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Reframing Steelhead Migration Behavior: A Population Perspective on Migration Rate and Survival Through the Columbia and Snake Rivers

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Reframing Steelhead Migration Behavior: A Population Perspective on Migration Rate and Survival Through the Columbia and Snake Rivers

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Abstract

Long-distance migrations present physiological and anthropogenic challenges for threatened Pacific salmon and steelhead (*Oncorhynchus* spp.). In salmonids, population-specific behaviors have evolved to cope with dynamic environmental conditions. Anthropogenic factors alter the survival benefits of various behaviors. Dams, for example, alter natural hydrological patterns, while harvest changes survival benefits. Thus, understanding how life history variation interacts with the combination of anthropogenic impacts and natural environmental variability is crucial for successful management of heavily regulated migration corridors and projections of impacts from climate change.

To investigate population-specific migration behavior and survival from Bonneville Dam to McNary Dam on the lower Columbia River, we studied 40,209 summer-run steelhead that had been individually tagged as juveniles and were detected during the 2004–16 adult migrations. To quantify the sensitivity of these behaviors to environmental and anthropogenic influences, we used mark–release–recapture models, generalized linear models, and two-dimensional mixture models.

We found distinct patterns in exposure to high river temperature, harvest, and survival related to different migration behavior of steelhead from the Upper Columbia, Snake River, and Middle Columbia River distinct population segments (DPSes). Life history variation resulted from different combinations of early and late arrival timing at Bonneville Dam, slow and fast travel times to McNary Dam, and years spent in the ocean (ocean age).

Temperature, origin, and ocean age were the most important predictors of both arrival timing and survival. In all major population groups (MPGs), steelhead returned later in warmer years, and hatchery fish returned later than wild fish. However, the effect of ocean age differed between populations, such that older fish arrived earlier than younger fish in early-migrating populations, but later than younger fish in late-migrating populations.

The probability of spending weeks to months in the lower Columbia River depended primarily on temperature and population; for example, Middle Columbia River steelhead had longer residence times in the lower river. However, migration delay was also associated with fallback, origin, and age. Survival was more sensitive to temperature for Upper Columbia steelhead than for other DPSes. Although high temperatures reduced survival in all populations, survival rates remained relatively high (73–90%) and consistent from 2004 to 2016, despite record-breaking temperatures during this period.

A greater sensitivity to temperature for Upper Columbia steelhead and a differentiation in return time of hatchery vs. wild Snake River steelhead were also major findings from this analysis. Proactive management plans informed by these insights could help threatened steelhead cope with increasing stress from climate change.

Acknowledgments

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Introduction

Pacific salmonids (*Oncorhynchus* spp.) in the Columbia River basin exhibit highly varied spawning migrations, with different populations historically entering freshwater at every month of the year. Summer steelhead (*O. mykiss*) have arguably the most complex migration among all salmonid ecotypes. Many steelhead populations comigrate, while some spend extended periods in mainstem rivers. Deciphering different behavior patterns among populations is often challenging.

While all interior Columbia River basin steelhead distinct population segments (DPSes) are listed as threatened under the U.S. Endangered Species Act, each population has individual recovery needs. Lack of accurate population-specific information on migration behavior has hindered management (Copeland et al. 2017), which seeks to balance the needs of fisheries, hydropower, and fish. New information on behavioral diversity among steelhead populations is needed to reach conservation goals.

Summer-run steelhead adults spend anywhere from one to 11 months in the lower Columbia and Snake Rivers before moving to natal tributaries to overwinter and spawn. Adults return to natal streams across a wide temporal window from spring to fall. These fish overwinter in diverse locations in mainstem and tributary habitat before spawning the following spring (Busby et al. 1996, Robards and Quinn 2002, Hess et al. 2016).

Steelhead that spawn, return to the ocean as adults, and sometimes return to spawn in a subsequent year are known as *kelts* (Keefer et al. 2008b, Copeland et al. 2017). Although repeat-spawners have become rare in the Columbia River watershed, adult steelhead regularly move both up and downriver, exhibiting complicated movement patterns.

Historically, summer-run steelhead have shown two distinct adult migration tendencies, with a smaller component of the run arriving at Bonneville Dam in early summer (termed A-Index) and a larger component arriving in late summer and early fall (termed B-Index). The latter group is thought to originate exclusively in the Snake River basin, specifically from a few populations in the Clearwater River and Salmon River MPGs (Ford et al. 2016).

Harvest guidelines were developed to distinguish the earlier A-Index from the later B-Index groups using date and size criteria: fish that passed Bonneville Dam between 1 July and 31 October and measured at least 78 cm fork length were classified as B-Index. However, recent genetic analyses (Nielsen et al. 2011, Matala et al. 2014, Copeland et al. 2017) have shown more overlap in migration date and size across populations than previously thought. These researchers cautioned that management plans based on date and size criteria alone might not lead to conservation success, because these criteria do not necessarily correspond to the factors that matter most for population viability.

Steelhead adult migration patterns appear to have changed over time from a strongly bimodal pattern of arrival at Bonneville Dam to a more continuous pattern (Robards and Quinn 2002). However, the relative roles of environmental factors and hatchery practices in changing migration timing have been difficult to isolate. Keefer et al. (2009) concluded that high mainstem temperatures caused fish to move into cool tributaries for days to weeks, with delayed migration associated with lower survival to natal basins. This pioneering work was based on limited data; however, its predictions can now be examined over a longer time series and a much wider range of temperatures utilizing PIT-tag detection data.

To explore run classification criteria other than date and size, and to evaluate the extent to which earlier predictions agree with present outcomes, we examined steelhead behavior and survival using a population-based approach. With 13 years of new data, larger sample sizes, and better population information, we undertook an analysis based on information from fish tagged as juveniles within the natal reaches of specific steelhead population groups (Ford et al. 2016). We then summarized how return timing corresponded to population of origin, juvenile migration history, and number of years spent in the ocean, along with environmental and anthropogenic factors.

Our objective was to provide insight into the relative impacts of environmental factors, fish management, and fisheries on adult migration behavior. An additional goal was to provide statistically robust information on how these factors influence survival from Bonneville Dam to McNary Dam. Specifically, we developed quantitative models to clarify the role of population origin, juvenile characteristics, environmental conditions, and adult migration history in shaping: 1) arrival timing, 2) travel time, and 3) survival. Results from these analyses can be used to anticipate risks to threatened steelhead from fishery catch and climate change.

We discuss three life history profiles identified from this analysis and how these profiles might help managers in: 1) adjusting harvest to reduce risk on the most vulnerable interior steelhead (Upper Columbia DPS wild runs), and 2) planning to address needs under climate change for steelhead that reside over long summer periods in the lower Columbia River (early Snake River and all Middle Columbia River DPS populations).

Methods

Study Fish

Inclusion Criteria

Study fish were identified using the Columbia Basin PIT-Tag Information System database.[1] To develop individual steelhead detection histories, we queried the database for steelhead tagged as juveniles from 2000–16 and interrogated as adults from 2004–16. These queries included only hatchery and wild summer steelhead.[2] Key data processing steps involved identifying major population groups (MPG) and separating juvenile from adult detections.

To identify whether fish originated from the Upper Columbia, Middle Columbia River, or Snake River DPS, we used river kilometer (RKM) of the release site (NWFSC 2015).[3] We used only fish with release sites upstream from McNary Dam and within the boundaries of a single MPG (Appendix A, Tables A1–A3). We identified fish at the population level if the release site was within the boundary of a single population, using boundaries specified by Ford et al. (2016). Hatchery fish were included only if they were identified as part of the official DPS designation (NMFS 2016b). To confirm the final hatchery dataset, we compared our data with data from a recent comprehensive examination of present and historical hatchery program status (S. Iltis, Columbia Basin Research, personal communication).

We identified juvenile steelhead using a combination of size and movement criteria, with a maximum size at tagging of 400 mm. To establish migration year, we used evidence of downstream movement as established by Columbia Basin Research (Iltis, personal communication). For some juvenile fish, the last detection downstream from release did not provide certain evidence of downstream movement. In these cases, we assigned migration year to the tagging year when tagging occurred before 1 June, and to the following year otherwise.

We determined that a fish was undergoing an adult migration if it was detected in an adult fish ladder and at least one year had elapsed between smolt year and fish ladder detection. Although summer steelhead adults are generally characterized by return dates from May through October (Busby et al. 1996), fish from summer-run populations return throughout the year. Spawning occurs in spring. Fish migrating in May could be either downstream migrating kelts, same-year spawners, or very early-returning next-spring spawners. To avoid including these other groups of fish, we used a 1 June cutoff as our "fish year." Thus we grouped all fish that migrated between 1 June and 31 May of the following year into a single "fish year," to pin them to their expected spawning cohort. For example, detection at Bonneville Dam in either June 2012 or in March 2013 would be assigned a migration year of 2012. For harvest management, these latter fish would be considered winter steelhead and assumed to have originated from lower or mid-Columbia River MPGs. However, because fish in our analysis were identified by source population, we did not need to assume origin.

[1] https://ptagis.org/

[2] Fish with records indicating Species Code 3, Run Codes 2 or 5, 0, or R, and Rear Codes H and W.

[3] Snake River: basin RKM 522; Middle Columbia River: RKMs ≥502 to <522; Upper Columbia: RKM ≥639.

For fish detected in adult fish ladders in multiple years, we used only the first adult migration in our analyses. We observed 1,080 steelhead in this category; all passed Lower Granite Dam or Rock Island/Rocky Reach Dam on their second upstream migration.

Dataset description

A total of 22,700 fish from the Upper Columbia DPS, 15,878 fish from the Snake River DPS, and 1,631 fish from the Middle Columbia River DPS met our criteria for analysis (Table 1). Of these, wild fish numbered 1,157 in the Upper Columbia DPS, 5,432 in the Snake River DPS, and 1,081 in the Middle Columbia River DPS (Table 1).

From 2004–07, the Upper Columbia DPS was represented almost entirely by hatchery fish (Table 2). After 2007, the large hatchery releases of tagged fish declined. Nonetheless, most Upper Columbia detections continued to be dominated by fish of hatchery origin (80–100% in the Methow, Okanogan, and Wenatchee populations). An exception was the Entiat population, which had only wild fish represented in our database.

The Snake River DPS had a variable proportion of hatchery fish among MPGs, with a small proportion from the Grand Ronde River (5%), an intermediate proportion from the Salmon River (48%), and higher proportions from the other MPGs (roughly 72%). The Middle Columbia River DPS had the lowest proportion of hatchery fish, with 46% hatchery fish in the Umatilla/Walla Walla MPG and only wild fish in the Yakima River MPG.

Covariates of Behavior and Survival

For covariate analyses of arrival date, travel time, and survival, we evaluated factors in three broad categories: fish characteristics, adult migration history, and environmental data.

Fish characteristics

To compare fish characteristics independent of adult migration metrics, we identified three covariates of behavior and survival. First, *fish origin* was defined as either hatchery or wild based on designation in PTAGIS. Second, *juvenile migration history* was classified as either in-river migrant or transported. Although juveniles from the Upper Columbia DPS were transported from McNary Dam in the early years, in this analysis we only compared transported vs. nontransported fish from the Snake River DPS. To increase migration survival, a portion of juvenile salmonids are collected at dams on the Snake River, transported downstream by barge, and released below Bonneville Dam, the most-downstream dam on the Columbia River (Gosselin and Anderson 2017). Transported fish were defined as those with the last juvenile detection location at the entrance to a transport collection raceway or facility sample (B. Sandford, NMFS/NWFSC, personal communication). Third, we calculated *ocean age*, or the number of years a fish spent in the ocean, by subtracting smolt year from adult migration year. We used ocean age rather than total fish age because steelhead can rear in freshwater for up to six years prior to transitioning to the smolt stage (Copeland et al. 2017), and we did not have enough information on wild fish ages at tagging to assess total fish age.

Table 1. Steelhead adult returns by distinct population segment (DPS) and major population group (MPG), with number of unique PIT-tagged adults detected in the Columbia River hydropower system by return year.

	Steelhead adult returns by year (*n*)													
DPS, *MPG*, Population	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**Total**
Upper Columbia DPS														
Upper Columbia MPG														
Entiat	0	0	3	8	8	75	74	57	28	42	68	56	33	452
Methow	785	1,882	3,081	467	15	114	62	272	181	230	193	267	102	7,651
Okanogan	124	356	466	73	17	10	9	118	136	93	149	135	62	1,748
Wenatchee	2,351	3,300	3,090	562	459	893	598	480	417	216	232	219	32	12,849
Snake River DPS														
Clearwater River MPG														
Lower Clearwater	12	19	21	39	42	89	381	350	362	112	259	221	335	2,242
Middle Fork Clearwater	31	29	20	23	65	90	158	82	52	48	210	87	43	938
South Fork Clearwater	11	5	18	7	30	54	347	437	346	138	132	151	178	1,854
Grand Ronde River MPG														
Lower Grand Ronde	6	0	1	11	7	27	32	149	83	6	16	15	13	366
Upper Grand Ronde	11	17	10	13	14	30	32	30	22	36	37	37	18	307
Wallowa	10	18	4	9	15	19	24	34	28	23	16	19	12	231
Imnaha River MPG														
Imnaha	89	69	54	68	158	887	569	540	232	430	540	574	214	4,424
Lower Snake River MPG														
Asotin	0	0	1	13	23	30	28	42	46	78	106	56	27	450
Tucannon	43	97	102	592	437	688	301	221	139	164	204	194	83	3,265
Salmon River MPG														
Lemhi	0	1	0	2	4	41	25	49	25	29	26	30	14	246
Middle Fork Salmon	2	3	11	4	9	47	22	29	24	41	36	19	0	247
South Fork Salmon	9	6	7	4	10	22	39	30	16	30	77	26	13	289
Lower Salmon	13	6	2	8	20	73	76	86	26	10	38	15	6	379
Upper Salmon	4	1	1	6	4	76	129	148	56	27	68	43	77	640
Middle Columbia River DPS														
Umatilla/Walla Walla MPG														
Walla Walla	8	44	44	33	84	165	147	165	136	72	109	111	63	1,181
Yakima River MPG														
Yakima	23	16	12	18	16	33	23	39	18	44	77	93	38	450
Totals:	**3,532**	**5,869**	**6,948**	**1,960**	**1,437**	**3,463**	**3,076**	**3,358**	**2,373**	**1,869**	**2,593**	**2,368**	**1,363**	**40,209**

Table 2. Steelhead population proportion of hatchery-origin fish by return year.

	Percent hatchery steelhead by adult return year												
DPS, *MPG*, Population	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**
Upper Columbia DPS													
Upper Columbia MPG													
Entiat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Methow	1.00	1.00	1.00	0.99	0.13	0.63	0.60	0.88	0.90	0.81	0.76	0.81	0.78
Okanogan	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.98	0.90	0.86	0.90
Wenatchee	1.00	1.00	1.00	0.99	0.97	0.92	0.87	0.89	0.92	0.85	0.81	0.80	0.63
Snake River DPS													
Clearwater River MPG													
Middle Fork Clearwater	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lower Clearwater	0.83	0.63	0.48	0.31	0.69	0.58	0.89	0.83	0.84	0.65	0.72	0.62	0.90
South Fork Clearwater	0.82	0.80	1.00	0.86	0.97	0.81	0.99	1.00	0.99	0.99	0.97	0.94	0.97
Grand Ronde River MPG													
Lower Grand Ronde	0.00	0.00	0.00	0.00	0.00	0.37	0.16	0.02	0.06	0.50	0.31	0.27	0.46
Upper Grand Ronde	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wallowa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Imnaha River MPG													
Imnaha	0.53	0.45	0.70	0.49	0.21	0.83	0.78	0.74	0.70	0.78	0.76	0.71	0.73
Lower Snake River MPG													
Asotin	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tucannon	0.23	0.62	0.76	0.93	0.97	0.93	0.86	0.77	0.61	0.74	0.71	0.69	0.89
Salmon River MPG													
Lemhi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Middle Fork Salmon	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
South Fork Salmon	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lower Salmon	0.00	0.00	0.00	0.00	0.00	0.51	0.92	0.91	0.88	0.90	0.95	0.87	0.33
Upper Salmon	0.67	1.00	0.00	1.00	0.75	0.99	0.99	0.97	0.98	0.77	0.95	0.88	0.91
Middle Columbia River DPS													
Umatilla/Walla Walla MPG													
Walla Walla	0.00	0.75	0.73	0.70	0.90	0.64	0.35	0.32	0.33	0.21	0.30	0.37	0.70
Yakima River MPG													
Yakima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Adult migration history

To explore how various aspects of adult migration history affected subsequent behavior and survival, we used *arrival date*, *travel time*, *fallback*, and *catch*. We defined arrival date as the first day a fish was detected at a dam, and calculated travel time by subtracting arrival date at Bonneville Dam from date of first detection at a given point upstream.

Fallback occurs when a fish ascends an adult ladder and then regresses downstream. Many of these fish are not detected on their way back downstream because they are unlikely to use the adult ladder or juvenile bypass routes, where most detectors are located. Therefore, we used the method developed by Burke et al. (2004) for identifying fallback in PIT-tagged fish. Briefly, we classified a fish as having fallen back if it was detected moving upstream in an adult ladder and then detected again after a lag of more than six hours, either in that same ladder, in a different ladder at the same dam, or at a downstream dam.

Finally, we used annual steelhead catch estimates within the harvest management zone between Bonneville and McNary Dams (Zone 6) as a predictor of survival within that reach. Commercial, sport, and tribal fisheries operate in the Columbia and Snake Rivers with different quotas for A- and B-index fish and rules for retention of wild fish. We summed all catch estimates for Zone 6, which included an expansion factor to account for mortality from catch and release (J. Jording, NMFS/WCR, personal communication). We weighted total catch by the sum of all steelhead counted at Bonneville Dam for that year (CBR 2019).

These catch estimates included catch in the mouths of coolwater tributaries, where up-river steelhead have been shown to reside temporarily during warmwater periods in the mainstem (Keefer et al. 2009). Specific coolwater fisheries included Drano Lake at the mouth of the Little White Salmon River, the lower Wind River, the lower Deschutes River to Sherars Falls, and Lake Umatilla below its confluence with the John Day River.

In addition to annual catch estimates, we used subannual catch estimates to explore how the seasonal patterns in catch overlapped with population arrival timing at Bonneville Dam. Weekly tribal and monthly nontribal catch reports for 2004–14 were used to derive a daily weighted catch index. Daily catch data were used to develop population-specific annual catch indices. For these indices, we interpolated linear catch data over the respective reporting periods and then divided by the corresponding daily window counts at Bonneville Dam (CBR 2019). We then summed daily weighted catch over all fish passage days in each population, each year. Note that this index did not account for variable residence time in Zone 6, but related strictly to passage day at Bonneville Dam.

Environmental data

To assess how environmental conditions affected migration timing and survival, we used daily average conditions at each dam, starting when the fish first arrived at that dam. Covariates included for this analysis were *temperature*, *flow*, *spill*, and *percentage of dissolved gas*. All of these variables were measured at all dams by the U.S. Army Corps of Engineers and recorded in the Columbia River Data Access in Real Time database (CBR 2019).

