (n) } \\ \hline \end{gathered}$ | Spawners at Sawtooth (n) |  | $\left.\begin{array}{c}\text { Passed } \\ \text { while } \\ \text { threshold } \\ \text { was met } \\ \text { or }\end{array}\right\}$ |  | Expected run survival (S) assuming $80 \%$ transport survival |  |  | Proportional increasein spawners |  |
| Year | Total at dam | ```Threshold \(\left(17^{\circ} \mathrm{C}\right)\) met or exceeded``` | Below threshold |  | Observed | With 20\% transported |  |  | Observed survival (S) | $\begin{gathered} \text { Transport } \\ 20 \% \text { of } \\ \text { run } \\ \hline \end{gathered}$ | $\begin{gathered} \text { Transport } \\ 100 \% \text { of } \\ \text { run } \\ \hline \end{gathered}$ | With 20\% transported | With $100 \%$ transported |
| Lower Granite Dam |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2010 | 31 | 27 | 4 | 5 | 24 | 24 | 14 | 87.1 | 77.4 | 77.4 | 83.9 | 1.000 | 1.083 |
| 2011 | 328 | 159 | 169 | 32 | 243 | 247 | 22 | 48.5 | 74.1 | 75.3 | 80.8 | 1.016 | 1.091 |
| 2012 | 63 | 59 | 4 | 12 | 38 | 40 | 28 | 93.7 | 60.3 | 63.5 | 79.4 | 1.053 | 1.316 |
| 2013 | 90 | 85 | 5 | 17 | 27 | 36 | 25 | 94.4 | 30 | 40 | 77.8 | 1.333 | 2.593 |

The actual transport benefit to the population depends on the proportion of fish transported fish and their rates of survival. Assuming a transport rate of $100 \%$ in 2013, and assuming those fish had an $80 \%$ rate of survival, the overall run survival would theoretically have improved from 13 to $49 \%$ (Bonneville Dam to Sawtooth, difference of $36 \%$ ). If we assume a sampling rate of $20 \%$, survival of the overall run would have improved to $28 \%$.

The net benefit of transportation for the population depends on how many fish reach Sawtooth Valley with versus without transportation. This proportional survival (i.e., the number of spawners simulated to reach Sawtooth/the number of spawners observed in that year) is shown in Figure 18. Improvement exceeded $30 \%$ in only one year, 2013, across all scenarios.


Figure 18. Proportional change in the number of fish simulated in each scenario to reach Sawtooth compared with the observed migrants for a given year. Improvement exceeded 30\% (horizontal line) in 2013 only.

The economic and logistical cost of transportation is likely related to the number of days transportation is necessary. A lthough we do not know exactly how many days fish would actually be transported, we know how many days the threshold was exceeded during fish passage. Figure 19 shows the proportional improvement (from Figure 18) as a function of the number of days the threshold was exceeded. For all triggers, lower thresholds entail more transportation days and a higher percentage of fish transported. Generally, they also have higher potential benefit in years with poor natural survival, but little effect in years such as 2010 and 2011.

Overall, the benefit was relatively low (less than 10\%) in many cases despite many transportation days simply because either relatively few fish were transported or because the in-river survival was already high (2010 and 2011), so a $20 \%$ sampling with only slightly higher survival has little total benefit.


Figure 19. Hypothetical improvement in the number of spawners (as a proportion of the actual number of spawners) under different transportation scenarios from 2010 to 2013, assuming $20 \%$ sampling of fish that exceeded the threshold for transport and $80 \%$ survival of transported fish. Multiple points per year describe different threshold levels for a given trigger (fewer days threshold was exceeded correspond to higher thresholds).

Another way to calculate the benefit to the population is to compare the cumulative survival from Bonneville Dam to Sawtooth with and without transportation. This approach complements the proportional increase in spawners because it places the benefit of transportation in the context of mortality that occurs throughout the migration, and also relates to targets for migration survival as a whole. Figure 20 shows this cumulative survival estimate, again assuming $20 \%$ sampling rate and $80 \%$ survival of transported fish, in relation to the observed annual survival.


Figure 20. Hypothetical improvement in total run survival from Bonneville Dam to Sawtooth under each scenario. Points show the scenario survival by year, trigger and threshold, assuming $20 \%$ sampling of fish that exceeded the threshold for transport and $80 \%$ survival of transported fish. Straight lines show the observed historical survival by year, for comparison.

This figure demonstrates that although transportation from Lower Granite might be the only feasible option, unless the sampling rate is much higher than $20 \%$ the impact on cumulative survival is relatively low. Furthermore, the threshold set for the trigger had relatively minor impact (most of the lines are pretty flat). This is because of the reduced number of fish that reached Lower Granite Dam in poor survival years compared with Bonneville Dam, and the effect of only transporting 20\% of those fish.

## Discussion

Because survival typically declines seasonally with the exception of potentially low survival in a few early migrants, day triggers showed an earlier-is-better tendency at all locations. This is not terribly meaningful, assuming that the survival of transported fish is higher than that of most in-river migrants. It is likely that this general strategy would lead to over-transportation in years with high in-river survival, such as 2011.

The probability of an individual fish surviving the migration was strongly correlated with temperature, with survival dropping below $50 \%$ when water temperature exceeded $18^{\circ} \mathrm{C}$ (Figure 15). However, this did not necessarily imply a substantial benefit to the population from transporting all fish that encounter such high temperatures. Transport benefit could be reduced either because of difficulties collecting fish under those conditions or because few fish passed and were sampled during the period when transport criteria were met.

The primary difference in temperature between 2013 and earlier years was not the maximum temperature, but the onset of warm temperatures early in the run (Figure 8). In fact, $95 \%$ of the run experienced temperatures over $17^{\circ} \mathrm{C}$ in 2013 . If collecting fish at such high temperatures is impractical due to handling stress, or if many fish have already died before reaching Lower Granite Dam, there might be little opportunity to improve survival by transporting fish. In these circumstances, initiating transport very quickly at the beginning of the run would also be a high priority. If the timing of warming is more critical than the high temperature itself, a useful strategy might be to combine temperature values and run-timing information.

The proportion of fish that would be transported under any given temperature trigger varied considerably from year to year (Figure 16). For example, using a trigger of $18^{\circ} \mathrm{C}$ at Lower Granite Dam, 23 and $92 \%$ of the fish would have been designated for transport in 2011 and 2013, respectively. Part of this variability stemmed from variability in the timing of onset of warm temperatures.

Overall, fish experienced high temperatures in 2012 and 2013, producing the highest theoretical transportation rates in these years based on temperature trigger scenarios (Figure 16). These years had the lowest conversion rates as well, and thus
would likely have benefitted the most from transportation. In fact, we found little benefit at all in other years (Figure 18).

We explored a hypothetical sampling rate of $20 \%$ and transport survival of $80 \%$, and calculated less than $10 \%$ increase in the number of spawners under most scenarios (Figure 19). The scenarios with the greatest benefit, that doubled the number of spawners, involved transporting fish from Bonneville Dam, and thereby avoiding all mortality within the hydrosystem. This option is currently not feasible. However, if a much higher proportion of hatchery releases were PIT tagged, Snake River fish could theoretically be detected in real time as they pass Bonneville Dam, and general features of migration timing could be assessed more readily. This would have the added benefit of allowing some features of juvenile history to be included in trigger criteria.

Our candidate scenario of transporting from Lower Granite Dam with a 20\% sampling rate and $80 \%$ survival improved cumulative migration survival (Bonneville Dam to Sawtooth) from the observed $13.2 \%$ to $17.6 \%$. This minor improvement stemmed from only 90 out of 205 fish surviving to Lower Granite Dam, sampling only 17-18 of these fish (depending on the threshold). Applying an $80 \%$ survival rate produced 36 spawners compared with the observed 27 spawners. Thus survival from Lower Granite Dam to Sawtooth improved by 33\%, but still only affected relatively few fish.

A further concern with transporting a large number of fish, or targeting a particular section of the run is that it risks precluding a natural response to warming temperature trends, such as the shift toward earlier migration exhibited in the run of Columbia River sockeye at large (Crozier et al. 2011). Although it might be necessary to carry the population through the next few years, further consideration should be devoted to longer-term implication for population resilience.

We could not optimize the transportation strategy because of lack of information regarding transport survival, sampling rate, and representativeness of the PIT-tagged population. The practicality of transporting fish when conditions are already stressful (e.g., over $18^{\circ} \mathrm{C}$ ) needs to be validated. If high temperatures during collection, for example, lower the survival of transported fish substantially, then one solution would be to collect them earlier in the migration, perhaps at Bonneville Dam. However, this option would require some means of identifying and collecting Snake River sockeye.

If a higher proportion of hatchery releases were PIT tagged, Snake River fish could be detected in real time as they pass Bonneville Dam, and general features of migration timing could be assessed more readily. Furthermore, additional experiments on adult transportation are needed to quantify transport survival and feasible sampling rates.

## Conclusions and Recommendations

After estimating conversion and fallback rates within individual and collective reaches of the hydrosystem, our objectives for this analysis were to ascertain the extent to which we could use existing PIT-tag data to a) identify useful predictors of reach survival for Snake River sockeye salmon and b) discern how these predictors might be used as "triggers" for transportation of adult fish to spawning grounds to improve survival.