We used daily mean temperature measured at the 0.5-m depth to estimate reservoir surface temperature. For these estimates, we prioritized temperature data from water-quality monitoring stations in the tailrace of each dam, rather than from those in the forebay.[4] Conditions in the tailrace are those first encountered at dams by adult migrants. However, in cases where data from the tailrace were not available, we used data from the forebay.[5] Hourly temperature was also monitored at various depths along a vertical string near the navigation locks at McNary, Ice Harbor, and Lower Granite Dams (USACE 2015). We used the 0.5-m depth string temperature data, when available, assuming that these data provide a more accurate description of the surface temperatures that fish encounter when they exit fish ladders.

We excluded individual temperature readings that were highly anomalous for the season and recorded at only one dam. To identify anomalous readings, we calculated average temperature across all years for each calendar day at each dam, and then examined individual readings that differed from this longterm average by more than 10°C. If nearby sites did not show a comparable anomaly, we replaced the anomalous value by interpolation. For example, two readings exceeded 30°C, were assumed to be errors, and were treated as missing data. Missing data for a single daily mean or series of two daily means were also linearly interpolated. For missing data in series up to 30 consecutive days, we regressed temperatures for the year with missing data against temperatures from the nearest dam during the same year. When more than 30 consecutive days were missing, we used data from water-quality monitoring stations at the nearest dam.

Environmental covariates varied systematically over the course of each season, with the strongest linear correlations between temperature and day. Flow and spill were also highly correlated with each other. To avoid problems with collinearity that would violate assumptions of regression analysis, we included only covariates with a correlation coefficient of less than 0.7 in the same model. For example, no model included both flow and spill; both covariates were considered individually. All continuous covariates were standardized by subtracting the mean and dividing by the standard deviation prior to model fitting, while fish origin, juvenile migration history, and fallback were treated as factors.

Data Analysis

We focused on three performance metrics of adult steelhead migration: First, we examined arrival date at Bonneville Dam and McNary Dam. Second, we calculated travel time between dams, focusing primarily on the reach from Bonneville Dam to McNary Dam. Third, we estimated detection efficiency and survival through the hydrosystem. Because each of these metrics was highly variable across populations and time, we used various modeling approaches to explore the factors that influenced them.

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[4] Project codes CCIW, TDDO, MCPW, IDSW, and LGNW.

[5] Project codes BON, TDA, MCN, IHR, LWG, PRD, RIS, RRH, and WEL. See the Columbia Basin Research Data Access in Real Time (Columbia River DART, http://www.cbr.washington.edu/dart) website for details.

Arrival timing

Arrival timing of the adult migration is an important tool for steelhead management, and arrival dates at Bonneville Dam contribute to the differentiation between A- and B-index types. To compare arrival timing among populations, we summarized arrival date by quantile at Bonneville, McNary, Ice Harbor, Lower Granite, Rock Island, and Rocky Reach Dams (5th, 25th, 50th, 75th, and 95th percentiles). Factors that influenced arrival date at Bonneville Dam were explored by modeling arrival date as a function of environmental conditions, ocean age, and fish origin. We fit these models to data from fish that arrived at Bonneville Dam between 1 June and 15 November. We included the first two weeks of November to ensure we captured nearly all of the run that was actively migrating, based on the quantile analysis.

To determine which covariates best predicted arrival day, we used multiple linear regression. Environmental covariates in these models consisted of annual monthly mean temperature, flow, and spill for July, August, and September. We used only one month per environmental covariate in each model to avoid temporal autocorrelation within each variable. Models also included the fish characteristic covariates of rearing origin, juvenile migration history, and ocean year.

Our initial analysis included MPG as a covariate in the regression. Because it was a significant factor, we applied a post-hoc Tukey Test to determine which MPGs were significantly different from each other. Based on the results of this analysis, we separated MPGs into two groups with arrival dates that differed significantly. These groups resembled previous designations of A- and B-index MPGs (Ford et al. 2016). In our analysis, the *early* group included the Upper Columbia, Grand Ronde River, Imnaha River, Lower Snake River, Umatilla/Walla Walla, and Yakima River MPGs. The *late* group consisted of the Clearwater River and Salmon River MPGs.

We ran models with all possible combinations of up to six covariates in a single model and then ranked models by Akaike information criterion (AIC, Burnham and Anderson 2002). Ranking by AIC produced a model-average object, where importance of a given variable was denoted by the proportion of top models (95% of AIC weight) that contained that variable. We implemented model averaging in the R (R Core Team 2019) `MuMIn` package (Barton 2018).

Travel time

For the Upper Columbia, Snake River, and Middle Columbia River DPSes, we summarized travel time between Bonneville and McNary Dams. For Snake River DPSes, we also summarized travel time from McNary to Ice Harbor and from Ice Harbor to Lower Granite Dams. Likewise, for Upper Columbia DPSes, we summarized travel time from McNary to Rock Island and Rock Island to Rocky Reach Dams. For these summaries, we included only populations with spawning tributaries upstream from the reach of interest.

Steelhead enter the Columbia River throughout the calendar year. However, for all three DPSes, travel time through the lower Columbia River differed between fish entering freshwater in summer and those entering at other times of the year. Travel times in salmon often show "long-tailed distributions." We therefore explored transformations visually, and found that by log-transforming travel times, the resulting times showed a distinct bimodal pattern, particularly in summer months (Figure 1).

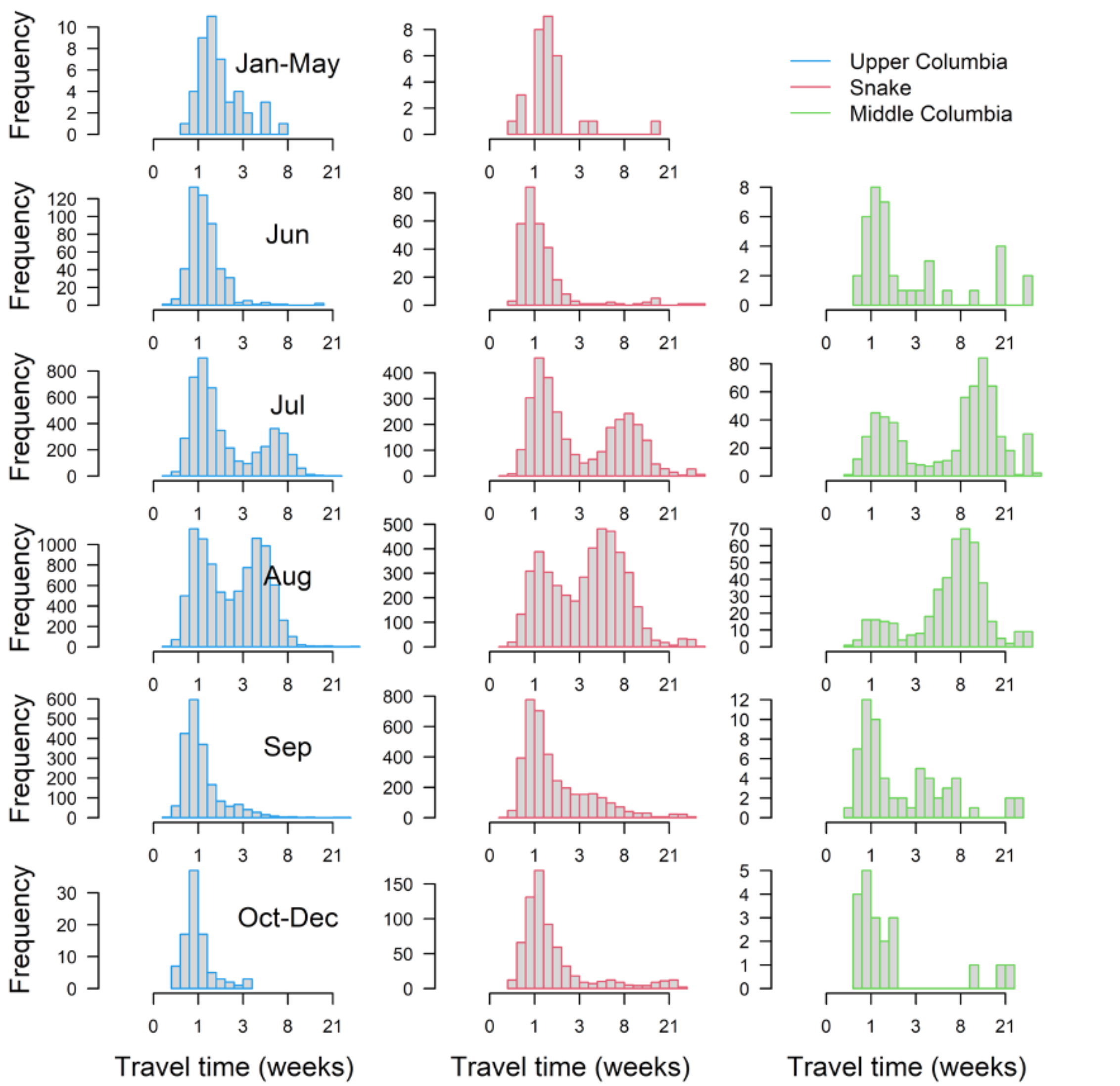


Figure 1. Distributions of travel time from Bonneville Dam to McNary Dam during Jan–May, Jun, Jul, Aug, Sep, and Oct–Dec for steelhead from the Upper Columbia, Snake River, and Middle Columbia River DPSes.

To characterize travel time in July and August for 22,298 fish, we used a two-dimensional mixture model (McLachlan and Peel 2000), where travel time was modeled as the sum of two separate distributions, a *slow* and a *fast* group, as follows:

$$\ln(T_{i,\lambda}) = p_{i,\lambda} \times N(\mu_{slow,i,\lambda}, \sigma_{slow,\lambda}) + (1 - p_{i,\lambda}) \times N(\mu_{fast,i,\lambda}, \sigma_{fast,\lambda}), \quad (1)$$

where T is the travel time for fish i from population group λ, N is a normal distribution defined by the mean μ and standard deviation σ for each group, and p is the probability of being in the slow group. The full mixture model included covariates that affected the mean time of slow and fast groups and the probability that an individual fish was in the slow group. The standard deviation σ did not include covariates in either group.

Our first step in travel-time analysis was to select a subset of all possible covariates for the fast and slow means separately, to facilitate convergence and reduce computation time for the full mixture model. To do this, we used a simple mixture model with no covariates to designate each fish as belonging to the slow or fast distribution.

The simple mixture model was implemented in R using functions from the `mixtools` package developed by Benaglia et al. (2009). This function fits a two-dimensional mixture model and assigns a probability p to each fish of being in the slow group (a fitted p). We fit separate models for each MPG (λ), and used the resulting fitted p to assign each fish to either the slow ($p_{i,\lambda} \geq 0.5$) or fast group ($p_{i,\lambda} < 0.5$).

We then conducted an exploratory analysis to identify the most important covariates for travel times of fast and slow fish, respectively. This step was a precursor to formal model selection of a subset of covariates within the mixture model. In the exploratory step, we separated fish classified as fast and slow from `mixtools`, and tested support for covariates using linear regression and model selection by AIC for each group separately. Possible covariates were hatchery or wild origin, number of fallbacks at Bonneville Dam, ocean age, temperature, spill, and flow on the day of passage at Bonneville Dam.

Travel times of fast and slow fish showed distinct responses to covariates. For slow fish, day of arrival was the only factor that was important and significant for all MPGs, so we carried it forward into the next step. Within the fast group, no covariates were consistently important across MPGs, but the most consistent factor was day of arrival, which was significant and important for half of the MPGs. However, the magnitude of the effect from day of arrival was small, so we elected to treat mean travel time for fast fish as a constant, with different values for each MPG.

In the second step, we selected the best covariates for p (the probability of being slow), given that the mean for the fast group was a constant and the mean for the slow group was a function of day. The `normalmixEM`[6] function of the `mixtools` package could not incorporate covariates in the distribution of means. Therefore, we used the mixture model code developed by Crozier et al. (2017). Possible covariates for p were the same as for those considered for the mean travel time of each group. We fit and compared models with up to three covariates for p separately for each MPG, considering all combinations of two covariates. Analysis of models with two covariates demonstrated that temperature was an important variable for all MPGs. Thus, to reduce computation time, we included temperature in all combinations with three covariates. We compared models using AIC, and reported the importance of covariates for p.

[6] *EM* = expectation–maximization.

Reach survival

To estimate annual reach survival and detection probability at dams, we used the Cormack–Jolly–Seber mark–recapture model implemented with the `marked` package (Laake et al. 2013) in R. We performed separate analyses for the Upper Columbia and Snake River DPSes, selecting the model with the lowest AIC score for each DPS. The majority of Middle Columbia River fish spawn in tributaries with confluences directly above McNary Dam, and thus do not necessarily migrate further upstream to reach natal tributaries; therefore, we simply reported observed annual survival rates from Bonneville Dam to McNary Dam.

For all fish in this analysis, we first generated a pseudo-detection history below Bonneville Dam (always 1) that was comparable to a release history. For fish from the Upper Columbia DPS, we estimated survival from Bonneville to McNary, McNary to Priest Rapids, and Priest Rapids to Rock Island Dams. For fish from the Snake River DPS, we estimated survival in reaches from Bonneville to The Dalles, The Dalles to McNary, McNary to Ice Harbor, and Ice Harbor to Lower Granite Dams.

We calculated detection probability at a given dam by searching for detections at any site upstream from the dam of interest (Table 3). However, upstream from Lower Granite Dam, the only detection points were in-stream monitoring systems. These systems have much lower detection rates than systems at dams, and did not produce enough detections for a realistic assessment of detection probability at Lower Granite Dam. We therefore generated a conservative pseudo-detection history above Lower Granite Dam that matched detection probability at Ice Harbor Dam, our best approximation.

Survival estimates were based on fish that had been released from sites upstream from either Rock Island Dam or Lower Granite Dam (i.e., we excluded Tucannon River and Ringold Springs hatchery fish). For both survival and detection terms, we tested models that included a single year effect across all reaches and that included a year-by-reach interaction. We also allowed an additive effect for MPG in the survival term.

Covariate models

Because adult detection rates at most dams were very high (>0.95), we reasoned that assuming perfect detection would not bias our analysis of factors affecting survival. We therefore conducted logistic regression analyses to investigate which covariates best predicted adult upstream survival. We analyzed factors that affected survival from Bonneville to McNary Dam for all DPSes. For the Snake River DPS, we analyzed factors affecting survival from McNary to Ice Harbor and from Ice Harbor to Lower Granite Dams, and from McNary to Priest Rapids and Priest Rapids to Rock Island Dams for the Upper Columbia DPS.

We hypothesized that drivers of interannual variation in survival may differ for late Clearwater River and Salmon River MPGs vs. early-arriving MGPs. Therefore, we analyzed the Clearwater River and Salmon River MPGs separately from the other, early MPGs.

Table 3. Counts of PIT-tagged steelhead in each population detected at each dam. Note that detection at The Dalles Dam began in 2012, while detection at all other sites occurred from 2004–16.

	Steelhead total adult detections (*n*)									
DPS, *MPG*, Population	**Bonneville**	**The Dalles**	**McNary**	**Ice Harbor**	**Lower Granite**	**Priest Rapids**	**Rock Island**	**Rocky Reach**	**Wells**	**Total**
Upper Columbia DPS										
Upper Columbia MPG										
Entiat	442	177	349	0	0	346	314	347	155	452
Methow	7,559	663	5,707	4	3	5,628	4,610	3,668	5,381	7,651
Okanogan	1,725	370	1,334	1	1	1,308	1,087	959	1,272	1,748
Wenatchee	12,678	596	9,127	68	16	5,281	4,007	2,351	1,905	12,849
Snake River DPS										
Clearwater River MPG										
Lower Clearwater	2,211	840	1,753	1,697	1,634	13	9	5	5	2,242
Middle Fork Clearwater	917	350	768	709	691	1	0	0	0	938
South Fork Clearwater	1,832	536	1,467	1,432	1,380	1	0	0	0	1,854
Grand Ronde River MPG										
Lower Grand Ronde	354	44	274	264	253	4	1	0	0	366
Upper Grand Ronde	305	109	238	226	218	6	4	3	2	307
Wallowa	230	65	191	177	172	4	1	1	0	231
Imnaha River MPG										
Imnaha	4,391	1,508	3,379	3,218	3,048	90	44	33	27	4,424
Lower Snake River MPG										
Asotin	447	234	349	329	308	16	9	7	3	450
Tucannon	3241	542	2,517	2,344	1,501	59	25	19	14	3,265
Salmon River MPG										
Lemhi	241	84	197	190	178	0	0	0	0	246
Middle Fork Salmon	244	85	185	181	181	2	1	1	1	247
South Fork Salmon	281	121	222	224	221	0	0	0	0	289
Lower Salmon	369	62	296	280	267	4	1	2	2	379
Upper Salmon	614	198	542	500	470	6	2	2	2	640
Middle Columbia River DPS										
Umatilla/Walla Walla MPG										
Walla Walla	1,170	296	957	434	147	21	11	5	3	1,181
Yakima River MPG										
Yakima	445	211	356	15	6	56	21	10	6	450

To determine whether early MPGs should be separated further, we looked for a significant MPG effect on survival using logistic regression. An effect from MPG was significant, and a post-hoc Tukey Test identified the Upper Columbia MPG as being different from the MPGs in the Snake River and Middle Columbia River DPSes, effectively recreating a DPS effect. We therefore separated the groups by DPS, with the Snake River DPS separated further into early and late MPGs.

We used the `dredge` function in the `MuMIn` package to run models with all possible covariate combinations with up to three covariates per model. Environmental and migration covariates were referenced to the day of passage at Bonneville Dam. We reported model-averaged coefficients and their significance and variable importance.

Survival of slow vs. fast fish

We hypothesized that if total mortality is a function of exposure time for steelhead, as it is for other Columbia River salmon (Crozier et al. 2017), then slow fish should have higher mortality than fast fish independently from other factors. We could not test this hypothesis directly because we could only categorize fish as fast or slow if they survived to McNary Dam.

Nonetheless, we could theoretically detect differential rates of mortality if that mortality was unrelated to characteristics that differentiated fast vs. slow groups. We tested whether fish expected to be slow when they passed Bonneville Dam had lower probabilities of detection at McNary Dam than fish expected to be fast. We used our final best mixture model for each MPG to assign a probability of being in the slow group for all fish detected at Bonneville Dam in July and August. We used a generalized linear model to determine whether the detection at McNary Dam was predicted by the probability of being assigned to the slow group.

To assess the quality of our assignment model, for each model of travel time for each MPG, we produced a contingency table ascribing numbers of fish predicted by the model to be fast or slow vs. numbers of fish observed to be fast or slow. We used these contingency tables to calculate sensitivity (rate at which observed slow fish are modeled as slow) and specificity (rate at which observed fast fish are modeled as fast) for each MPG (Fielding and Bell 1997).