Specifically, we explored potential transportation triggers by comparing the survival rates of various proportions of the population and developing transportation scenarios based on different types of triggers (date and temperature). Scenarios were then constructed for different locations of potential transport (Bonneville, Ice Harbor, or Lower Granite Dam) and different threshold values for each transportation trigger.

Based on results from the overall analysis, we identified five areas of outstanding need for data important to the management of adult Snake River sockeye:

1) Refine understanding of how thermal experience affects survival, especially to determine the relative roles of acute vs. cumulative thermal stress for both survival and fallback
2) Explore factors that affect migration timing both between years and within a year, and the extent to which run timing affects losses in the Bonneville to McNary Dam reach, and tolerance of warm years
3) Better discriminate among the influences of flow, spill, and gas, especially for fallback at Columbia River dams and survival through the Snake River
4) Obtain more accurate estimates of fallback rates
5) Pursue a more conclusive evaluation of whether juvenile transportation influences fallback and adult survival

Two basic types of information are needed to resolve these gaps. Each of these categories of information have multiple components that span a range of complexity and benefit.

First, further monitoring is required. Three types of monitoring would be helpful: a) monitoring from passive collection and analysis of additional years of PIT-tag data, b) radio telemetry data to better resolve the spatial and temporal patterns of fish movement, and finally c) data-intensive tags to record features such as depth and temperature will address most of these issues to some extent.

Second, to better resolve issues that will continue to be confounded, active experimentation is necessary. We recommend experimental manipulations of a) temperature exposure, b) gas, spill, and flow, c) juvenile transport and hatchery practices,
and finally d) adult transportation to tease apart the causal factors that underlie correlations apparent in the historical record.

To explain why each of these elements is necessary, we link our specific recommendations (shown in italic below) to conclusions that emerged from our analysis.

1) Refine understanding of how thermal experience affects survival, especially to determine the relative roles of acute vs. cumulative thermal stress for both survival and fallback

The most consistently significant predictor of survival across reaches was thermal exposure. Temperatures measured at Lower Granite Dam and Anatone were less predictive of survival from Lower Granite Dam to Sawtooth than those measured at Ice Harbor Dam. This finding is consistent with the concept of delayed or cumulative effects of thermal stress.

However, our lack of information on specific temperature exposure within the hydrosystem limits our ability to separate the potential immediate or delayed effects of temperature. We know little about the exact temperatures fish encounter and almost nothing about their behavioral and sublethal response to thermal conditions, such as whether they select thermal refugia or whether cumulative thermal effects exact an energetic cost on fecundity, even for survivors (Mann 2007).

To distinguish whether cumulative temperature effects or specific exposure to acute thermal stress is more important, a finer scale understanding is needed of the thermal choices individuals make, along with experimental validation of consequent mortality. To better specify these risks, we need to know fish location more precisely, ideally with temperature loggers that can calculate thermal loads for individual fish.

One aspect of fish behavior that would be particularly useful is the depth distribution of sockeye salmon. We had to make simplifying assumptions about temporal and spatial fish distribution in the water column in order to "assign" a temperature exposure. As evidenced by the variability in string temperatures at any given time, fish could thermoregulate to some extent simply by adjusting their depth.

Studies using radio telemetry and data-intensive tags (i.e., depth meter and temperature recorders) would help clarify the thermal habitats adult sockeye select during migration (informing both acute and cumulative effects).

Experimental thermal exposure followed by intensive monitoring of condition and survival would help to 1) identify delayed effects of exposure in the hydrosystem that might affect fish upstream in the Snake and Salmon Rivers, 2) determine thresholds of exposure tolerance and 3) separate confounded environmental factors. Conditions within and upstream of the hydrosystem might continue to be correlated in future years.
2) Explore factors that affect migration timing both between years and within a year, and the extent to which run timing affects losses in the Bonneville to McNary Dam reach, and tolerance of warm years

We observed variation in run timing among years that affected exposure to high temperatures in the Snake and Salmon River and presumably cumulative run survival.

Run timing also affects the differentiation between Snake River and upper Columbia River sockeye, which affects exposure to the Zone 6 fishery. We observed lower survival of Snake River fish relative to upper Columbia River fish between The Dalles Dam and McNary Dam in 2012 and 2013. The reasons for this are unclear and warrant further study.

## Additional monitoring and modeling of run timing is needed to understand potential natural adaptation to rising river temperature due to climate change and to manage the Zone 6 fishery. It will also help inform hatchery practices that currently strive to maintain the existing genetic variation in run timing.

If Snake River sockeye could be selectively tagged at Bonneville Dam, examination of physical condition could test for condition-related sources of mortality unrelated to the fishery. Furthermore, radio tags would help to specify the location and timing of loss within the Bonneville to McNary Dam reach. Combined with more detailed harvest information, this data could help resolve the role of the fishery in losses of Snake River sockeye salmon.
3) Better discriminate among the influences of flow, spill, and gas, especially for fallback at Columbia River dams and survival through the Snake River

Although temperature was generally the most important environmental variable for both survival and fallback, dissolved gas, spill and flow were also selected in some models. These factors are typically correlated. Better discrimination of the causal drivers of mortality and fallback would help inform management of spill regimes.

Direct manipulation of spill regimes and fine-scale modeling of dissolved gases, as well as better resolution of fish location are needed to test the relative importance of these factors.
4) Obtain more accurate estimates of fallback rates

We inferred fallbacks based on the direction of movement through the fish ladder, appearance at multiple ladders, or long breaks in ladder detections.

We recommend radio telemetry as the method best suited for documenting fallbacks. These analyses are required for understanding the causes of fallback and ultimately correcting window counts.
5) Pursue a more conclusive evaluation of whether juvenile transportation influences fallback and adult survival

Our analysis suffered from unbalanced representation of various factor levels across years, particularly for juvenile history traits.

## Experimental manipulations of juvenile transportation protocols would help test whether juvenile transportation affects adult homing and fallback.

In general, ongoing monitoring of adult migration fate is needed. We demonstrated challenges for forecasting by trying to predict survival in 2013 based on data from prior years. Although temperature emerged as a key driving factor, the magnitude of negative effects of higher temperature was underestimated, especially for survival from Ice Harbor Dam to the Sawtooth Valley.

Additional years of data and modeling are crucial for exploring a wider range of environmental conditions and identifying other factors that might have led to the low survival in 2013.

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## Appendix

Appendix Table A. Results of trigger analysis for all transportation scenarios. We assume $80 \%$ survival of transported fish, and that the $20 \%$ that are transported are randomly selected, with the remainder surviving at the observed in-river survival rate. Threshold is ${ }^{\circ} \mathrm{C}$ or Julian date, depending on trigger.


Appendix Table 1. Continued.


Appendix Table 1. Continued.