Results

Date of Arrival

Overall median arrival date at Bonneville Dam was 10 August for upriver steelhead. However, individual MPGs varied in arrival timing (Figure 2). Median arrival was relatively early for the Yakima River, Grande Ronde River, Lower Snake River, and Umatilla/Walla Walla MPGs (25, 29, 31, and 31 July, respectively), followed closely by the Imnaha and Upper Columbia MPGs (5 and 9 August, Table 4). All of these MPGs showed unimodal arrival patterns and were grouped as *early* MPGs. The Salmon River populations had median arrival dates from 10 August to 12 September, and Clearwater River populations centered on dates in September. All populations in these MPGs were placed in the *late* group.

Arrival distribution at McNary Dam was similar to that at Bonneville Dam for the late Clearwater River and Salmon River MPGs in terms of breadth of the migration window (approximately 60 and 80 days, respectively), but differed among early MPGs (Figure 3). For early MPGs, arrival dates were more protracted at McNary Dam than at Bonneville Dam (106 vs. 66 days, on average, between the 5th and 95th quantiles; Tables 4 and 5). For early fish, the arrival distribution at McNary Dam was not only more protracted, but appeared bimodal at both the population and MPG levels.

For the Snake River DPS as a whole, the strong bimodality observed at Bonneville Dam decreased as fish moved upstream. The range in median arrival among Snake River MPGs diminished from 44 days at Bonneville Dam to 29 days at McNary Dam, 22 days at Ice Harbor Dam, and 19 days at Lower Granite Dam (Tables 4–6). Thus, as it progressed, the migration became increasingly synchronized.

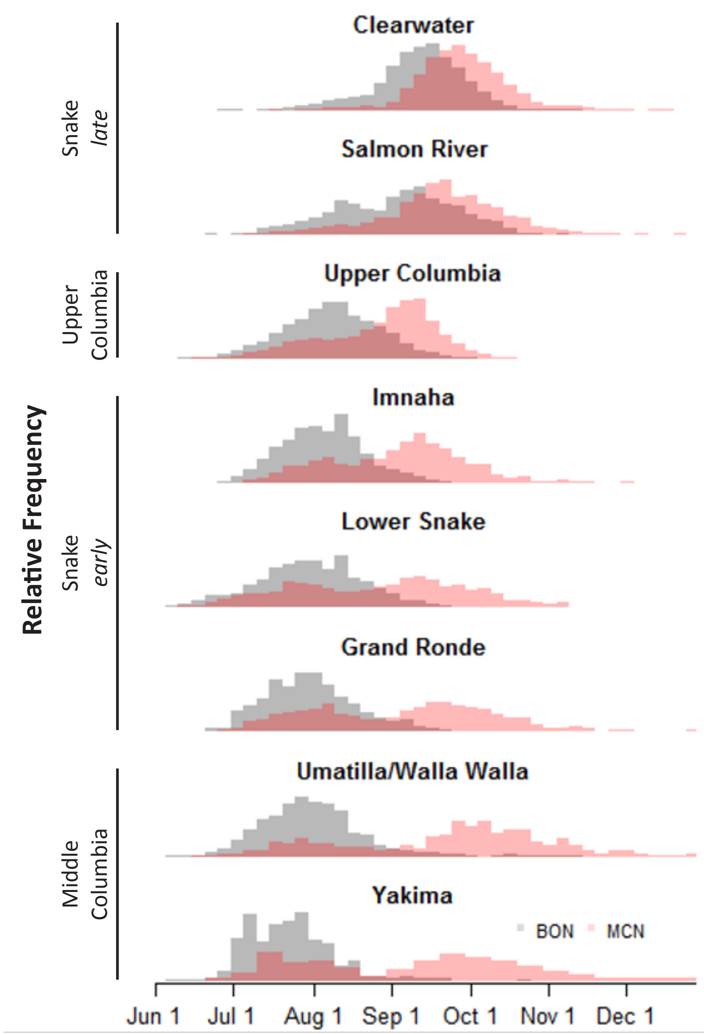


Figure 2. Relative frequency of arrival day for PIT-tagged steelhead by MPG, showing comparisons of arrival day at Bonneville (gray) and McNary (pink) Dams.

Table 4. Arrival date, by quantile, for adult steelhead at Bonneville Dam.

DPS, *MPG*, Population	**Steelhead date of arrival (quantile)** 5th	25th	50th	75th	95th	**Timing group**
Upper Columbia DPS						
Upper Columbia MPG						
Entiat	6 Jul	22 Jul	2 Aug	15 Aug	3 Sep	Early
Methow	9 Jul	27 Jul	8 Aug	20 Aug	7 Sep	Early
Okanogan	5 Jul	27 Jul	9 Aug	22 Aug	10 Sep	Early
Wenatchee	14 Jul	30 Jul	11 Aug	23 Aug	11 Sep	Early
Snake River DPS						
Clearwater River MPG						
Lower Clearwater	28 Jul	29 Aug	11 Sep	21 Sep	7 Oct	Late
Middle Fork Clearwater	13 Aug	1 Sep	9 Sep	19 Sep	30 Sep	Late
South Fork Clearwater	18 Aug	6 Sep	15 Sep	26 Sep	11 Oct	Late
Grand Ronde River MPG						
Lower Grand Ronde	11 Jul	27 Jul	8 Aug	21 Aug	8 Sep	Early
Upper Grand Ronde	2 Jul	16 Jul	25 Jul	4 Aug	25 Aug	Early
Wallowa	3 Jul	13 Jul	26 Jul	5 Aug	2 Sep	Early
Imnaha River MPG						
Imnaha	11 Jul	25 Jul	5 Aug	15 Aug	4 Sep	Early
Lower Snake River MPG						
Asotin	27 Jun	19 Jul	30 Jul	12 Aug	3 Sep	Early
Tucannon	24 Jun	18 Jul	1 Aug	15 Aug	9 Sep	Early
Salmon River MPG						
Lemhi	13 Jul	30 Jul	10 Aug	22 Aug	10 Sep	Late
Middle Fork Salmon	25 Jul	13 Aug	26 Aug	7 Sep	20 Sep	Late
South Fork Salmon	9 Aug	26 Aug	8 Sep	15 Sep	30 Sep	Late
Lower Salmon	22 Jul	20 Aug	10 Sep	25 Sep	11 Oct	Late
Upper Salmon	26 Jul	23 Aug	12 Sep	27 Sep	14 Oct	Late
Middle Columbia River DPS						
Umatilla/Walla Walla MPG						
Walla Walla	4 Jul	19 Jul	31 Jul	11 Aug	8 Sep	Early
Yakima River MPG						
Yakima	1 Jul	10 Jul	22 Jul	2 Aug	28 Aug	Early

Table 5. Arrival date, by quantile, for adult steelhead at McNary Dam.

DPS, *MPG*, Population	Steelhead date of arrival (quantile) **5th**	**25th**	**50th**	**75th**	**95th**	**Timing group**
Upper Columbia DPS						
Upper Columbia MPG						
Entiat	14 Jul	1 Aug	20 Aug	9 Sep	5 Oct	Early
Methow	17 Jul	11 Aug	30 Aug	10 Sep	25 Sep	Early
Okanogan	12 Jul	11 Aug	2 Sep	12 Sep	29 Sep	Early
Wenatchee	22 Jul	13 Aug	30 Aug	10 Sep	26 Sep	Early
Snake River DPS						
Clearwater River MPG						
Lower Clearwater	18 Aug	16 Sep	26 Sep	7 Oct	5 Nov	Late
Middle Fork Clearwater	6 Sep	17 Sep	28 Sep	8 Oct	7 Nov	Late
South Fork Clearwater	5 Sep	18 Sep	28 Sep	10 Oct	7 Nov	Late
Grand Ronde River MPG						
Lower Grand Ronde	24 Jul	14 Aug	15 Sep	2 Oct	27 Nov	Early
Upper Grand Ronde	9 Jul	1 Aug	12 Sep	5 Oct	9 Nov	Early
Wallowa	12 Jul	29 Jul	26 Aug	1 Oct	19 Nov	Early
Imnaha River MPG						
Imnaha	22 Jul	15 Aug	7 Sep	21 Sep	22 Oct	Early
Lower Snake River MPG						
Asotin	6 Jul	2 Aug	6 Sep	28 Sep	29 Oct	Early
Tucannon	1 Jul	28 Jul	30 Aug	22 Sep	27 Oct	Early
Salmon River MPG						
Lemhi	27 Jul	18 Aug	6 Sep	18 Sep	16 Oct	Late
Middle Fork Salmon	5 Aug	31 Aug	11 Sep	21 Sep	7 Oct	Late
South Fork Salmon	27 Aug	10 Sep	18 Sep	26 Sep	11 Oct	Late
Lower Salmon	10 Aug	17 Sep	30 Sep	14 Oct	30 Nov	Late
Upper Salmon	9 Aug	16 Sep	30 Sep	14 Oct	18 Dec	Late
Middle Columbia River DPS						
Umatilla/Walla Walla MPG						
Walla Walla	17 Jul	28 Aug	1 Oct	23 Oct	2 Mar	Early
Yakima River MPG						
Yakima	12 Jul	1 Aug	17 Sep	12 Oct	4 Dec	Early

Table 6. Arrival date, by quantile, for adult steelhead at Ice Harbor and Lower Granite Dams.

	Steelhead date of arrival (quantile)				
Dam, *MPG*	**5th**	**25th**	**50th**	**75th**	**95th**
Ice Harbor Dam					
Clearwater River MPG	5 Sep	19 Sep	30 Sep	11 Oct	4 Nov
Grand Ronde River MPG	16 Jul	21 Aug	19 Sep	8 Oct	11 Nov
Imnaha River MPG	1 Jul	4 Aug	8 Sep	28 Sep	29 Oct
Lower Snake River MPG	28 Jul	29 Aug	13 Sep	28 Sep	27 Oct
Salmon River MPG	9 Aug	11 Sep	23 Sep	8 Oct	6 Nov
Lower Granite Dam					
Clearwater River MPG	11 Sep	25 Sep	5 Oct	17 Oct	9 Nov
Grand Ronde River MPG	26 Jul	7 Sep	26 Sep	12 Oct	7 Nov
Imnaha River MPG	12 Jul	31 Aug	17 Sep	3 Oct	30 Oct
Lower Snake River MPG	13 Aug	11 Sep	22 Sep	5 Oct	31 Oct
Salmon River MPG	29 Aug	17 Sep	29 Sep	13 Oct	5 Nov

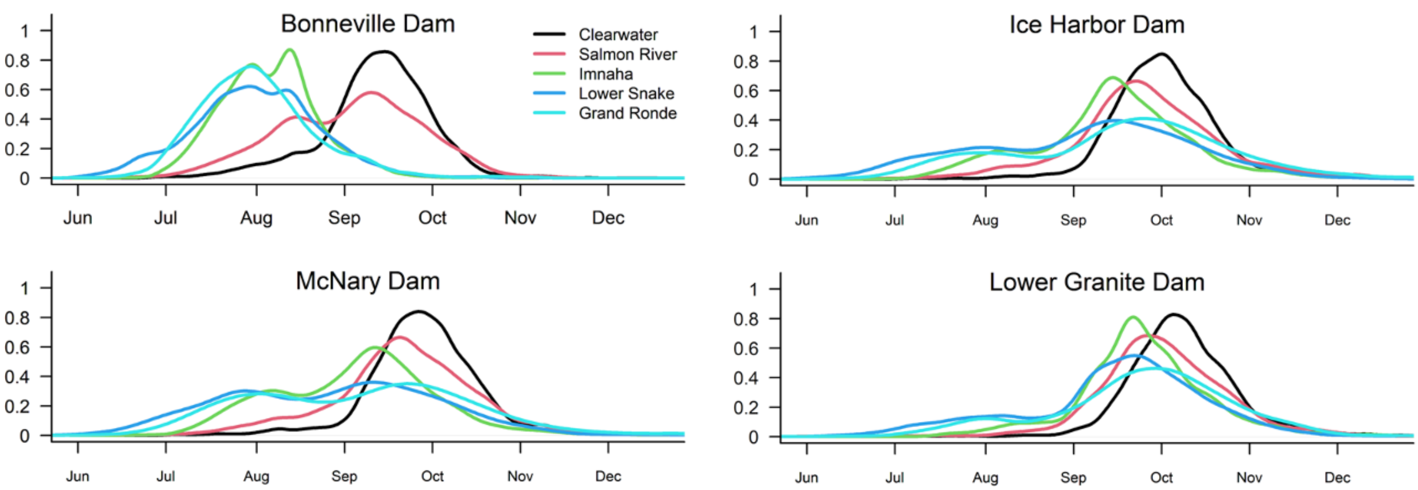


Figure 3. Relative frequency of arrival day at four dams for PIT-tagged Snake River DPS steelhead. The y-axis is scaled for each MPG to show relative peaks in relation to date, rather than magnitude.

Median arrival date at Bonneville also varied by year, but the rank order of years differed between early and late populations (Figure 4). For early populations, median arrival day was earliest in 2008 (22 July) and latest in 2006 (13 August). For late populations, the earliest arrival was 1 September in both 2007 and 2009, and the latest was 18 September in both 2012 and 2016.

Due to differing travel times, the order of arrival of fish was different at McNary Dam than at Bonneville Dam. The four Upper Columbia populations were among those arriving earliest at McNary Dam (median arrival day, 2 September or earlier), along with the Wallowa, Asotin, and Tucannon populations. By 10 September, 75% of the Upper Columbia MPG had passed McNary Dam (Table 5). Next to pass were the Imnaha River and Lower Snake River MPGs, with 75% arriving by 20 September. The Middle Columbia River DPS was the last to pass McNary Dam, with the interquartile range lingering until late October.

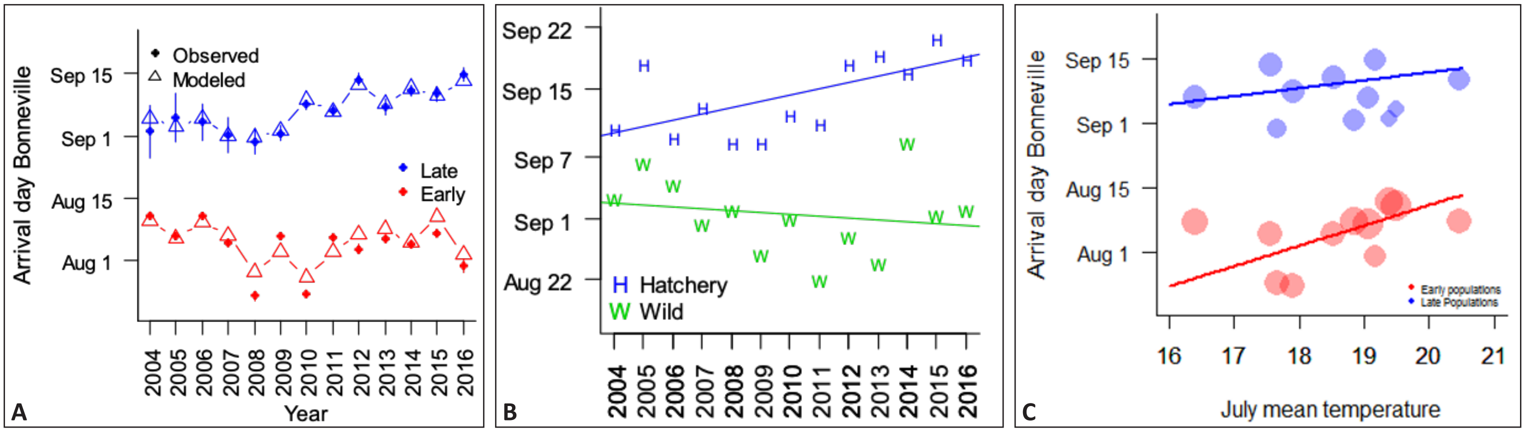


Figure 4. Mean date of arrival at Bonneville Dam for early (Upper Columbia, Middle Columbia River, and early Snake River DPSes) and late (Clearwater River and Salmon River) MPGs. A) Observed mean dates of arrival, and those predicted by the covariate model. B) Median dates of arrival of hatchery and wild fish with separate trend lines. C) Arrival day as a function of temperature, with dots scaled by sample size and temperature binned into 11 groups.

Covariates of Arrival Timing

Key factors that determined arrival day were the same for early and late MPGs. July temperature, a discharge variable (flow or spill), hatchery origin, ocean age, and juvenile migration history each appeared in the model with the lowest AIC, although the coefficient for juvenile migration was not significant and had low importance for the early group (Table 7). However, the relative magnitude of environmental factors and hatchery effects differed between groups, as did the direction of the age effect.

For the early group, July temperature had the largest effect (Figure 4C). Environmental effects were weaker in the late group, but still significant and in the same direction (Table 7). For all MPGs, coefficients for both factors were positive, indicating arrival was later in years that were warmer and had higher flow or spill. Generally, temperature and flow are negatively correlated, but in this case, the two factors balanced each other out to some extent. Temperature had the dominant effect, but the response was tempered in the high-flow years of 2011 and 2012, and in the low-flow year of 2015.

Table 7. Covariates of arrival timing of Snake River DPS steelhead at Bonneville Dam showing model-average coefficients and variable importance.

Covariate	Coefficient	Importance
Early Snake River and Middle Columbia River MPGs		
Intercept	66.73	n/a
Temperature (Jul)	5.02	1.00
Flow (Aug)	4.09	1.00
Fish origin	−2.09	1.00
Ocean age	−2.90	1.00
Late Snake River MPGs		
Intercept	101.40	n/a
Temperature (Jul)	1.70	1.00
Spill (Sep)	0.62	1.00
Fish origin	−7.15	1.00
Ocean age	2.90	1.00
Juvenile migration	1.88	1.00

Early and late groups contrasted in whether older or younger fish came back first (Table 7). In all early MPGs, 2-ocean fish arrived 4.7 days earlier, on average, than 1-ocean fish (Figure 5). In late MPGs, on the other hand, average arrival date was later—10 September for 2-ocean fish vs. 31 August for 1-ocean fish. This probably explains why using a cutoff date to define the B-index has been relatively successful (Figure 5).

Wild fish arrived earlier than hatchery fish in all populations (Figure 5). However, for the late group, fish origin was the dominant factor affecting arrival day (Table 7). Fish origin had a similarly important but weaker magnitude of effect in the early group.

The discharge variable selected for the late group was September spill, despite the fact that spill is usually near zero at this time of year. Nonetheless, model fit was significantly worse for flow compared to spill (ΔAIC of 57 compared to a model with September flow, vs. 31 with August flow). Fish transported as juveniles arrived about 1 day later than those that had migrated in-river, and juvenile migration history was a significant effect for late-group MPGs.