| Scenario |  | Passage condition (n) |  |  | Transported | Spawners at Sawtooth |  | Passed while threshold met (\%) |  | Survival assuming $80 \%$ transport Proportional increase survival in spawners |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Threshold | Year | Total at dam | Threshold met | Below threshold | $\begin{gathered} 20 \% \text { sample } \\ (\mathrm{n}) \end{gathered}$ | Observed | With 20\% transported |  |  | Observed survival | With 20\% transported | With 100\% transported | With 20\% transported | With 100\% transported |
| Trigger: Temperature at Bonneville ( ${ }^{\circ} \mathrm{C}$ ) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 14 | 2010 | 40 | 40 | 0 | 8 | 24 | 26 | 21 | 100 | 60 | 65 | 80.0 | 1.083 | 1.333 |
| 15 | 2010 | 40 | 39 | 1 | 8 | 24 | 26 | 20 | 97.5 | 60 | 65 | 80.0 | 1.083 | 1.333 |
| 16 | 2010 | 40 | 28 | 12 | 6 | 24 | 26 | 16 | 70 | 60 | 65 | 80.0 | 1.083 | 1.333 |
| 17 | 2010 | 40 | 12 | 28 | 2 | 24 | 25 | 8 | 30 | 60 | 62.5 | 72.5 | 1.042 | 1.208 |
| 18 | 2010 | 40 | 8 | 32 | 2 | 24 | 25 | 6 | 20 | 60 | 62.5 | 70.0 | 1.042 | 1.167 |
| 19 | 2010 | 40 | 2 | 38 | 0 | 24 | 24 | 2 | 5 | 60 | 60 | 65.0 | 1.000 | 1.083 |
| 20 | 2010 | 40 | 0 | 40 | 0 | 24 | 24 | 0 | 0 | 60 | 60 | 60.0 | 1.000 | 1.000 |
| 14 | 2011 | 516 | 515 | 1 | 103 | 250 | 282 | 37 | 99.8 | 48.4 | 54.7 | 80.0 | 1.128 | 1.652 |
| 15 | 2011 | 516 | 490 | 26 | 98 | 250 | 281 | 32 | 95 | 48.4 | 54.5 | 78.3 | 1.124 | 1.616 |
| 16 | 2011 | 516 | 356 | 160 | 71 | 250 | 274 | 24 | 69 | 48.4 | 53.1 | 71.5 | 1.096 | 1.476 |
| 17 | 2011 | 516 | 79 | 437 | 16 | 250 | 256 | 15 | 15.3 | 48.4 | 49.6 | 53.7 | 1.024 | 1.108 |
| 18 | 2011 | 516 | 4 | 512 | 1 | 250 | 251 | 4 | 0.8 | 48.4 | 48.6 | 49.0 | 1.004 | 1.012 |
| 19 | 2011 | 516 | 1 | 515 | 0 | 250 | 250 | 1 | 0.2 | 48.4 | 48.4 | 48.6 | 1.000 | 1.004 |
| 20 | 2011 | 516 | 0 | 516 | 0 | 250 | 250 | 0 | 0 | 48.4 | 48.4 | 48.4 | 1.000 | 1.000 |
| 14 | 2012 | 122 | 122 | 0 | 24 | 39 | 51 | 31 | 100 | 32 | 41.8 | 80.3 | 1.308 | 2.513 |
| 15 | 2012 | 122 | 120 | 2 | 24 | 39 | 51 | 29 | 98.4 | 32 | 41.8 | 79.5 | 1.308 | 2.487 |
| 16 | 2012 | 122 | 87 | 35 | 17 | 39 | 48 | 19 | 71.3 | 32 | 39.3 | 72.1 | 1.231 | 2.256 |
| 17 | 2012 | 122 | 34 | 88 | 7 | 39 | 44 | 9 | 27.9 | 32 | 36.1 | 50.0 | 1.128 | 1.564 |
| 18 | 2012 | 122 | 13 | 109 | 3 | 39 | 40 | 5 | 10.7 | 32 | 32.8 | 36.9 | 1.026 | 1.154 |
| 19 | 2012 | 122 | 0 | 122 | 0 | 39 | 39 | 0 | 0 | 32 | 32 | 32.0 | 1.000 | 1.000 |
| 20 | 2012 | 122 | 0 | 122 | 0 | 39 | 39 | 0 | 0 | 32 | 32 | 32.0 | 1.000 | 1.000 |
| 14 | 2013 | 205 | 205 | 0 | 41 | 27 | 54 | 32 | 100 | 13.2 | 26.3 | 80.0 | 2.000 | 6.074 |
| 15 | 2013 | 205 | 205 | 0 | 41 | 27 | 54 | 32 | 100 | 13.2 | 26.3 | 80.0 | 2.000 | 6.074 |
| 16 | 2013 | 205 | 205 | 0 | 41 | 27 | 54 | 32 | 100 | 13.2 | 26.3 | 80.0 | 2.000 | 6.074 |
| 17 | 2013 | 205 | 195 | 10 | 39 | 27 | 53 | 29 | 95.1 | 13.2 | 25.9 | 77.6 | 1.963 | 5.889 |
| 18 | 2013 | 205 | 95 | 110 | 19 | 27 | 42 | 16 | 46.3 | 13.2 | 20.5 | 49.3 | 1.556 | 3.741 |
| 19 | 2013 | 205 | 29 | 176 | 6 | 27 | 32 | 9 | 14.1 | 13.2 | 15.6 | 24.4 | 1.185 | 1.852 |
| 20 | 2013 | 205 | 2 | 203 | 0 | 27 | 27 | 2 | 1 | 13.2 | 13.2 | 14.1 | 1.000 | 1.074 |

Appendix Table 1. Continued.