Overall, model predictions of arrival time at Bonneville fit observed arrival times slightly better in the late than in the early group (Figure 4A). Interestingly, the late group had a significant trend toward later arrival for hatchery fish based on linear regression ($F_{1,11} = 5.586$, $P = 0.038$; Figure 4B), but the trend was not significant for wild fish ($F_{1,11} = 0.5018$, $P = 0.49$). From 2004 to 2009, average arrival date at Bonneville Dam was 1 September, while from 2010 to 2016 it was 10 September. The percentage of hatchery fish in our sample doubled from 35% in the first period to 70% in the more-recent period. All model predictions fell within the confidence interval of the late-group observations. The early group exhibited no long-term trend in arrival date, but dates varied by up to 3 weeks, from 18 July in 2008 and 2010 to 2 August in 2010 and 2011.

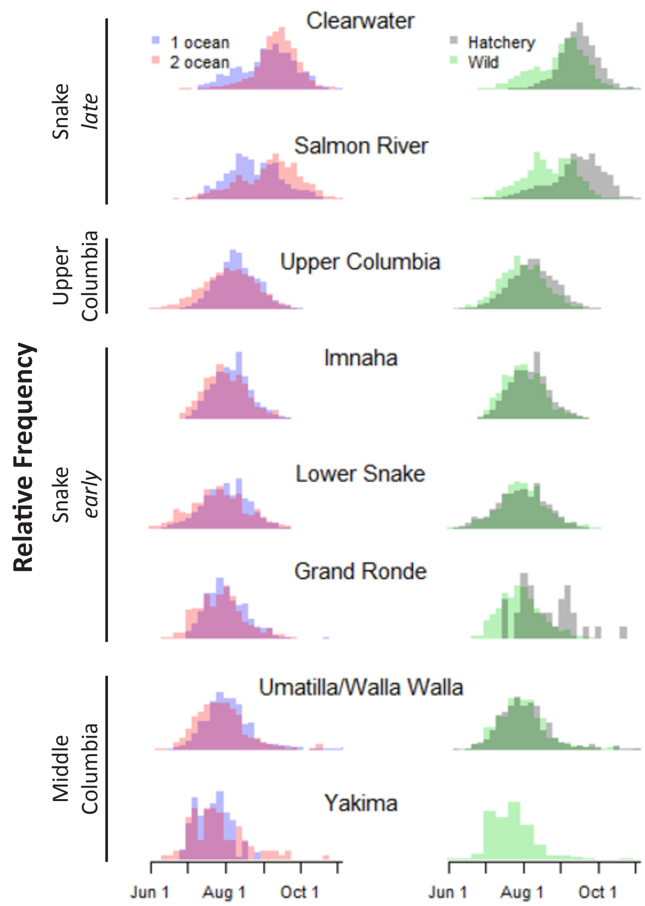


Figure 5. Relative frequency of arrival day for PIT-tagged steelhead by MPG, showing comparisons of arrival day at Bonneville Dam for 1- vs. 2-ocean fish (left panels) and for hatchery vs. wild fish (right panels).

Travel Time

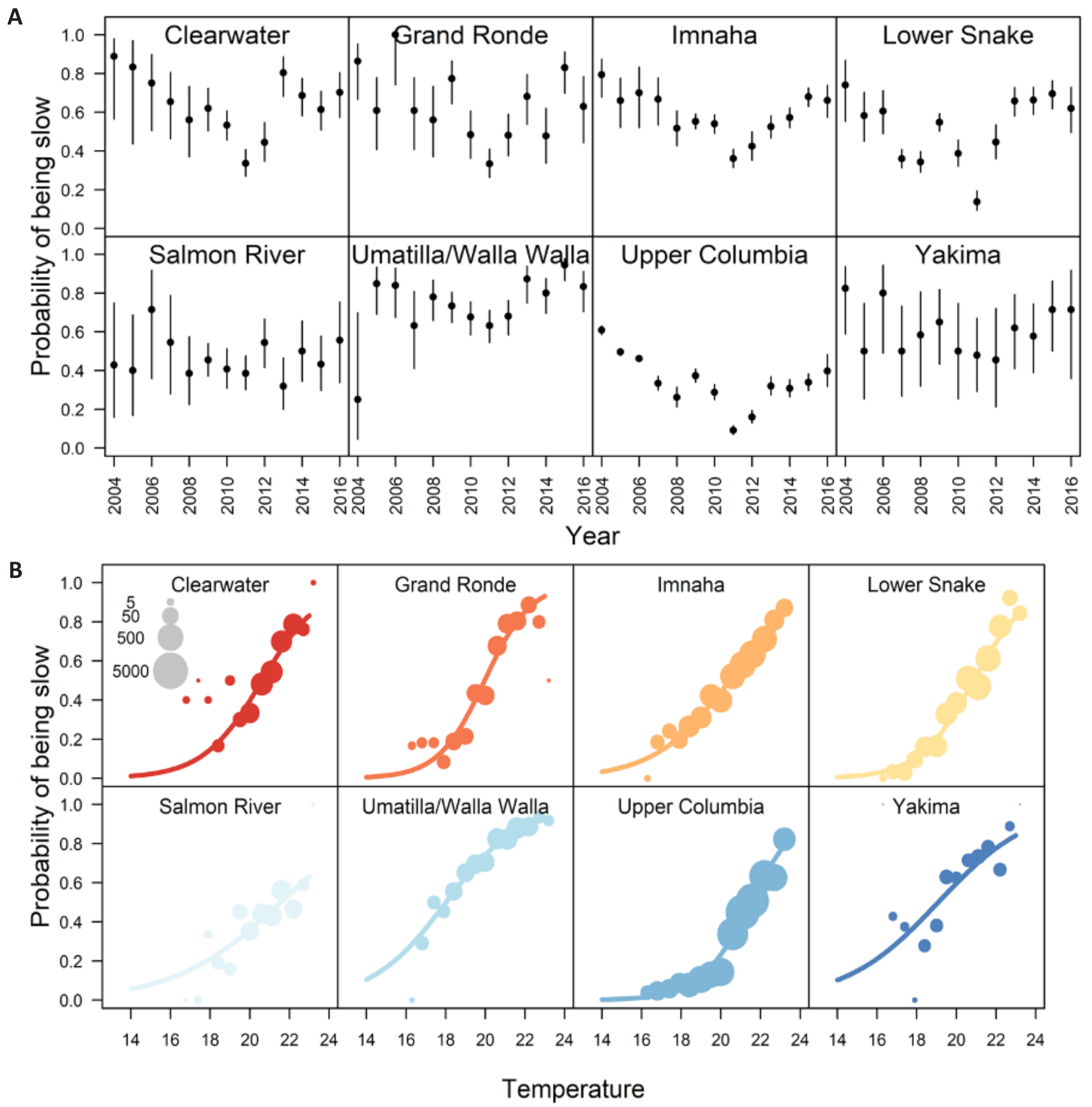
Observed shifts in arrival time from a bimodal to a unimodal distribution as fish moved upstream can be explained by looking directly at travel time from Bonneville Dam to McNary Dam. In this reach, travel time varied seasonally, with fast fish migrating year-round and slow fish primarily appearing in summer for all DPSs. The delay of the slow fish smoothed out the initial bump in arrival date at Bonneville Dam, which then merged with the rest of the run at other dams. The bimodal distribution in travel time from Bonneville Dam to McNary Dam therefore only appeared in summer (Figure 1). The slow group formed in June/July, peaked in August, and largely disappeared in October. This time frame was consistent with the period over which mean daily temperature at Bonneville Dam exceeded 19°C (9 July–28 September).

While all MPGs exhibited both fast and slow movement through this reach, they did so in varying proportions (Figure 6). The means of the slow annual proportions tended to be higher for the more-central MPGs (0.75 in Umatilla/Walla Walla, 0.61 in Yakima River) and lower in the interior MPGs (0.47 in Salmon River, 0.34 in Upper Columbia). Proportions of slow fish also varied by year, with most MPGs experiencing minimums in 2011 and maximums in 2015. For example, respective proportions of slow fish from Upper Columbia and Umatilla/Walla Walla populations ranged from 0.09–0.34 and 0.63–0.94 between 2011 and 2015.

Average travel time from Bonneville Dam to McNary Dam was 7 days for fast fish and 33 days for slow fish from all populations combined (Table 8). Annual travel times are shown in Appendix A, Table A-4. In Snake River reaches from McNary to Ice Harbor and from Ice Harbor to Lower Granite Dams, travel time distributions exhibited one large mode and a long right tail (Appendix B, Figure B-1).

Table 8. Median travel times, in days, between reaches. Table shows separate travel times for fast vs. slow fish in the reach from Bonneville Dam to McNary Dam.

	Steelhead median travel time (in days)							
	BON to MCN							
DPS, *MPG*	**Fast**	**Slow**	**Slow (%)**	**MCN to IHR**	**IHR to LWG**	**PRD to RIS**	**RIS to RRH**	**RRH to WEL**
Upper Columbia DPS								
Upper Columbia MPG	8.2	31.0	38.6	—	—	4.1	1.9	3.0
Snake River DPS (late)								
Clearwater River MPG	8.7	37.7	29.3	2.5	6.9	—	—	—
Salmon River MPG	9.9	37.2	32.6	2.3	6.8	—	—	—
Snake River DPS (early)								
Grand Ronde River MPG	9.1	54.8	53.4	2.8	7.8	—	—	—
Imnaha River MPG	10.1	42.2	52.2	3.1	8.1	—	—	—
Lower Snake River MPG	8.2	47.7	45.4	2.7	9.2	—	—	—
Middle Columbia River DPS								
Umatilla/Walla Walla MPG	10.0	67.8	71.0	—	—	5.9	30.5	2.4
Yakima River MPG	8.4	66.5	57.8	—	—	6.6	2.2	5.9



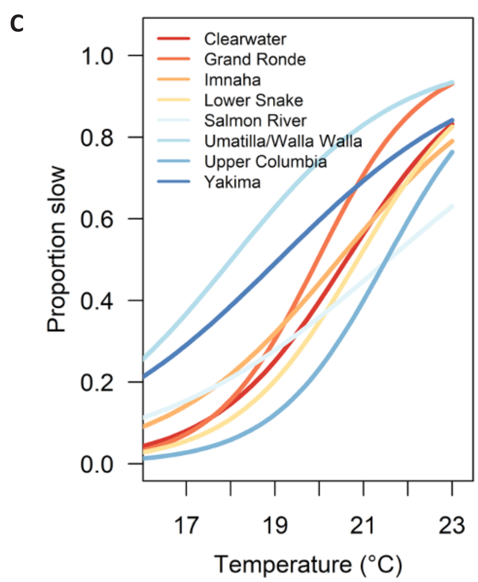


Figure 6. Propensity to exhibit slow travel time from Bonneville Dam to McNary Dam, by MPG, across years (A) and temperatures (B and C). Points in A show the median, while lines show the interquartile range each year. The size of the circles in B indicates the number of fish that passed BON in that temperature bin. For comparison of fits across MPGs, the fitted lines from B are plotted together in C.

Mixture model results

For nearly all MPGs, the best mixture model predicting travel time included two additional covariates for *p* besides temperature (Table 9). An exception was the Umatilla/Walla Walla MPG, for which the best model included only one additional covariate. For slow fish from all MPGs combined, on average, the best model included *day* as a covariate for the mean (Appendix A, Table A-5). Model selection generally found strong support for the effect of two variables. *Temperature* at Bonneville was the most important covariate for *p* for all MPGs (Table 9). Higher temperatures increased the probability of being in the slow group (Figure 6). The importance of other factors varied by MPG.

Aside from temperature, different covariates were important for different populations, but for most populations, a single model was strongly supported. *Fallback* was an important predictor for the Clearwater River, Lower Snake River, Imnaha River, and Umatilla/Walla Walla MPGs; *ocean age*, *fish origin*, and *juvenile transportation* were in the top models for three populations each. *Spill* influenced Upper Columbia MPG populations (Table 9).

Table 9. Delta AIC table showing covariates for *p* for all two- and three-covariate models within 2 AIC of the top model for each steelhead MPG.

MPG	Equation	ΔAIC	Cumulative model weight
Upper Columbia	*p ~ temperature + ocean age + spill*	0.000	1.0
Clearwater River	*p ~ temperature + fish origin + fallback*	0.000	0.8
Grand Ronde River	*p ~ temperature + transport + fish origin*	0.000	0.4
	p ~ temperature + transport + flow	1.618	0.2
Imnaha River	*p ~ temperature + transport + fallback*	0.000	1.0
Lower Snake River	*p ~ temperature + ocean age + fallback*	0.000	1.0
Salmon River	*p ~temperature + transport + fish origin*	0.000	0.7
Umatilla/Walla Walla	*p ~ temperature + fallback*	0.000	0.4
	p ~ temperature + fallback + ocean age	0.394	0.3
	p ~ temperature + fallback + spill	1.993	0.1
Yakima River	*p ~ temperature + ocean age*	0.000	0.3
	p ~ temperature + ocean age + spill	1.101	0.2
	p ~ temperature + ocean age + flow	1.663	0.1
	p ~ temperature + ocean age + fallback	1.998	0.1

Linking migration behavior with survival

Among all DPSes combined, fish predicted to be in the slow group were significantly less likely to be detected at McNary Dam than fish predicted to be in the fast group. This difference was also significant within the Upper Columbia and early Snake River MPGs. However, it was not significant within the late Snake River or the Middle Columbia River MPGs (Table 10). This result supported the hypothesis that slow fish experience higher mortality than fast fish, but with important differences between MPGs.

Combined, the models had better true slow rates (sensitivity: 64–91% correct) than true fast rates (specificity: 27–60% correct; Appendix A, Table A-6). Among fast fish miscategorized as slow by the models, all passed Bonneville Dam at temperatures exceeding 19°C, and 95% passed at temperatures of 21°C or higher. Steelhead response to high temperatures was therefore more variable than expected, with a substantial proportion of fish transiting directly through the lower Columbia River regardless of temperature.

Table 10. Generalized linear model results for probability of detection at McNary Dam as a function of predicted membership in slow vs. fast migration groups (*pSlow*).

DPS	Estimate	Standard error	z value	Pr(>|z|)
Upper Columbia				
Intercept	0.879	0.016	54.697	<2e–16***
pSlow	–0.194	0.016	–12.079	<2e–16***
Snake River (late)				
Intercept	1.301	0.069	18.878	<2e–16***
pSlow	–0.017	0.059	–0.285	0.776
Snake River (early)				
Intercept	1.218	0.029	42.135	<2e–16***
pSlow	–0.116	0.024	–4.936	6.31e–05***
Middle Columbia River				
Intercept	1.431	0.099	14.518	<2e–16***
pSlow	-0.045	0.065	–0.695	0.487
All groups				
Intercept	1.025	0.013	78.464	<2e–16***
pSlow	–0.092	0.012	–7.957	1.77e–15***

Reach-Specific Survival Estimates

Detection probability

Estimated detection efficiency was higher than 0.95 at all dams except Rock Island (Table 11). Rock Island Dam had the lowest and most variable detection probabilities, ranging from 0.66 to 0.95, with the lowest probabilities occurring in 2005, 2008, 2012, and 2014 (range 0.66–0.79). For the Upper Columbia DPS, the best mark–recapture model included a reach and year interaction term for detection probability, as year effects differed among dams. For Snake River MPGs, the best mark–recapture model had a year and dam effect on the detection term, but no interaction between year and dam, with detection probabilities at all dams similarly low or high in a given year.

Table 11a. Detection efficiency for Upper Columbia DPS steelhead. Standard error shown in parentheses. Dashes indicate years prior to the installation of PIT-tag monitoring systems.

Year	Bonneville Dam	The Dalles Dam	McNary Dam	Priest Rapids Dam	Rock Island Dam
2004	0.955 (0.256)	—	0.953 (0.010)	0.952 (0.035)	0.734 (1.254)
2005	0.991 (0.067)	—	0.972 (0.003)	0.949 (0.005)	0.763 (0.065)
2006	0.994 (0.051)	—	0.987 (0.002)	0.982 (0.003)	0.816 (0.056)
2007	0.992 (0.331)	—	0.975 (0.006)	0.987 (0.005)	0.898 (0.253)
2008	0.978 (6.534)	—	0.963 (0.031)	0.975 (0.032)	0.790 (0.039)
2009	0.989 (0.296)	—	0.981 (0.005)	0.988 (0.006)	0.982 (0.107)
2010	0.987 (0.465)	—	0.978 (0.006)	0.977 (0.011)	0.971 (0.121)
2011	0.983 (0.004)	—	0.979 (0.005)	0.980 (0.031)	0.938 (0.325)
2012	0.979 (0.005)	—	0.979 (0.006)	0.985 (0.005)	0.784 (0.207)
2013	0.986 (0.102)	0.979 (0.007)	0.976 (0.007)	0.988 (0.046)	0.896 (0.044)
2014	0.969 (0.497)	0.971 (0.007)	0.961 (0.009)	0.955 (0.009)	0.657 (0.136)
2015	0.977 (0.008)	0.975 (0.007)	0.980 (0.006)	0.976 (0.133)	0.946 (0.594)
2016	0.971 (1.442)	0.955 (0.016)	0.954 (0.019)	0.960 (0.016)	0.914 (0.022)

Table 11b. Detection efficiency for Snake River DPS steelhead. Standard error shown in parentheses. Dashes indicate years prior to the installation of PIT-tag monitoring systems.

Year	Bonneville Dam	The Dalles Dam	McNary Dam	Ice Harbor Dam	Lower Granite Dam
2004	0.857 (0.017)	—	0.886 (0.015)	0.905 (0.013)	0.977 (0.005)
2005	0.967 (0.009)	—	0.975 (0.007)	0.979 (0.006)	0.995 (0.002)
2006	0.965 (0.010)	—	0.973 (0.008)	0.978 (0.007)	0.995 (0.002)
2007	0.978 (0.007)	—	0.983 (0.005)	0.986 (0.005)	0.997 (0.001)
2008	0.988 (0.004)	—	0.991 (0.003)	0.993 (0.002)	0.998 (0.001)
2009	0.993 (0.002)	—	0.995 (0.001)	0.996 (0.001)	0.999 (0.000)
2010	0.989 (0.002)	—	0.992 (0.001)	0.993 (0.001)	0.998 (0.000)
2011	0.986 (0.002)	—	0.989 (0.002)	0.991 (0.001)	0.998 (0.000)
2012	0.989 (0.002)	—	0.991 (0.002)	0.993 (0.001)	0.998 (0.000)
2013	0.981 (0.003)	0.991 (0.002)	0.985 (0.003)	0.988 (0.002)	0.997 (0.001)
2014	0.986 (0.002)	0.991 (0.002)	0.990 (0.002)	0.991 (0.001)	0.998 (0.000)
2015	0.989 (0.002)	0.994 (0.001)	0.992 (0.002)	0.993 (0.001)	0.999 (0.000)
2016	0.979 (0.003)	0.986 (0.003)	0.984 (0.003)	0.987 (0.002)	0.997 (0.001)

Estimated survival

For the Upper Columbia DPS, the best mark–recapture model also had an interaction between reach and year in the survival term. As in the Snake River DPS, survival for the Upper Columbia DPS was lowest in the reach from Bonneville Dam to McNary Dam (Table 12). Survival ranged from a low of 0.73 in 2013 and 2016 to a high of 0.82 in 2004. Survival from McNary Dam to Priest Rapids Dam was very high, about 0.98 every year. In the reach from Priest Rapids Dam to Rock Island Dam, detection rates were low in certain years, causing apparent survival to underestimate actual survival. Modeled survival was near 0.97 after 2004 (Figure 7C).

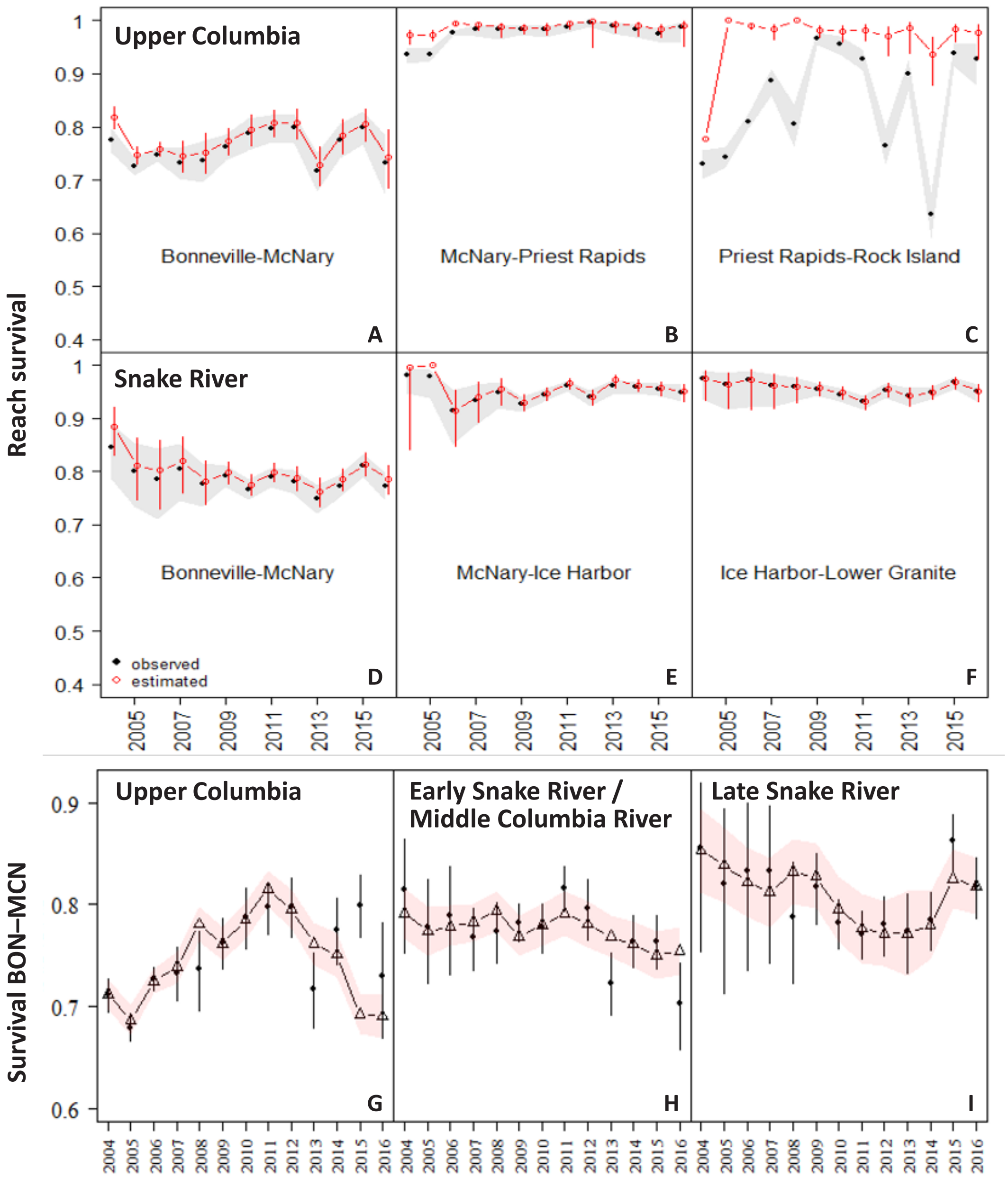


Figure 7. Steelhead survival, 2004–16. Top two rows compare apparent survival with mark–release–recapture model survival estimates for Upper Columbia (A–C) and Snake River DPS steelhead (all MPGs, D–F). Bottom row compares apparent survival from Bonneville Dam to McNary Dam with the covariate model fits for Upper Columbia (G), early Snake River (H), and late Snake River MPGs (I). Polygons show confidence intervals around model estimates; error bars show confidence limits for apparent survival.

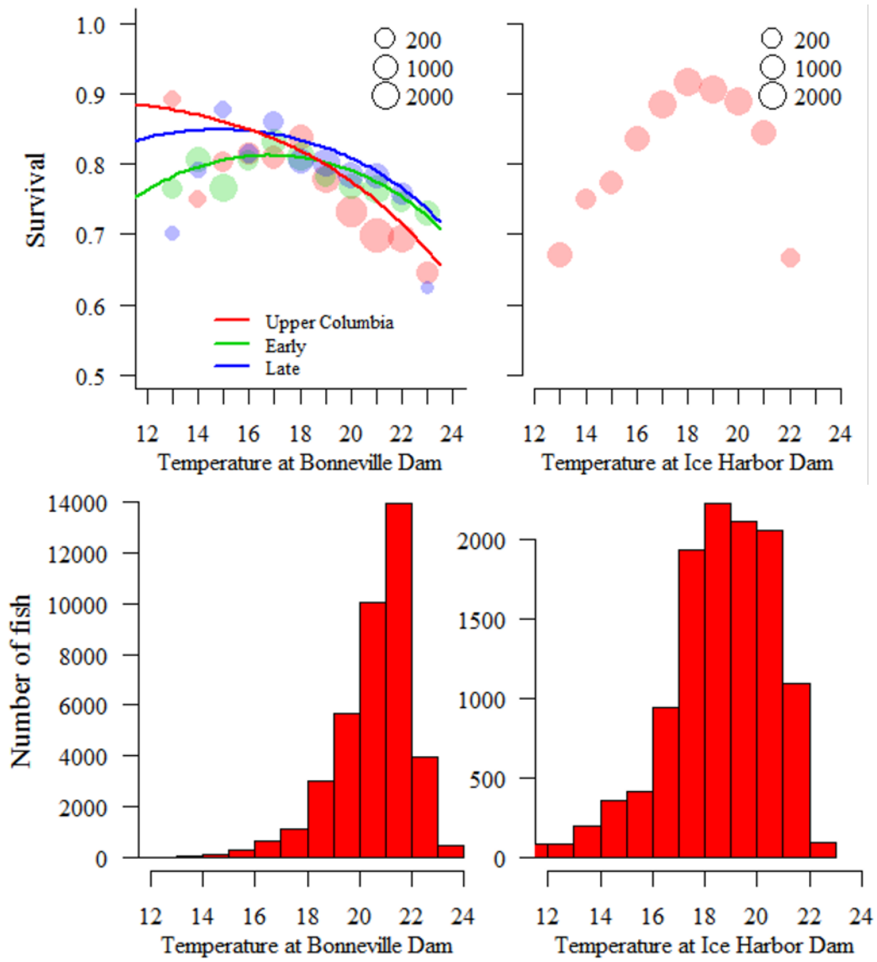


Figure 8. (top) Survival as a function of temperature on date of arrival in the reach from Bonneville Dam to McNary Dam (left) and from Ice Harbor Dam to Lower Granite Dam (right). Temperatures were rounded down to the nearest whole number. Circle size is proportional to the number of fish in each temperature bin. (bottom) Respective distribution of temperatures experienced by fish at Bonneville Dam (left) and Ice Harbor Dam (right).

Table 12a. Upper Columbia DPS survival estimates based on mark–recapture analysis.

Year	BON–TDA	TDA–MCN	BON–MCN	MCN–PRD	PRD–RIS
2004			0.82 (0.01)	0.97 (0.01)	0.73 (0.02)
2005			0.75 (0.01)	0.97 (0.01)	0.99 (0.04)
2006			0.76 (0.01)	0.99 (0.00)	0.99 (0.00)
2007			0.75 (0.01)	0.99 (0.00)	0.98 (0.01)
2008			0.75 (0.02)	0.99 (0.01)	1.00 (0.00)
2009			0.77 (0.01)	0.99 (0.00)	0.98 (0.01)
2010			0.80 (0.02)	0.99 (0.01)	0.98 (0.01)
2011			0.81 (0.01)	0.99 (0.00)	0.99 (0.01)
2012			0.81 (0.01)	1.00 (0.00)	1.00 (0.00)
2013	0.83 (0.02)	0.88 (0.02)	0.73 (0.02)	0.99 (0.00)	0.99 (0.01)
2014	0.87 (0.01)	0.90 (0.01)	0.79 (0.02)	0.99 (0.01)	0.98 (0.01)
2015	0.87 (0.01)	0.93 (0.01)	0.81 (0.02)	0.98 (0.01)	0.99 (0.01)
2016	0.87 (0.02)	0.86 (0.03)	0.74 (0.03)	0.99 (0.01)	0.97 (0.01)

Table 12b. Estimated survival, by reach, for individual and combined Snake River MPGs.

		Estimated survival of Snake River DPS				
Reach	**Year**	**All MPGs**	**Clearwater River MPG**	**Grande Ronde River MPG**	**Imnaha River MPG**	**Salmon River MPG**
BON–MCN	2004	0.87 (0.02)	0.882 (0.024)	0.871 (0.025)	0.894 (0.021)	0.896 (0.020)
	2005	0.81 (0.03)	0.809 (0.031)	0.794 (0.032)	0.827 (0.029)	0.831 (0.028)
	2006	0.80 (0.03)	0.796 (0.035)	0.780 (0.036)	0.815 (0.032)	0.819 (0.031)
	2007	0.82 (0.03)	0.816 (0.029)	0.801 (0.029)	0.834 (0.026)	0.837 (0.025)
	2008	0.78 (0.02)	0.778 (0.024)	0.761 (0.022)	0.799 (0.021)	0.802 (0.020)
	2009	0.80 (0.01)	0.801 (0.015)	0.785 (0.011)	0.819 (0.012)	0.823 (0.011)
	2010	0.78 (0.01)	0.765 (0.016)	0.748 (0.012)	0.787 (0.012)	0.790 (0.010)
	2011	0.80 (0.01)	0.789 (0.014)	0.773 (0.011)	0.809 (0.011)	0.812 (0.009)
	2012	0.79 (0.01)	0.774 (0.016)	0.757 (0.014)	0.795 (0.014)	0.799 (0.011)
	2013	0.76 (0.01)	0.758 (0.018)	0.740 (0.015)	0.780 (0.015)	0.784 (0.013)
	2014	0.78 (0.01)	0.777 (0.016)	0.760 (0.012)	0.798 (0.012)	0.801 (0.011)
	2015	0.81 (0.01)	0.812 (0.015)	0.797 (0.012)	0.830 (0.012)	0.833 (0.011)
	2016	0.79 (0.01)	0.774 (0.018)	0.757 (0.016)	0.795 (0.015)	0.798 (0.013)
	Mean	0.798	0.795	0.779	0.814	0.817
MCN–IHR	2004	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
	2005	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
	2006	0.915 (0.026)	0.912 (0.027)	0.904 (0.029)	0.921 (0.024)	0.923 (0.024)
	2007	0.941 (0.018)	0.940 (0.019)	0.934 (0.020)	0.946 (0.017)	0.948 (0.016)
	2008	0.956 (0.012)	0.955 (0.012)	0.950 (0.013)	0.960 (0.011)	0.960 (0.010)
	2009	0.931 (0.007)	0.932 (0.009)	0.925 (0.008)	0.939 (0.007)	0.940 (0.007)
	2010	0.946 (0.006)	0.944 (0.007)	0.938 (0.007)	0.950 (0.006)	0.951 (0.006)
	2011	0.966 (0.005)	0.964 (0.005)	0.961 (0.005)	0.968 (0.005)	0.969 (0.004)
	2012	0.941 (0.007)	0.937 (0.009)	0.931 (0.009)	0.944 (0.007)	0.945 (0.007)
	2013	0.970 (0.006)	0.971 (0.006)	0.969 (0.007)	0.975 (0.006)	0.975 (0.005)
	2014	0.961 (0.006)	0.960 (0.006)	0.957 (0.006)	0.965 (0.005)	0.966 (0.005)
	2015	0.957 (0.006)	0.956 (0.007)	0.952 (0.007)	0.961 (0.006)	0.962 (0.006)
	2016	0.950 (0.008)	0.946 (0.009)	0.941 (0.010)	0.952 (0.008)	0.953 (0.008)
IHR–LWG	2004	0.972 (0.012)	0.972 (0.013)	0.969 (0.014)	0.975 (0.011)	0.975 (0.011)
	2005	0.973 (0.036)	0.964 (0.016)	0.961 (0.017)	0.968 (0.014)	0.969 (0.014)
	2006	1.000 (0.000)	0.971 (0.017)	0.968 (0.018)	0.974 (0.015)	0.975 (0.014)
	2007	0.962 (0.015)	0.961 (0.016)	0.958 (0.017)	0.966 (0.014)	0.966 (0.014)
	2008	0.960 (0.011)	0.959 (0.012)	0.955 (0.013)	0.964 (0.010)	0.964 (0.010)
	2009	0.956 (0.006)	0.958 (0.007)	0.954 (0.007)	0.963 (0.006)	0.963 (0.005)
	2010	0.946 (0.006)	0.945 (0.007)	0.940 (0.007)	0.951 (0.006)	0.952 (0.006)
	2011	0.931 (0.006)	0.928 (0.008)	0.921 (0.008)	0.936 (0.007)	0.937 (0.006)
	2012	0.954 (0.007)	0.951 (0.008)	0.947 (0.008)	0.957 (0.007)	0.958 (0.006)
	2013	0.943 (0.009)	0.943 (0.009)	0.937 (0.009)	0.949 (0.008)	0.950 (0.008)
	2014	0.949 (0.006)	0.948 (0.007)	0.943 (0.007)	0.954 (0.006)	0.954 (0.006)
	2015	0.974 (0.013)	0.967 (0.006)	0.964 (0.006)	0.971 (0.005)	0.972 (0.005)
	2016	0.956 (0.022)	0.946 (0.010)	0.941 (0.010)	0.952 (0.008)	0.953 (0.008)
BON–TDA	2013	n/a	0.858 (0.018)	0.835 (0.013)	0.865 (0.014)	0.891 (0.010)
	2014	n/a	0.877 (0.016)	0.857 (0.011)	0.883 (0.011)	0.906 (0.008)
	2015	n/a	0.910 (0.013)	0.894 (0.010)	0.915 (0.010)	0.932 (0.007)
	2016	n/a	0.875 (0.018)	0.854 (0.014)	0.881 (0.013)	0.904 (0.009)
TDA–MCN	2013	n/a	0.880 (0.017)	0.860 (0.013)	0.886 (0.013)	0.908 (0.010)
	2014	n/a	0.885 (0.015)	0.866 (0.011)	0.891 (0.011)	0.912 (0.008)
	2015	n/a	0.891 (0.015)	0.873 (0.011)	0.897 (0.011)	0.917 (0.008)
	2016	n/a	0.871 (0.018)	0.850 (0.015)	0.878 (0.014)	0.901 (0.010)

For the Snake River DPS, the best-fitting mark–recapture model had an interaction between reach and year in the survival term and an MPG effect. The late Clearwater River and Salmon River MPGs had higher survival than the early MPGs (Figure 7, Table 11). Reach-specific survival for the Snake River DPS was lowest in the reach from Bonneville Dam to McNary Dam, ranging between 0.76 and 0.87 in all years since 2004. For the years 2004 and 2005, survival was estimated at 100%, though sample sizes were very small for these years. Across all years and MPGs, survival from McNary Dam to Lower Granite Dam was near 90%, ranging from 0.88 to 0.97 across years; means per MPG ranged from 0.89–0.92.

Factors influencing survival from Bonneville Dam to McNary Dam

The main factors that influenced apparent survival were *temperature*, *fish origin*, *ocean age*, and *catch* (Appendix A, Table A-7). In all three model averages, older fish and hatchery fish were less likely to survive to McNary Dam (Table 13; note that a positive coefficient for fish origin indicates an advantage for wild fish). Temperature had a significant negative effect in all cases (Figure 8). In late populations that migrate as summer is waning and temperatures are dropping, temperature was strongly negatively correlated with arrival date, and the two factors performed similarly.

Early populations (Upper Columbia and Middle Columbia River DPSes, and early Snake River MPGs) were susceptible to negative effects of high spill as well. A juvenile migration history of transportation had a negative effect on survival during adult migration for both early and late Snake River fish in the affected populations.

A large part of the tribal fishery targets upriver fall Chinook salmon with steelhead primarily as bycatch, so overlap with steelhead occurs mostly in September. Smaller, nontribal fisheries target steelhead, and therefore display a different seasonal pattern. We used the weekly catch metric to estimate the variation across populations in their exposure to the fishery. Catch exposure based on arrival date at Bonneville Dam varied among populations (Table 14).

Table 13. Generalized linear model results for survival in the reach from Bonneville Dam to McNary Dam.

Covariate	Coefficient	Importance
Upper Columbia MPG		
Intercept	1.1286	n/a
Temperature	−0.2408	1.00
Spill	−0.1084	1.00
Fish origin	0.0614	0.89
Ocean age	−0.1721	1.00
Catch	0.1414	1.00
Late Snake River MPGs		
Intercept	1.3891	n/a
Temperature	−0.1640	1.00
Fish origin	0.0788	1.00
Juvenile migration	−0.0661	1.00
Ocean age	−0.1410	1.00
Early Snake River and Middle Columbia River MPGs		
Intercept	1.3028	n/a
$Temperature^2$	−0.0220	0.89
Temperature	−0.1292	1.00
Spill	−0.0861	0.93
Fish origin	0.0659	1.00
Juvenile migration	−0.0878	1.00
Ocean age	−0.0772	1.00
Catch	−0.0572	0.81

Peak catch in Zone 6 occurred in September, and overlapped most with the Clearwater River and Salmon River populations (Appendix B, Figure B-2). Models indicated that catch had a significant and important negative effect on adult migration survival in the Clearwater River and Salmon River MPGs.

The Upper Columbia MPG model did not capture survival very well compared with other models, particularly after 2012. This model included a surprising positive effect of catch, which did not produce very good fits. Additional work is necessary to improve the covariates that are relevant for this MPG.

Table 14. Average weekly catch rate (weekly catch/ weekly counts at Bonneville Dam) of PIT-tagged fish, by MPG, and the proportion of at least 2-ocean fish among hatchery and wild steelhead.