| Scenario |  | Passage condition (n) |  |  |  | Spawners at Sawtooth |  |  |  | Survival assuming $80 \%$ transport Proportional increase survival in spawners |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Threshold | Year | Total at dam | Threshold met | Below threshold |  | Observed | With $20 \%$ transported |  |  | Observed survival | With 20\% transported | With $100 \%$ transported | With 20\% transported | With $100 \%$ transported |
| Trigger: String temperature at Lower Granite ( ${ }^{\circ} \mathrm{C}$ ) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 15 | 2010 | 30 | 30 | 0 | 6 | 23 | 23 | 16 | 100 | 76.7 | 76.7 | 80.0 | 1.000 | 1.043 |
| 16 | 2010 | 30 | 30 | 0 | 6 | 23 | 23 | 16 | 100 | 76.7 | 76.7 | 80.0 | 1.000 | 1.043 |
| 17 | 2010 | 30 | 30 | 0 | 6 | 23 | 23 | 16 | 100 | 76.7 | 76.7 | 80.0 | 1.000 | 1.043 |
| 18 | 2010 | 30 | 26 | 4 | 5 | 23 | 23 | 14 | 86.7 | 76.7 | 76.7 | 83.3 | 1.000 | 1.087 |
| 19 | 2010 | 30 | 17 | 13 | 3 | 23 | 23 | 10 | 56.7 | 76.7 | 76.7 | 86.7 | 1.000 | 1.130 |
| 20 | 2010 | 30 | 12 | 18 | 2 | 23 | 23 | 8 | 40 | 76.7 | 76.7 | 86.7 | 1.000 | 1.130 |
| 21 | 2010 | 30 | 5 | 25 | 1 | 23 | 23 | 4 | 16.7 | 76.7 | 76.7 | 76.7 | 1.000 | 1.000 |
| 22 | 2010 | 30 | 4 | 26 | 1 | 23 | 23 | 3 | 13.3 | 76.7 | 76.7 | 73.3 | 1.000 | 0.957 |
| 23 | 2010 | 30 | 0 | 30 | 0 | 23 | 23 | 0 | 0 | 76.7 | 76.7 | 76.7 | 1.000 | 1.000 |
| 15 | 2011 | 328 | 326 | 2 | 65 | 243 | 247 | 35 | 99.4 | 74.1 | 75.3 | 79.9 | 1.016 | 1.078 |
| 16 | 2011 | 328 | 314 | 14 | 63 | 243 | 247 | 31 | 95.7 | 74.1 | 75.3 | 80.2 | 1.016 | 1.082 |
| 17 | 2011 | 328 | 200 | 128 | 40 | 243 | 248 | 24 | 61 | 74.1 | 75.6 | 81.4 | 1.021 | 1.099 |
| 18 | 2011 | 328 | 102 | 226 | 20 | 243 | 246 | 19 | 31.1 | 74.1 | 75 | 78.7 | 1.012 | 1.062 |
| 19 | 2011 | 328 | 25 | 303 | 5 | 243 | 245 | 13 | 7.6 | 74.1 | 74.7 | 76.8 | 1.008 | 1.037 |
| 20 | 2011 | 328 | 17 | 311 | 3 | 243 | 244 | 11 | 5.2 | 74.1 | 74.4 | 76.5 | 1.004 | 1.033 |
| 21 | 2011 | 328 | 4 | 324 | 1 | 243 | 244 | 3 | 1.2 | 74.1 | 74.4 | 75.0 | 1.004 | 1.012 |
| 22 | 2011 | 328 | 0 | 328 | 0 | 243 | 243 | 0 | 0 | 74.1 | 74.1 | 74.1 | 1.000 | 1.000 |
| 23 | 2011 | 328 | 0 | 328 | 0 | 243 | 243 | 0 | 0 | 74.1 | 74.1 | 74.1 | 1.000 | 1.000 |
| 15 | 2012 | 63 | 63 | 0 | 13 | 38 | 41 | 32 | 100 | 60.3 | 65.1 | 79.4 | 1.079 | 1.316 |
| 16 | 2012 | 63 | 63 | 0 | 13 | 38 | 41 | 32 | 100 | 60.3 | 65.1 | 79.4 | 1.079 | 1.316 |
| 17 | 2012 | 63 | 63 | 0 | 13 | 38 | 41 | 32 | 100 | 60.3 | 65.1 | 79.4 | 1.079 | 1.316 |
| 18 | 2012 | 63 | 60 | 3 | 12 | 38 | 40 | 29 | 95.2 | 60.3 | 63.5 | 79.4 | 1.053 | 1.316 |
| 19 | 2012 | 63 | 56 | 7 | 11 | 38 | 40 | 26 | 88.9 | 60.3 | 63.5 | 81.0 | 1.053 | 1.342 |
| 20 | 2012 | 63 | 55 | 8 | 11 | 38 | 41 | 25 | 87.3 | 60.3 | 65.1 | 81.0 | 1.079 | 1.342 |
| 21 | 2012 | 63 | 37 | 26 | 7 | 38 | 40 | 19 | 58.7 | 60.3 | 63.5 | 79.4 | 1.053 | 1.316 |
| 22 | 2012 | 63 | 30 | 33 | 6 | 38 | 40 | 14 | 47.6 | 60.3 | 63.5 | 76.2 | 1.053 | 1.263 |
| 23 | 2012 | 63 | 8 | 55 | 2 | 38 | 38 | 6 | 12.7 | 60.3 | 60.3 | 61.9 | 1.000 | 1.026 |

Appendix Table 1. Continued.