		Frequency of 2-ocean steelhead	
MPG	**Catch rate (BON)**	**Hatchery**	**Wild**
Upper Columbia	0.037	0.43	0.71
Clearwater River	0.197	0.89	0.80
Grand Ronde River	0.059	0.33	0.53
Lower Snake River	0.051	0.25	0.57
Imnaha River	0.056	0.24	0.44
Salmon River	0.162	0.74	0.69
Umatilla/Walla Walla	0.058	0.44	0.48
Yakima River	0.052	—	0.38

Factors influencing survival in the Snake River

Survival was high in the Snake River reaches from McNary to Ice Harbor and from Ice Harbor to Lower Granite Dams (>92%, Table 12). In both reaches, spill had a negative effect on survival (Table 15). Hatchery fish, with more fallbacks and longer travel times, had lower survival. Transport negatively affected survival in both reaches. Although all of these coefficients were statistically significant, their magnitude was relatively small. In both reaches, model predictions were very similar to observed apparent survival, and small variations from year to year were well represented by the model (Figure 7, panels E and F).

Table 15. Generalized linear model results for survival in the Snake River reaches.

Covariate	Coefficient	Importance
McNary Dam to Ice Harbor Dam		
Intercept	3.9491	n/a
Temperature	0.1930	1.00
Spill	−0.1563	1.00
Fish origin	0.1021	0.97
Juvenile migration	−0.2670	1.00
Ocean age	0.1646	1.00
Fallback	−0.3854	1.00
Travel time	−0.2388	1.00
Ice Harbor Dam to Lower Granite Dam		
Intercept	3.0357	n/a
Temperature	0.2854	1.00
Spill	−0.2229	1.00
Fish origin	0.1862	1.00
Juvenile migration	−0.0870	1.00
Fallback	−0.1629	1.00

Discussion

Overview of Behavior Patterns

Adult arrival timing, migration rate, and survival through the mainstem Columbia and Snake Rivers have important implications for recovery planning and long-term persistence of upriver steelhead. Three general patterns emerged as the product of different combinations of 1) early vs. late arrival timing at Bonneville Dam, 2) slow vs. fast travel time to McNary Dam, and 3) the number of years fish had spent in the ocean. These behavior combinations determine exposure of adult steelhead to mainstem river temperature and harvest, and they produced distinct patterns in survival specific to each DPS.

Our models quantified the sensitivity of arrival timing, migration rate, and survival to various influences, such as environmental conditions and hatchery origin. Proactive management plans can incorporate these insights to help steelhead cope with increasing stress from climate change (IPCC 2014, EPA 2016, Dalton et al. 2017). Such plans are essential in addressing the ongoing challenges to recovery of threatened wild steelhead.

Upper Columbia DPS steelhead stocks are at the greatest risk from a conservation standpoint, because wild populations continue to have the lowest replacement rates, and hatchery supplementation dominates the basin (Ford et al. 2016). Although Upper Columbia steelhead populations are considered part of the A-index, we found that a majority of wild fish (71%) had spent at least two years in the ocean, which is typically associated with the B-index.

Wild Upper Columbia DPS steelhead that were ocean-age 2 or more returned in the earliest group to pass Bonneville Dam (earlier than 1-ocean fish, and earlier than hatchery fish). They therefore encountered slightly lower temperatures at Bonneville Dam, but faced rising temperatures as they moved upstream. Older wild fish tended to use thermal refuges at a very low rate, despite a mean passage temperature at Bonneville Dam of 20.2°C. Therefore, they were relatively vulnerable to high mainstem temperatures and summer Chinook salmon gillnet fisheries that select for larger fish.

Overall, the survival of Upper Columbia DPS steelhead was 2.3% lower than that of other early runs (early Snake River and Middle Columbia River MPGs), and 5% lower than that of late Snake River MPGs. This ratio held for wild and hatchery fish separately. Upper Columbia stocks also showed a steeper decline in survival at higher temperatures than other DPSes (Figure 8), raising concern that they might be especially sensitive to warming temperatures.

Middle Columbia River DPS steelhead spent a median of 53 days in the lower Columbia River, the longest of any DPS. These stocks had the earliest arrival date at Bonneville Dam and the latest passage date at McNary Dam. The degree day metric multiplies the number of days at a given temperature by the duration of time at that temperature; it is an indication of cumulative thermal exposure. If Middle Columbia River steelhead spent all of that time within the mainstem, they would have experienced the highest cumulative thermal exposure of all DPSes, with a median 950 degree days (vs. 200–360 degree days for other DPSes, Figure 9). However, if fish spent most of this time in thermal refuges, then actual degree days are much fewer.

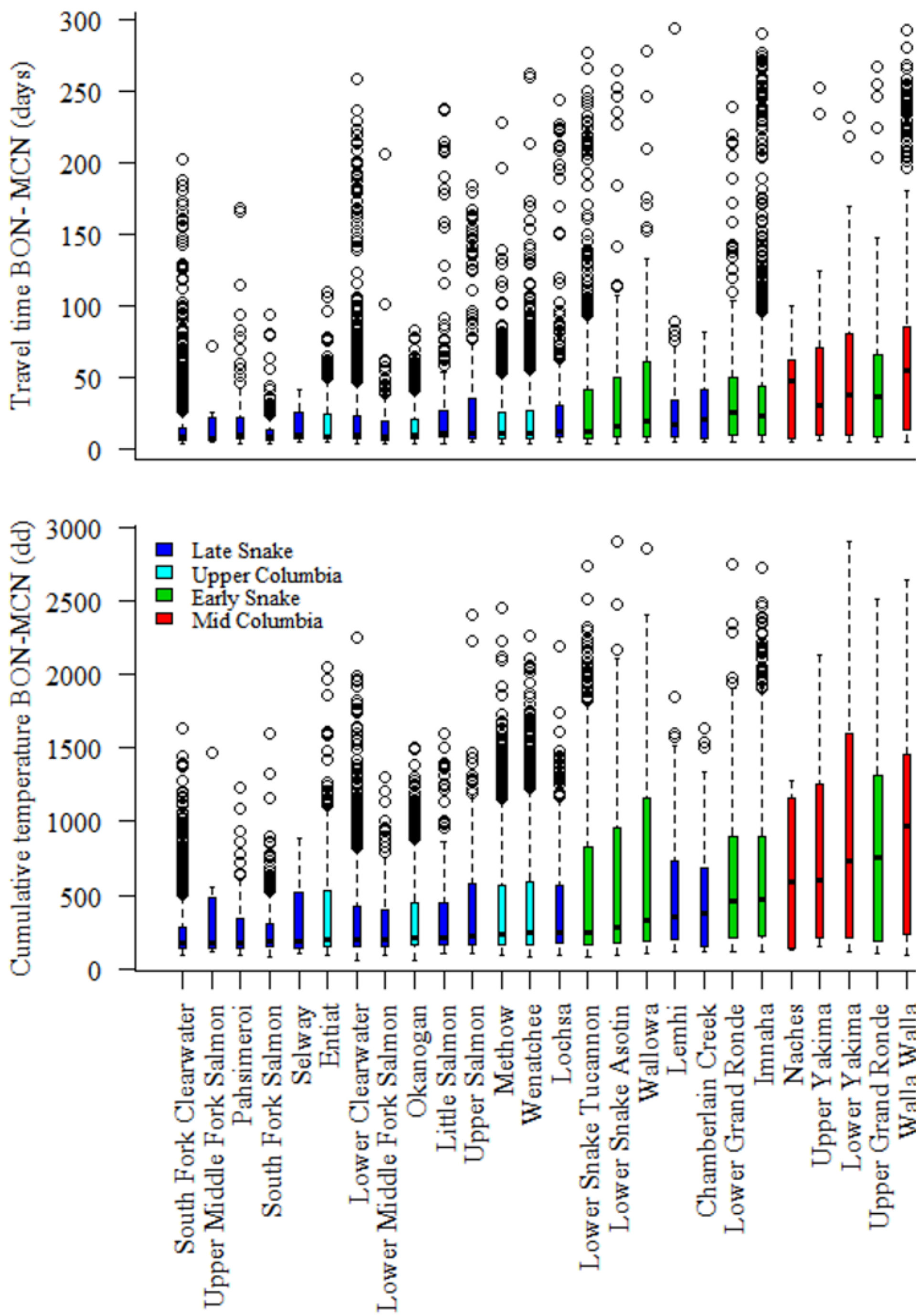


Figure 9. Travel time from Bonneville Dam to McNary Dam and cumulative degree days in this reach, based on temperatures at Bonneville Dam. Fish are grouped into populations based on release site.

The Middle Columbia River DPS also had the highest proportion of slow fish, and slow fish from this DPS had the longest median travel times. Despite long travel times from Bonneville Dam to McNary Dam, overall survival was relatively high for this DPS (mean 80%). Middle Columbia River steelhead presumably made the most use of thermal refuges, and hence will depend most on protection of these refuges as the Columbia River continues to warm.

Behavior of the Snake River DPS was highly diverse, with clear behavioral differences between low- and high-elevation MPGs. The Snake River DPS thus separated naturally into early and late components, typically conforming with A- and B-index populations. Run timing of the early and late groups was distinct (Figure 10), despite the unimodal appearance of the run as a whole pointed out by Robards and Quinn (2002). As those authors suggested, a large number of hatchery fish obscures the distinction between the two modes. This bimodality might have been more clear if we had not lumped populations by MPG. The Salmon River MPG in particular includes both A- and B-index populations. However, regardless of our categorization, overall behavioral characteristics were relatively clear.

We noted that the majority of wild fish spent at least two years in the ocean, even in the early (A-index) MPGs. It would be interesting to know whether 2-ocean fish from A-index populations are as large as those from B-index populations, because length also affects fecundity and fishery quotas. However, proportions of 2-ocean fish from our analysis were consistent with those observed by Copeland et al. (2017) for Snake River steelhead. Early MPGs of the Snake River DPS had arrival times similar to those of the Upper Columbia and Middle Columbia River DPSes, but an intermediate use of the slow migration strategy. The survival profile of early Snake River MPGs was also intermediate and distinctly lower than that of the late Snake River MPGs. Late Snake River MPGs experienced lower temperatures, the shortest residence times, and the highest proportions of 2-ocean fish in both hatchery and wild groups.

All Snake River MPGs moved relatively quickly and cohesively after passing McNary Dam to complete the long migration to their spawning grounds.

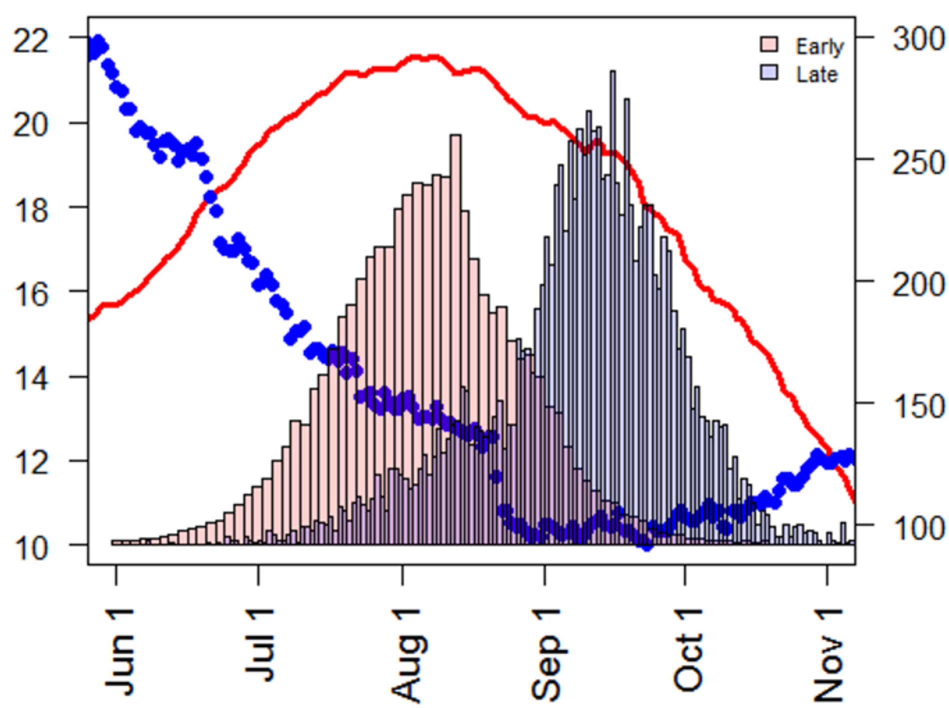


Figure 10. Daily average temperature (red line), flow (blue points), and passage (histogram) at Bonneville Dam for early- and late-migrating groups of steelhead.

Factors Affecting Arrival Time

Arrival timing at Bonneville Dam

Annual variation and long-term trends in steelhead arrival timing reflect both biological plasticity and anthropogenic factors. Early runs have been arriving later since the 1930s. Robards and Quinn (2002) attributed this long-term trend to hatchery practices and changing hydrology, especially from hydropower development and anthropogenic climate change. Our observation that arrival of early populations was very sensitive to environmental factors was consistent with their explanation. We did not observe a trend in environmental factors during our study period (Figure 11), but we expect Columbia River temperatures to continue to warm over the next few decades, leading to progressively later steelhead arrival.

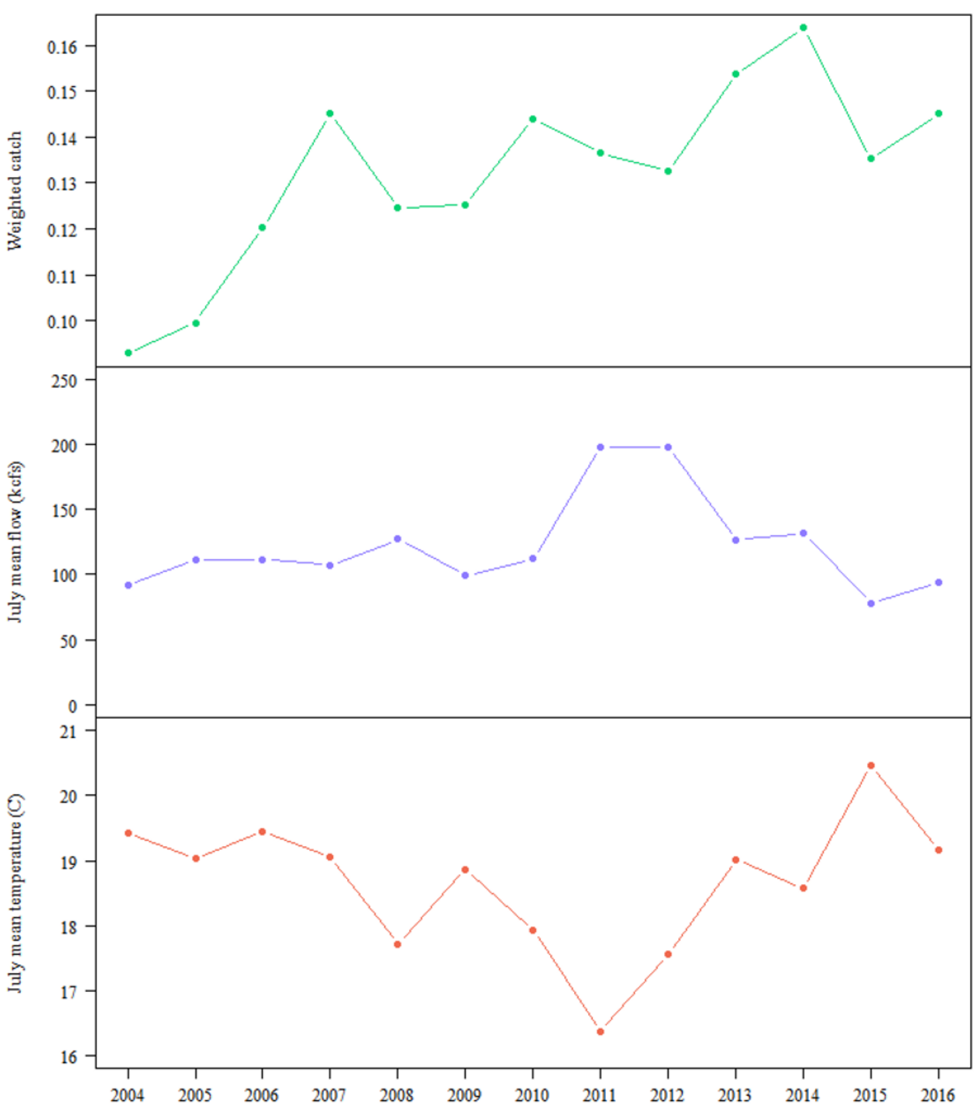


Figure 11. (A) Total annual catch in Zone 6. (B) Mean flow in July. (C) Temperature (°C) at Bonneville Dam.

Over the six decades of their study, Robards and Quinn (2002) found that late populations were more stable in arrival timing than early populations. In contrast to this finding, we observed a temporal trend in the late populations. Later arrival of the Clearwater River and Salmon River MPGs mostly reflected increased proportions of hatchery fish in the Upper Salmon and Lower Salmon populations, as well as in the South Fork Clearwater and Lower Clearwater populations.

However, even considering only hatchery fish, we found a significant trend toward later arrival. Whether this trend reflected active selection in hatcheries, selection by fisheries, or a shift in representation of different stocks within the hatcheries was not clear. Our analyses confirmed that hatchery fish arrived at Bonneville Dam later than wild fish in all MPGs. Hatchery fish arrived about one week later in the early MPGs, and two weeks later in the late MPGs.

Fast vs. slow migration from Bonneville Dam to McNary Dam

Throughout the year, most steelhead pass from Bonneville Dam to McNary Dam within about one week. However, the proportion of fish that delay migration through this reach by weeks or even months is highly temperature-sensitive. As pointed out by Keefer et al. (2009), a majority of fish that encounter temperatures above 19°C at Bonneville Dam delay migration. All early MPGs entered the Columbia River when the average temperature was above 20°C. Nonetheless, their propensity to suspend migration was not just a function of temperature. Across temperatures, migration delays occurred at a higher rate in the Middle Columbia River DPS than in the Upper Columbia or Snake River DPSes.

Additional predictors for slow migration included the number of fallbacks at Bonneville Dam, juvenile transportation, temperature, and ocean age (Appendix A, Table A-8). Fallbacks could be a cause or a result of the slowed migration strategy. If fish are meandering around the lower Columbia River, they might fall back over Bonneville Dam as a secondary characteristic of this larger meandering. They could also be retreating to cooler water in the estuary. In general, hatchery fish had a higher probability of being slow than wild fish. Hatchery fish may have weaker homing ability than wild fish, or reduced incentive based on distance because hatcheries tend to be located farther downstream than wild spawning areas in many river basins (Keefer and Caudill 2013).

Factors Affecting Estimated Survival

Temperature

For all MPGs, survival between Bonneville Dam and McNary Dam was strongly predicted by temperature. Temperature was followed by ocean age, catch rate, and fish origin as predictors.

These factors impact survival in numerous ways. For example, higher temperatures might have reduced survival through physiological stress, considering that temperatures were relatively close to the critical maximums reported for this species (Richter and Kolmes 2005). Declines in survival from Ice Harbor Dam to Lower Granite Dam at temperatures over 21°C were consistent with this hypothesis.