| Scen | ario | Passage condition (n) |  |  |  |  | ners at tooth |  |  | Survival assuming $80 \%$ transport Proportional increase survival in spawners |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Threshold | Year | Total at dam | Threshold met | Below threshold |  | Observed | With 20\% transported |  |  | Observed survival | With 20\% transported | With $100 \%$ transported | With 20\% transported | With $100 \%$ transported |
| Trigger: String temperature at Lower Granite ( ${ }^{\circ} \mathrm{C}$ ), continued |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 15 | 2013 | 91 | 91 | 0 | 18 | 27 | 36 | 29 | 100 | 29.7 | 39.6 | 80.2 | 1.333 | 2.704 |
| 16 | 2013 | 91 | 91 | 0 | 18 | 27 | 36 | 29 | 100 | 29.7 | 39.6 | 80.2 | 1.333 | 2.704 |
| 17 | 2013 | 91 | 91 | 0 | 18 | 27 | 36 | 29 | 100 | 29.7 | 39.6 | 80.2 | 1.333 | 2.704 |
| 18 | 2013 | 91 | 90 | 1 | 18 | 27 | 36 | 28 | 98.9 | 29.7 | 39.6 | 79.1 | 1.333 | 2.667 |
| 19 | 2013 | 91 | 90 | 1 | 18 | 27 | 36 | 28 | 98.9 | 29.7 | 39.6 | 79.1 | 1.333 | 2.667 |
| 20 | 2013 | 91 | 87 | 4 | 17 | 27 | 36 | 27 | 95.6 | 29.7 | 39.6 | 78.0 | 1.333 | 2.630 |
| 21 | 2013 | 91 | 85 | 6 | 17 | 27 | 36 | 26 | 93.4 | 29.7 | 39.6 | 76.9 | 1.333 | 2.593 |
| 22 | 2013 | 91 | 64 | 27 | 13 | 27 | 34 | 18 | 70.3 | 29.7 | 37.4 | 65.9 | 1.259 | 2.222 |
| 23 | 2013 | 91 | 20 | 71 | 4 | 27 | 29 | 8 | 22 | 29.7 | 31.9 | 42.9 | 1.074 | 1.444 |
| Trigger: Day at Lower Granite (Julian date) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 181 | 2010 | 31 | 29 | 2 | 6 | 24 | 24 | 15 | 93.5 | 77.4 | 77.4 | 80.6 | 1.000 | 1.042 |
| 189 | 2010 | 31 | 22 | 9 | 4 | 24 | 24 | 11 | 71 | 77.4 | 77.4 | 87.1 | 1.000 | 1.125 |
| 197 | 2010 | 31 | 7 | 24 | 1 | 24 | 24 | 4 | 22.6 | 77.4 | 77.4 | 80.6 | 1.000 | 1.042 |
| 205 | 2010 | 31 | 1 | 30 | 0 | 24 | 24 | 1 | 3.2 | 77.4 | 77.4 | 80.6 | 1.000 | 1.042 |
| 213 | 2010 | 31 | 0 | 31 | 0 | 24 | 24 | 0 | 0 | 77.4 | 77.4 | 77.4 | 1.000 | 1.000 |
| 221 | 2010 | 31 | 0 | 31 | 0 | 24 | 24 | 0 | 0 | 77.4 | 77.4 | 77.4 | 1.000 | 1.000 |
| 229 | 2010 | 31 | 0 | 31 | 0 | 24 | 24 | 0 | 0 | 77.4 | 77.4 | 77.4 | 1.000 | 1.000 |
| 237 | 2010 | 31 | 0 | 31 | 0 | 24 | 24 | 0 | 0 | 77.4 | 77.4 | 77.4 | 1.000 | 1.000 |
| 181 | 2011 | 328 | 328 | 0 | 66 | 243 | 247 | 37 | 100 | 74.1 | 75.3 | 79.9 | 1.016 | 1.078 |
| 189 | 2011 | 328 | 318 | 10 | 64 | 243 | 247 | 32 | 97 | 74.1 | 75.3 | 80.2 | 1.016 | 1.082 |
| 197 | 2011 | 328 | 200 | 128 | 40 | 243 | 248 | 24 | 61 | 74.1 | 75.6 | 81.4 | 1.021 | 1.099 |
| 205 | 2011 | 328 | 58 | 270 | 12 | 243 | 246 | 16 | 17.7 | 74.1 | 75 | 77.7 | 1.012 | 1.049 |
| 213 | 2011 | 328 | 11 | 317 | 2 | 243 | 244 | 8 | 3.4 | 74.1 | 74.4 | 75.6 | 1.004 | 1.021 |
| 221 | 2011 | 328 | 5 | 323 | 1 | 243 | 244 | 4 | 1.5 | 74.1 | 74.4 | 75.3 | 1.004 | 1.016 |
| 229 | 2011 | 328 | 1 | 327 | 0 | 243 | 243 | 1 | 0.3 | 74.1 | 74.1 | 74.4 | 1.000 | 1.004 |
| 237 | 2011 | 328 | 1 | 327 | 0 | 243 | 243 | 1 | 0.3 | 74.1 | 74.1 | 74.4 | 1.000 | 1.004 |
| 181 | 2012 | 63 | 62 | 1 | 12 | 38 | 40 | 31 | 98.4 | 60.3 | 63.5 | 81.0 | 1.053 | 1.342 |

Appendix Table 1. Continued.

| Scenario |  | Passage condition (n) |  |  |  | Spawners at Sawtooth |  |  |  | Survival assuming $80 \%$ transport Proportional increase survival in spawners |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Threshold | Year | Total at dam | Threshold met | Below threshold |  | Observed | With 20\% transported |  |  | Observed survival | With 20\% transported | With $100 \%$ transported | With 20\% transported | With $100 \%$ transported |
| Trigger: Day at Lower Granite (Julian date), continued |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 189 | 2012 | 63 | 53 | 10 | 11 | 38 | 41 | 24 | 84.1 | 60.3 | 65.1 | 79.4 | 1.079 | 1.316 |
| 197 | 2012 | 63 | 31 | 32 | 6 | 38 | 41 | 16 | 49.2 | 60.3 | 65.1 | 82.5 | 1.079 | 1.368 |
| 205 | 2012 | 63 | 13 | 50 | 3 | 38 | 39 | 8 | 20.6 | 60.3 | 61.9 | 68.3 | 1.026 | 1.132 |
| 213 | 2012 | 63 | 5 | 58 | 1 | 38 | 39 | 5 | 7.9 | 60.3 | 61.9 | 65.1 | 1.026 | 1.079 |
| 221 | 2012 | 63 | 2 | 61 | 0 | 38 | 38 | 2 | 3.2 | 60.3 | 60.3 | 63.5 | 1.000 | 1.053 |
| 229 | 2012 | 63 | 2 | 61 | 0 | 38 | 38 | 2 | 3.2 | 60.3 | 60.3 | 63.5 | 1.000 | 1.053 |
| 237 | 2012 | 63 | 2 | 61 | 0 | 38 | 38 | 2 | 3.2 | 60.3 | 60.3 | 63.5 | 1.000 | 1.053 |
| 181 | 2013 | 90 | 86 | 4 | 17 | 27 | 35 | 26 | 95.6 | 30 | 38.9 | 77.8 | 1.296 | 2.593 |
| 189 | 2013 | 90 | 60 | 30 | 12 | 27 | 35 | 19 | 66.7 | 30 | 38.9 | 73.3 | 1.296 | 2.444 |
| 197 | 2013 | 90 | 33 | 57 | 7 | 27 | 32 | 11 | 36.7 | 30 | 35.6 | 55.6 | 1.185 | 1.852 |
| 205 | 2013 | 90 | 25 | 65 | 5 | 27 | 31 | 7 | 27.8 | 30 | 34.4 | 51.1 | 1.148 | 1.704 |
| 213 | 2013 | 90 | 6 | 84 | 1 | 27 | 28 | 4 | 6.7 | 30 | 31.1 | 35.6 | 1.037 | 1.185 |
| 221 | 2013 | 90 | 1 | 89 | 0 | 27 | 27 | 1 | 1.1 | 30 | 30 | 31.1 | 1.000 | 1.037 |
| 229 | 2013 | 90 | 1 | 89 | 0 | 27 | 27 | 1 | 1.1 | 30 | 30 | 31.1 | 1.000 | 1.037 |
| 237 | 2013 | 90 | 0 | 90 | 0 | 27 | 27 | 0 | 0 | 30 | 30 | 30.0 | 1.000 | 1.000 |
| Trigger: Day at Ice Harbor (Julian date) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 176 | 2010 | 30 | 29 | 1 | 6 | 21 | 22 | 18 | 96.7 | 70 | 73.3 | 80.0 | 1.048 | 1.143 |
| 182 | 2010 | 30 | 25 | 5 | 5 | 21 | 22 | 14 | 83.3 | 70 | 73.3 | 83.3 | 1.048 | 1.190 |
| 189 | 2010 | 30 | 12 | 18 | 2 | 21 | 22 | 7 | 40 | 70 | 73.3 | 86.7 | 1.048 | 1.238 |
| 195 | 2010 | 30 | 7 | 23 | 1 | 21 | 21 | 4 | 23.3 | 70 | 70 | 76.7 | 1.000 | 1.095 |
| 202 | 2010 | 30 | 1 | 29 | 0 | 21 | 21 | 1 | 3.3 | 70 | 70 | 73.3 | 1.000 | 1.048 |
| 208 | 2010 | 30 | 1 | 29 | 0 | 21 | 21 | 1 | 3.3 | 70 | 70 | 73.3 | 1.000 | 1.048 |
| 215 | 2010 | 30 | 0 | 30 | 0 | 21 | 21 | 0 | 0 | 70 | 70 | 70.0 | 1.000 | 1.000 |

Appendix Table 1. Continued.


Appendix Table 1. Continued.