In the Snake River, cumulative degree days are relatively well correlated with temperature on date of passage at Ice Harbor Dam (Keefer and Caudill 2016). This relationship is not apparent in the lower Columbia River, where steelhead tend to use cooler tributaries to avoid high temperatures. Use of thermal refuges in the lower Columbia River appeared to buffer temperature impacts for some DPSes more than others.

Migration rate

Our finding that fish never detected at McNary Dam had higher probabilities of being in the slow group than the fast group was consistent with the results of Keefer et al. (2009). They found that fish using thermal refuges were more likely to be caught in recreational fisheries and had lower survival. However, because temperature was a strong predictor both of survival and of being in the slow group, we could not differentiate temperature vs. slow migration rate as causal factors of mortality.

Fish in the slow group experienced greater exposure to catch below McNary Dam, which might have contributed to their higher mortality. Some mortality might also result from compounded weakness due to poor physical condition and cumulative exposure to stressful environmental conditions. In Chinook salmon, longer travel times are correlated with higher mortality (Caudill et al. 2007, Crozier et al. 2017).

However, steelhead from the Middle Columbia River DPS, which spent the most time downstream of McNary Dam, had relatively high survival. This suggests that steelhead may be more resilient to time-dependent mortality than Chinook or sockeye salmon. For the Middle Columbia River DPS, the survival benefits of slow travel (avoiding high temperatures) appeared to outweigh the survival costs (greater catch exposure).

Survival estimates were generally lower in the early group, at 68–80% in the Upper Columbia DPS alone, and 73–83% in the entire early group in variation across years. In comparison, survival ranged from 76–86% for the late Snake River DPS group. Temperature on day of passage at Bonneville Dam was the strongest individual predictor of survival, with estimates dropping from above 80% during temperatures of 13–17°C to 67% when the river reached 23°C. A majority of steelhead (61%) entered the Bonneville Dam to McNary Dam reach at temperatures of 20–22°C, and thus had an expected temperature-determined survival of about 73%. This estimate included observed catch rates, so reducing catch would increase estimated survival at high temperatures.

As the Columbia Basin warms in response to greenhouse gas emissions, an increasing number of steelhead will likely encounter temperatures above 23°C, and this could further depress survival. Providing adequate thermal refuges will likely be a crucial management tool to preserve these threatened fish.

Mean temperatures in tributary streams will also increase over time. To the extent that mortality is caused by fisheries rather than by direct thermal stress, these fish can be protected using fishery management strategies. It is also possible that later-arriving populations have been selected for, and that wild fish from these populations might shift to later run timing. However, no indication of such shifts in wild fish has been observed thus far.

Fish age

As a covariate of survival, fish age also interacts with catch. Older, larger fish are more likely to be caught for various reasons. Anglers prefer larger fish in recreational fisheries; larger size also increases the risk of bycatch, as larger fish are more likely to be caught in gillnets targeting Chinook salmon. Steelhead MPGs differed in the percentage of older upstream migrants. Most early-run hatchery steelhead populations are dominated by 1-ocean fish, while wild fish tend to be older.

In the late Clearwater River and Salmon River MPGs, a majority of both hatchery and wild fish spent two or more years in the ocean. These 2-ocean, late-arriving hatchery fish were caught primarily during fall fisheries, which traditionally class larger, late-run fish as B-index. Finally, fish age affected temperature exposure because older fish tend to arrive later than younger fish in early runs and earlier than younger fish in late runs. In both cases, older fish encounter higher temperatures than younger fish, putting them at greater risk from climate change.

Catch

Estimating the effect of catch on steelhead survival was difficult because our index of catch was not sensitive to specific dates or locations, and thus did not necessarily reflect the catch exposure of individual fish. Furthermore, harvest might have been under-reported, especially during periods when catch rates near quotas could shut down the fishery. We used the annual sum of all catch as an index due to a) difficulty in identifying B-index fish, and b) the wide variation in travel time through the Zone 6 fishery.

Peak harvest occurs in September, when many Middle Columbia River and early Snake River DPS steelhead are still downstream of McNary Dam. Thus, fish may have been harvested by the fishery weeks instead of days after passing Bonneville Dam. Taking travel-time behavior into account could help managers develop catch targets that are more population-specific. However, better monitoring of catch is essential to refine our understanding of population impacts.

We focused on survival to first detection at upstream dams for each DPS because we were interested in the behaviors most pertinent to tolerance of high temperatures and peak harvest periods in fall. It is interesting to note, however, that after passing Lower Granite Dam, steelhead may reverse direction and return to the hydrosystem to overwinter. Keefer et al. (2008a) found that in January, one-quarter of radio-tagged Clearwater River steelhead were in the lower Columbia River, and one-half were in Lower Granite Lake. They reported that steelhead from the Salmon and lower Snake Rivers were even more likely to be downstream of Lower Granite Dam in January. The winter behavior could therefore also be described as mixtures of different distributions of time spent in different reaches, and each one would be associated with its own exposure to different risk factors.

Overshoot and straying

Steelhead wander widely in the Columbia River basin prior to spawning, and may linger upstream from a spawning tributary before returning downstream. This behavior is known as *overshoot* (Boggs et al. 2004). If the fish does not ultimately return to the natal basin, it is usually called *straying.* Our study focused on first detections at each dam, so we looked only at the initial residence in the lower Columbia River for our differentiation between fast and slow behaviors. Fish might have returned to this reach later, but that was not included in our analysis.

We only included fish whose natal tributaries were upstream from McNary Dam in our analysis, so no detections at McNary Dam were considered overshoot. We did observe fish that strayed or overshot upstream from McNary Dam. Out of 12,378 Snake River DPS migrants that were detected at McNary Dam, 206 (1.7%) were detected at one or more of the upper Columbia River dams. Of those, 125 (61%) were subsequently detected at a Snake River dam. On the other hand, the remaining 81 fish (0.6%) might be considered strays to the Upper Columbia DPS.

A much smaller percentage of steelhead from the Upper Columbia DPS were detected in the Snake River (72/16,445, 0.4%). Of them, 18 (25%) were later detected at an upper Columbia River dam, whereas the remaining 54 (0.3%) would be considered strays.

One possible explanation for the higher percentage of Snake River fish that moved into Upper Columbia (1.7%) compared with the percentage of Upper Columbia fish that strayed into Snake River (0.4%) is that the Snake River fish were showing a preference for cooler river temperatures in the upper Columbia River, but this behavior did not interfere with successful migration overall. Most of these fish successfully returned to the natal branch, so it seems generally consistent with other steelhead behavioral adaptations to the river environment.

We do not know whether any of these fish actually spawned. Using radio-tagging data, Keefer et al. (2009) were able to determine that fish that delayed over summer were less likely to enter a natal tributary than fish that did not delay (68.7% vs. 76.8%). Keefer et al. (2008a) found equally complex behaviors over winter, when over 60% of the fish from some populations, especially from the Clearwater River, resided within the hydrosystem instead of spending winter within the tributary. These fish had higher survival than those that did not overwinter within the hydrosystem (82% vs. 62% were considered successful migrants). Keefer et al. (2009) attributed the difference in these outcomes for slow fish in summer vs. winter largely to patterns in harvest. It is difficult to know what the historical survival rates might have been that selected for these slow-migration behaviors, but presumably they tended to produce higher survival than direct movement into natal tributaries.

Conclusion

In summary, we found that steelhead DPSes in the Columbia River basin have variable mortality risk in relation to environmental factors as well as to hydrosystem and fishery management actions, and that this variability stems from distinct behavior patterns. Temperature was a strong predictor of individual survival, which suggests vulnerability in relation to climate change. However, steelhead have complex behavioral responses to warm temperature, such as reverse migration, delayed arrival, and use of thermal refuges. These behaviors appear to be sufficient to allow them to tolerate the current range of temperatures, and even extreme temperatures over this time period. In 2015, in particular, steelhead survival was relatively high, despite record hot temperatures in July and catastrophic run failures for comigrating sockeye salmon (NMFS 2016a). These responses may ultimately cause survival of steelhead to fluctuate less than that of Chinook or sockeye salmon, especially in the Snake River DPS.

Life history diversity and flexibility are key to steelhead population viability (Greene et al. 2010, Schindler et al. 2010). Robards and Quinn (2002) noted that the adult steelhead migration window has shifted, and will perhaps continue to do so. This moving window, coupled with the behavioral flexibility of steelhead, may enable these fish to maintain their steady survival rate in coming decades.

References

Barton, K. 2018. MuMIn: Multi-Model Inference. R package version 1.40.4.

Benaglia, T., D. Chauveau, D. Hunter, and D. Young. 2009. mixtools: An R Package for Analyzing Finite Mixture Models. Journal of Statistical Software 32(6):1–29.

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

Burke, B. J., T. J. Bohn, S. L. Downing, M. A. Jepson, and C. A. Peery. 2004. Dam passage and fallback by Chinook salmon and steelhead as determined by Passive Integrated Transponder tags and radio tags. Northwest Fisheries Science Center, Seattle.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag, New York.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. Northwest Fisheries Science Center, Seattle.

Caudill, C. C., W. R. Daigle, M. L. Keefer, C. T. Boggs, M. A. Jepson, B. J. Burke, R. W. Zabel, T. C. Bjornn, and C. A. Peery. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition-dependent mortality? Canadian Journal of Fisheries and Aquatic Sciences 64(7):979–995.

CBR (Columbia Basin Research). 2019. Columbia River Data Access in Real Time (DART). University of Washington, School of Fisheries and Aquatic Sciences, Seattle. Available: http://www.cbr.washington.edu/dart (June 2019).

Copeland, T., M. W. Ackerman, K. K. Wright, and A. Byrne. 2017. Life history diversity of Snake River steelhead populations between and within management categories. North American Journal of Fisheries Management 37(2):395–404.

Crozier, L. G., T. E. Bowerman, B. J. Burke, M. L. Keefer, and C. C. Caudill. 2017. High-stakes steeplechase: A behavior-based model to predict individual travel times through diverse migration segments. Ecosphere 8(10):e01965.

Dalton, M. M., K. D. Dello, L. Hawkins, P. W. Mote, and D. E. Rupp. 2017. The third Oregon climate assessment report. Oregon Climate Change Research Institute, Oregon State University, Corvallis, Oregon.

EPA (U.S. Environmental Protection Agency). 2016. Climate change indicators in the United States. U.S. Environmental Protection Agency, Washington, D.C.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24(1):38–49.

Ford, M. J., K. Barnas, T. Cooney, L. G. Crozier, M. Diaz, J. J. Hard, E. E. Holmes, D. M. Holzer, R. G. Kope, P. W. Lawson, M. Liermann, J. M. Myers, M. Rowse, D. J. Teel, D. M. V. Doornik, T. C. Wainwright, L. A. Weitkamp, and M. Williams. 2016. 2015 Status Review Update for Pacific Salmon and Steelhead Listed under the Endangered Species Act: Pacific Northwest. Northwest Fisheries Science Center, Seattle. Available: www.fisheries.noaa.gov/resource/publication-database/northwest-fisheries-science-center-publications-database (June 2019).

Gosselin, J. L., and J. J. Anderson. 2017. Combining Migration History, River Conditions, and Fish Condition to Examine Cross-Life-Stage Effects on Marine Survival in Chinook Salmon. Transactions of the American Fisheries Society 146(3):408–421.

Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2010. Improved viability of populations with diverse life-history portfolios. Biology Letters 6(3):382–386.

Hess, M. A., J. E. Hess, A. P. Matala, R. A. French, C. A. Steele, J. C. Lovtang, and S. R. Narum. 2016. Migrating adult steelhead utilize a thermal refuge during summer periods with high water temperatures. ICES Journal of Marine Science 73(10):2616–2624.

IPCC (Intergovernmental Panel on Climate Change). 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2008a. Overwintering distribution, behavior, and survival of adult summer steelhead: Variability among Columbia river populations. North American Journal of Fisheries Management 28(1):81–96.

Keefer, M. L., and C. C. Caudill. 2013. Homing and straying by anadromous salmonids: A review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24(1):333–368.

Keefer, M. L., and C. C. Caudill. 2016. Estimating thermal exposure of adult summer steelhead and fall Chinook salmon migrating in a warm impounded river. Ecology of Freshwater Fish 25(4):599–611.

Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): Variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences 66(10):1734–1747.

Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008b. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): Implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65(12):2592–2605.

Laake, J. L., D. S. Johnson, and P. B. Conn. 2013. marked: An R package for maximum-likelihood and MCMC analysis of capture-recapture data. Methods in Ecology and Evolution 4:885–890.

Matala, A. P., M. W. Ackerman, M. R. Campbell, and S. R. Narum. 2014. Relative contributions of neutral and non-neutral genetic differentiation to inform conservation of steelhead trout across highly variable landscapes. Evolutionary Applications 7(6):682–701.

McLachlan, G., and D. Peel. 2000. Finite Mixture Models. John Wiley & Sons, Inc. Wiley-Interscience Publication, New York.

Nielsen, J. L., A. Byrne, S. L. Graziano, and C. C. Kozfkay. 2011. Steelhead Genetic Diversity at Multiple Spatial Scales in a Managed Basin: Snake River, Idaho. North American Journal of Fisheries Management 29(3):680–701.

NMFS (National Marine Fisheries Service). 2016a. 2015 adult sockeye salmon passage report. Available: www.columbiariverkeeper.org/sites/default/files/2017/08/8.pdf (December 2020).

NMFS (National Marine Fisheries Service). 2016b. West Coast salmon & steelhead listings. NOAA Fisheries West Coast Region, Seattle.

NWFSC (Northwest Fisheries Science Center). 2015. Status Review update for the Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. NWFSC, Seattle.

R Core Team. 2019. R version 3.6.2: A language and environmental for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Robards, M. D., and T. P. Quinn. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. Transactions of the American Fisheries Society 131(3):523–536.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465(7298):609–612.

USACE (U.S. Army Corps of Engineers). 2015. Columbia River Basin Water Management. Northwestern Division, U.S. Army Corps of Engineers. Portland, Oregon. Available: www.nwd.usace.army.mil/CRWM/ (June 2015).

Appendix A: Supplemental Data Tables

Table A-1. Release sites from the PTAGIS database used to determine final steelhead tag groups from populations and major population groups (MPGs) within the Upper Columbia and Snake River distinct population segments (DPSes).

DPS, *MPG*, Population	**PTAGIS release site**
Upper Columbia DPS	
Upper Columbia MPG	
Entiat	Entiat River
	Mad River (Entiat River watershed)
	Tillicum Creek, tributary to Mad River
Methow	Beaver Creek, Methow River
	Chewuch River
	Gold Creek, Methow River
	Libby Creek, Methow River
	Little Bridge Creek, tributary to Twisp River
	Methow Hatchery
	Methow River
	Methow Smolt Trap at McFarland Creek Road Bridge
	South Fork Gold Creek, Methow River watershed
	Twisp Acclimation Pond (Methow Salmon Recovery Foundation)
	Twisp River
	Winthrop National Fish Hatchery
	Wolf Creek, Methow River
Okanogan	Okanogan River
	Omak Creek (tributary to Okanogan River)
	Salmon Creek (tributary to Okanogan River)
	Similkameen River
	Stapaloop Creek, in Okanogan River basin
Wenatchee	Chiwaukum Creek, tributary to Wenatchee River
	Chiwawa Rearing Pond
	Chiwawa River
	Chiwawa River Trap, 0.5 km below CHIP acclimation pond
	DRY—Release into the Forebay within 0.5 km upstream of Dam
	Lower Wenatchee trap, 2.8 km below Mission Creek
	Nason Creek (tributary to Wenatchee River)
	Peshastin River
	Ringold Hatchery
	Rolfing Acclimation Pond, Wenatchee River Basin
	Upper Wenatchee smolt trap just below Lake Wenatchee
	Upper Wenatchee trap, 4 km above Chiwawa River
	Wenatchee River
	Wenatchee River trap at West Monitor Bridge

Table A-1 (continued). Release sites from the PTAGIS database used to determine final steelhead tag groups from populations and major population groups (MPGs) within the Upper Columbia and Snake River distinct population segments (DPSes).

DPS, *MPG*, Population	**PTAGIS release site**
Snake River DPS	
Clearwater River MPG	
Lower Clearwater	Big Bear Creek, Potlatch River
	Cedar Creek, Potlatch River watershed
	Clearwater Trap
	Corral Creek, Potlatch River watershed
	Dworshak NFH, release into mainstem Clearwater River
	East Fork Potlatch River
	Eldorado Creek
	Lapwai Creek
	Little Bear Creek, Potlatch River watershed
	Lolo Creek
	Mission Creek
	Pine Creek, Potlatch River watershed
	Potlatch River
	Sweetwater Creek, Lapwai Creek watershed
	Webb Creek, Lapwai Creek watershed
	West Fork Little Bear Creek, Potlatch River watershed
Middle Fork Clearwater	Boulder Creek
	Brushy Fork Creek
	Colt Kill Creek—Replaces WHITSC
	Crooked Fork Creek Trap
	Fish Creek
	Fish Creek Trap
	Gedney Creek
	Moose Creek (Selway River)
	North Fork Moose Creek, Selway River
	O'Hara Creek
South Fork Clearwater	American River
	Clear Creek
	Crooked River
	Crooked River Pond
	Crooked River Trap
	Kooskia National Fish Hatchery
	Meadow Creek, South Fork Clearwater
	Mill Creek, SF Clearwater River
	Newsome Creek
	Red River
	Red River Rearing Pond
	Red River Trap
	South Fork Clearwater River
Grande Ronde River MPG	
Lower Grande Ronde	Cottonwood Acclimation Pond
	Grande Ronde River Trap

Table A-1 (continued). Release sites from the PTAGIS database used to determine final steelhead tag groups from populations and major population groups (MPGs) within the Upper Columbia and Snake River distinct population segments (DPSes).

DPS, *MPG*, Population	**PTAGIS release site**
Snake River DPS (continued)	
Grande Ronde River MPG (continued)	
Upper Grande Ronde	Catherine Creek
	Grande Ronde River—Wallowa River to headwaters (RKM 131–325)
	Little Catherine Creek
	Lookingglass Creek
Wallowa	Lostine River
	Minam River
Imnaha River MPG	
Imnaha	Big Sheep Creek
	Imnaha Trap
	Little Sheep Facility
Lower Snake River MPG	
Asotin	Asotin Creek, Snake River above Clarkston, WA
	Charley Creek, Asotin Creek watershed
	North Fork Asotin Creek
	South Fork Asotin Creek
Tucannon	Snake River—Palouse River to Clearwater River (RKM 96–224)
	Tucannon River
Salmon River MPG	
Lemhi	Bohannon Creek, Lemhi River Basin
	Hayden Creek, Lemhi River Basin
	Kenney Creek, Lemhi River Basin
	Lemhi Little Springs Creek
	Lemhi River
	Lemhi River Weir
	Panther Creek (Salmon River)
	Wimpey Creek, Lemhi River Basin
Middle Fork Salmon	Bear Valley Creek
	Big Creek, Middle Fork Salmon River
	Cabin Creek, Big Creek watershed, MF Salmon River
	Camas Creek, Middle Fork Salmon River
	Loon Creek
	Lower Marsh Creek Trap at RKM 8
	Marsh Creek
	Marsh Creek Trap
	Middle Fork Salmon River—Loon Creek to headwaters (RKM 73–170)
	Monumental Creek, Big Creek watershed, MF Salmon River
	Rapid River, Middle Fork Salmon River
	Sulphur Creek, Middle Fork Salmon River
	Yellowjacket Creek, tributary of Camas Creek

Table A-1 (continued). Release sites from the PTAGIS database used to determine final steelhead tag groups from populations and major population groups (MPGs) within the Upper Columbia and Snake River distinct population segments (DPSes).

DPS, *MPG*, Population	**PTAGIS release site**
Snake River DPS (continued)	
Salmon River MPG (continued)	
South Fork Salmon	Johnson Creek Trap
	Knox Bridge, SF Salmon River
	Lake Creek
	Lick Creek
	Lower SF Salmon River Trap at RKM 61
	Secesh River
	Secesh River Screw Trap
	SF Salmon River Trap
Lower Salmon	Bargamin Creek
	Chamberlain Creek
	Horse Creek
	Little Salmon River
	Rapid River Smolt Trap
	Rapid River, Little Salmon River
	West Fork Chamberlain Creek
	Whitebird Creek
Upper Salmon	East Fork Salmon River
	Pahsimeroi River Trap
	Salmon River—Pahsimeroi River to headwaters (RKM 489–650)
	Sawtooth Trap
	Slate Creek, upper Salmon River
	Squaw Creek Acclimation Pond
	Squaw Creek, Salmon River
	West Fork Yankee Fork Salmon River
	Yankee Fork Salmon River

Table A-2. Release sites from the PTAGIS database used to determine final steelhead tag groups from populations and major population groups (MPGs) within the Middle Columbia River distinct population segment (DPS).

DPS, *MPG*, Population	**PTAGIS release site**
Middle Columbia River DPS	
Umatilla/Walla Walla MPG	
Walla Walla	Dayton Acclimation Pond
	Mill Creek, Walla Walla River
	South Fork Walla Walla River
	Touchet River
	Walla Walla River
	Yellowhawk Creek, Walla Walla River
Yakima River MPG	
Yakima	Ahtanum Creek, Yakima River
	Chandler Canal (Prosser Dam)—headgate to diversion screen (RKM 000–002)
	Natches River
	North Fork Teanaway River
	ROZ—Release into the Facility Bypass Flume/Pipe
	ROZ—Release into the tailrace within 0.5 km downstream of Dam
	Satus Creek, Yakima River
	Teanaway River
	Toppenish Creek
	Yakima River—mouth to Naches River (RKM 0–187)
	Yakima River—Naches River to headwaters (RKM 187–345)

Table A-3. List of hatcheries included, and PTAGIS sites excluded, from analysis.

Hatcheries included)	**PTAGIS release sites excluded**
Tucannon River	Wells Dam
Dworshak National Fish Hatchery	Tumwater Dam
Lolo Creek	Rock Island Dam
North Fork Clearwater River	Rocky Reach Dam
East Fork Salmon River	Priest Rapids Dam
Little Sheep Creek/Imnaha River	Wanapum Dam
Wenatchee River	McNary Dam
Wells Hatchery	Snake Trap
Winthrop National Fish Hatchery	Salmon River Trap
Omak Creek	Lower Granite Dam
Ringold	Lower Monumental Dam
	Ice Harbor Dam

Table A-4. Median yearly travel time, by DPS.

Year	BON to MCN		MCN to IHR	IHR to LWG	MCN to PRD	PRD to RIS	RIS to RRH	RRH to WEL
	Fast	Slow						
Upper Columbia DPS								
2004	29.1	7.0	6.8	6.0	6.1	3.8	n/a	n/a
2005	30.2	7.5	12.9	11.9	7.2	4.2	204.7	3.0
2006	27.4	7.8	28.0	10.6	6.2	4.1	1.7	2.9
2007	25.8	7.9	20.5	8.7	6.8	4.1	2.5	3.5
2008	19.2	8.4	n/a	n/a	6.9	4.6	2.3	5.0
2009	25.8	7.8	3.3	4.9	5.7	4.3	2.1	3.5
2010	24.7	8.1	n/a	n/a	6.9	4.6	3.0	4.3
2011	17.8	8.2	n/a	n/a	7.9	4.1	2.1	3.0
2012	20.9	8.0	n/a	n/a	7.9	4.1	2.0	3.1
2013	30.3	7.3	n/a	n/a	6.0	3.8	1.8	2.4
2014	26.6	7.1	2.0	4.1	5.8	4.4	1.8	2.7
2015	29.1	6.8	1.8	5.3	5.7	4.0	1.7	2.5
2016	27.0	6.7	n/a	n/a	5.7	4.1	1.8	3.0
Snake River DPS								
2004	39.0	7.1	2.1	6.3	n/a	n/a	n/a	n/a
2005	41.6	7.6	2.7	7.7	11.3	n/a	n/a	n/a
2006	42.3	8.0	2.8	6.9	11.7	n/a	n/a	n/a
2007	37.0	7.5	3.0	9.2	12.2	5.3	1.6	4.0
2008	32.9	8.2	2.8	8.8	19.4	16.0	22.7	3.9
2009	35.8	7.9	2.7	7.4	12.1	8.2	2.1	5.5
2010	33.2	8.0	2.8	7.3	13.8	4.2	8.3	18.7
2011	27.2	8.1	2.7	7.0	23.7	6.2	1.9	2.3
2012	31.5	8.0	3.3	7.2	30.1	7.7	2.5	2.8
2013	37.6	7.9	2.5	8.0	8.5	5.2	4.4	2.9
2014	36.4	7.9	2.7	7.9	9.9	5.1	1.1	2.1
2015	42.0	7.1	2.5	7.7	7.4	4.2	2.5	2.7
2016	38.3	7.6	2.3	7.1	18.0	6.0	2.7	5.7
Middle Columbia River DPS								
2004	63.3	7.1	5.4	4.9	10.1	n/a	n/a	n/a
2005	64.7	7.9	4.9	10.0	11.7	4.7	n/a	n/a
2006	61.0	7.7	6.1	20.1	12.0	5.9	n/a	n/a
2007	48.8	8.6	5.1	10.1	35.9	7.7	n/a	n/a
2008	70.6	8.4	5.1	18.9	17.4	6.2	2.2	n/a
2009	63.6	7.3	3.9	9.6	11.0	10.0	4.2	5.1
2010	65.8	8.9	5.2	12.5	12.0	5.9	3.1	29.0
2011	74.1	9.7	13.1	20.4	13.6	3.9	n/a	n/a
2012	70.6	8.8	49.3	10.9	n/a	n/a	n/a	n/a
2013	64.5	6.6	4.3	7.5	8.2	5.8	2.1	2.9
2014	78.3	8.1	7.1	8.5	15.8	5.5	n/a	n/a
2015	61.7	6.2	4.1	14.6	104.0	4.7	117.2	2.4
2016	69.8	7.4	6.0	10.6	10.2	8.0	3.1	5.9

Table A-5. Delta AIC for best mixture models of steelhead travel time from Bonneville Dam to McNary Dam, by MPG, in each model parameter tier. *Key to MPGs*: UC = Upper Columbia, CR = Clearwater River, GRR = Grande Ronde River, IR = Imnaha River, LSR = Lower Snake River, SR = Salmon River, UWW = Umatilla/Walla Walla, YR = Yakima River.

Model	*k*	UC	CR	GRR	IR	LSR	SR	UWW	YR
P0 + P1 + P2 + P3 + M0 + D	9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
P0 + P1 + P2 + M0 + D	8	56.2	17.1	2.9	15.5	1.1	29.6	10.7	0.0
P0 + P1 + M0 + D	7	94.9	37.2	1.1	30.1	24.8	69.4	13.6	3.0
P0 + M0 + D	6	2,662.3	587.0	345.8	1,093.2	906.7	287.4	560.8	75.4
P0 + P1 + M0	6	3,916.5	676.8	615.8	763.2	1,930.2	499.1	766.8	187.1
P0 + M0	5	4,099.0	779.1	413.9	1,302.9	997.2	327.7	668.5	105.1

Table A-6. Contingency table rates for all MPGs. Sensitivity reflects percentages of observed slow fish that were modeled as slow, specificity reflects percentages of observed fast fish that were modeled as fast.

MPG	Sensitivity (%)	Specificity (%)
Upper Columbia	60	64
Clearwater River	56	75
Grande Ronde River	58	84
Imnaha River	40	84
Lower Snake River	52	78
Salmon River	27	89
Umatilla/Walla Walla	32	91
Yakima River	52	81

Table A-7. Observed yearly mean survival of PIT-tagged steelhead from Bonneville Dam to McNary Dam (with 95% confidence intervals).

Year	Upper Columbia DPS	Snake River DPS (late)	Snake River DPS (early)	Middle Columbia River DPS
2004	0.721 (0.706–0.737)	0.756 (0.653–0.836)	0.824 (0.757–0.875)	0.810 (0.637–0.908)
2005	0.681 (0.669–0.693)	0.814 (0.708–0.888)	0.756 (0.692–0.810)	0.870 (0.758–0.931)
2006	0.728 (0.718–0.739)	0.838 (0.742–0.903)	0.779 (0.711–0.835)	0.800 (0.682–0.887)
2007	0.730 (0.703–0.755)	0.828 (0.739–0.891)	0.772 (0.740–0.801)	0.730 (0.591–0.829)
2008	0.737 (0.697–0.774)	0.793 (0.729–0.846)	0.774 (0.740–0.804)	0.770 (0.675–0.840)
2009	0.762 (0.736–0.786)	0.819 (0.783–0.851)	0.778 (0.757–0.797)	0.820 (0.764–0.872)
2010	0.786 (0.755–0.814)	0.782 (0.757–0.804)	0.760 (0.732–0.785)	0.890 (0.830–0.928)
2011	0.797 (0.770–0.822)	0.774 (0.749–0.796)	0.817 (0.792–0.840)	0.820 (0.762–0.869)
2012	0.794 (0.764–0.821)	0.783 (0.755–0.808)	0.776 (0.740–0.809)	0.870 (0.811–0.917)
2013	0.716 (0.678–0.751)	0.772 (0.731–0.809)	0.723 (0.690–0.754)	0.710 (0.615–0.788)
2014	0.771 (0.737–0.802)	0.783 (0.753–0.809)	0.760 (0.731–0.786)	0.790 (0.718–0.848)
2015	0.799 (0.767–0.828)	0.856 (0.826–0.882)	0.762 (0.733–0.789)	0.780 (0.701–0.837)
2016	0.729 (0.668–0.783)	0.820 (0.789–0.847)	0.692 (0.643–0.737)	0.770 (0.668–0.851)

Table A-8. Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
BON	**Upper Columbia**			
	2004	3,114	100	109
	2005	5,488	126	131
	2006	6,622	292	304
	2007	1,104	67	70
	2008	497	30	30
	2009	1,086	49	50
	2010	740	41	42
	2011	919	75	82
	2012	749	56	68
	2013	576	41	43
	2014	635	30	32
	2015	669	27	29
	2016	231	8	8
	Snake River			
	2004	224	14	16
	2005	264	14	21
	2006	246	16	23
	2007	792	54	58
	2008	829	49	51
	2009	2,165	109	118
	2010	2,145	113	124
	2011	2,197	170	186
	2012	1,439	124	147
	2013	1,165	87	102
	2014	1,742	105	121
	2015	1,469	98	107
	2016	1,001	48	52
	Middle Columbia River			
	2004	29	6	6
	2005	59	0	0
	2006	55	7	7
	2007	51	6	9
	2008	99	8	10
	2009	186	9	9
	2010	160	13	13
	2011	196	15	16
	2012	147	14	15
	2013	102	6	6
	2014	147	8	10
	2015	141	9	9
	2016	77	4	5

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
TDA	**Upper Columbia**			
	2012	7	0	0
	2013	472	18	20
	2014	554	10	10
	2015	578	9	9
	2016	197	1	1
	Snake River			
	2012	10	2	2
	2013	994	48	63
	2014	1,538	62	82
	2015	1,334	71	110
	2016	903	29	33
	Middle Columbia River			
	2012	0	0	0
	2013	83	1	1
	2014	126	2	2
	2015	119	2	2
	2016	66	0	0

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
MCN	**Upper Columbia**			
	2004	2,352	132	138
	2005	3,771	239	251
	2006	4,855	326	335
	2007	810	62	65
	2008	369	34	35
	2009	832	43	45
	2010	584	58	63
	2011	739	49	50
	2012	605	66	70
	2013	416	30	33
	2014	496	23	23
	2015	543	19	19
	2016	169	7	7
	Snake River			
	2004	193	13	14
	2005	209	21	24
	2006	201	29	43
	2007	622	99	139
	2008	652	93	103
	2009	1,710	160	190
	2010	1,669	151	176
	2011	1,769	156	181
	2012	1,137	135	148
	2013	870	67	81
	2014	1,360	110	119
	2015	1,189	60	64
	2016	801	47	51
	Middle Columbia River			
	2004	25	1	1
	2005	52	2	2
	2006	45	5	5
	2007	37	2	2
	2008	76	6	7
	2009	155	12	12
	2010	143	19	20
	2011	161	24	25
	2012	131	15	16
	2013	73	6	6
	2014	117	5	5
	2015	111	3	4
	2016	60	1	1

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	**DPS**, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
IHR	**Upper Columbia**			
	2004	13	2	3
	2005	20	2	2
	2006	33	3	3
	2007	3	0	0
	2008	0	0	0
	2009	1	0	0
	2010	0	0	0
	2011	0	0	0
	2012	0	0	0
	2013	0	0	0
	2014	1	0	0
	2015	2	0	0
	2016	0	0	0
	Snake River			
	2004	194	5	7
	2005	204	11	11
	2006	181	3	3
	2007	544	43	54
	2008	612	36	39
	2009	1,600	63	70
	2010	1,593	80	88
	2011	1,714	73	80
	2012	1,078	30	31
	2013	840	59	83
	2014	1,312	36	41
	2015	1,134	42	46
	2016	769	12	12
	Middle Columbia River			
	2004	5	0	0
	2005	17	2	2
	2006	17	0	0
	2007	15	0	0
	2008	32	2	2
	2009	63	8	8
	2010	63	3	3
	2011	61	7	12
	2012	40	4	4
	2013	17	3	4
	2014	37	5	6
	2015	51	2	2
	2016	27	1	2

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
LWG	**Upper Columbia**			
	2004	3	0	0
	2005	6	2	2
	2006	6	1	1
	2007	1	0	0
	2008	0	0	0
	2009	1	0	0
	2010	0	0	0
	2011	0	0	0
	2012	0	0	0
	2013	0	0	0
	2014	1	1	1
	2015	2	1	1
	2016	0	0	0
	Snake River			
	2004	206	25	30
	2005	180	38	53
	2006	154	25	37
	2007	420	119	177
	2008	473	101	138
	2009	1,389	238	289
	2010	1,445	244	282
	2011	1,530	298	344
	2012	988	124	137
	2013	765	147	183
	2014	1,203	203	237
	2015	1,070	209	219
	2016	714	244	253
	Middle Columbia River			
	2004	2	0	0
	2005	4	0	0
	2006	5	1	1
	2007	5	2	2
	2008	9	0	0
	2009	29	6	11
	2010	24	6	7
	2011	17	3	3
	2012	16	5	6
	2013	5	0	0
	2014	12	6	6
	2015	12	1	1
	2016	12	1	1

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
PRD	**Upper Columbia**			
	2004	1,182	11	11
	2005	2,455	33	33
	2006	3,516	76	78
	2007	703	21	22
	2008	369	17	17
	2009	826	31	31
	2010	577	22	23
	2011	736	25	26
	2012	609	31	37
	2013	418	22	22
	2014	493	29	34
	2015	533	19	20
	2016	168	4	7
	Snake River			
	2004	0	0	0
	2005	2	0	0
	2006	3	0	0
	2007	21	2	2
	2008	6	0	0
	2009	40	1	1
	2010	18	0	0
	2011	20	2	2
	2012	15	2	2
	2013	31	1	2
	2014	30	0	0
	2015	14	0	0
	2016	6	1	1
	Middle Columbia River			
	2004	1	0	0
	2005	4	0	0
	2006	3	0	0
	2007	2	0	0
	2008	6	1	1
	2009	7	1	1
	2010	8	1	1
	2011	4	0	0
	2012	0	0	0
	2013	5	0	0
	2014	7	0	0
	2015	5	0	0
	2016	4	0	0

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
RIS	**Upper Columbia**			
	2004	835	10	11
	2005	1,735	41	46
	2006	2,688	62	70
	2007	617	17	19
	2008	299	6	6
	2009	807	23	24
	2010	561	32	36
	2011	691	16	16
	2012	471	10	10
	2013	379	6	10
	2014	318	2	2
	2015	508	1	1
	2016	160	2	3
	Snake River			
	2004	0	0	0
	2005	0	0	0
	2006	0	0	0
	2007	8	1	1
	2008	2	0	0
	2009	19	3	3
	2010	7	0	0
	2011	14	2	2
	2012	6	1	1
	2013	17	3	3
	2014	13	1	1
	2015	8	0	0
	2016	3	0	0
	Middle Columbia River			
	2004	0	0	0
	2005	2	0	0
	2006	1	0	0
	2007	1	0	0
	2008	2	0	0
	2009	3	0	0
	2010	5	0	0
	2011	1	0	0
	2012	0	0	0
	2013	4	0	0
	2014	3	1	1
	2015	2	0	0
	2016	1	0	0

Table A-8 (continued). Fallback counts for steelhead at Columbia and Snake River dams, 2004–16.

Dam	DPS, Year	Number of fish detected at BON	Total number of fish that fell back	Total number of fallback events
RRH	**Upper Columbia**			
	2005	40	5	5
	2006	3,046	70	78
	2007	604	23	24
	2008	311	38	41
	2009	622	39	46
	2010	447	42	52
	2011	596	43	59
	2012	478	13	14
	2013	303	6	6
	2014	343	1	1
	2015	421	1	1
	2016	152	2	4
	Snake River			
	2005	0	0	0
	2006	0	0	0
	2007	7	0	0
	2008	1	0	0
	2009	15	0	0
	2010	6	0	0
	2011	8	0	0
	2012	4	0	0
	2013	11	0	1
	2014	12	0	1
	2015	6	0	0
	2016	3	0	0
	Middle Columbia River			
	2005	0	0	0
	2006	0	0	0
	2007	0	0	0
	2008	1	0	0
	2009	3	0	0
	2010	4	0	0
	2011	0	0	0
	2012	0	0	0
	2013	1	0	1
	2014	1	0	1
	2015	1	0	0
	2016	1	0	0

Appendix B: Supplemental Figures

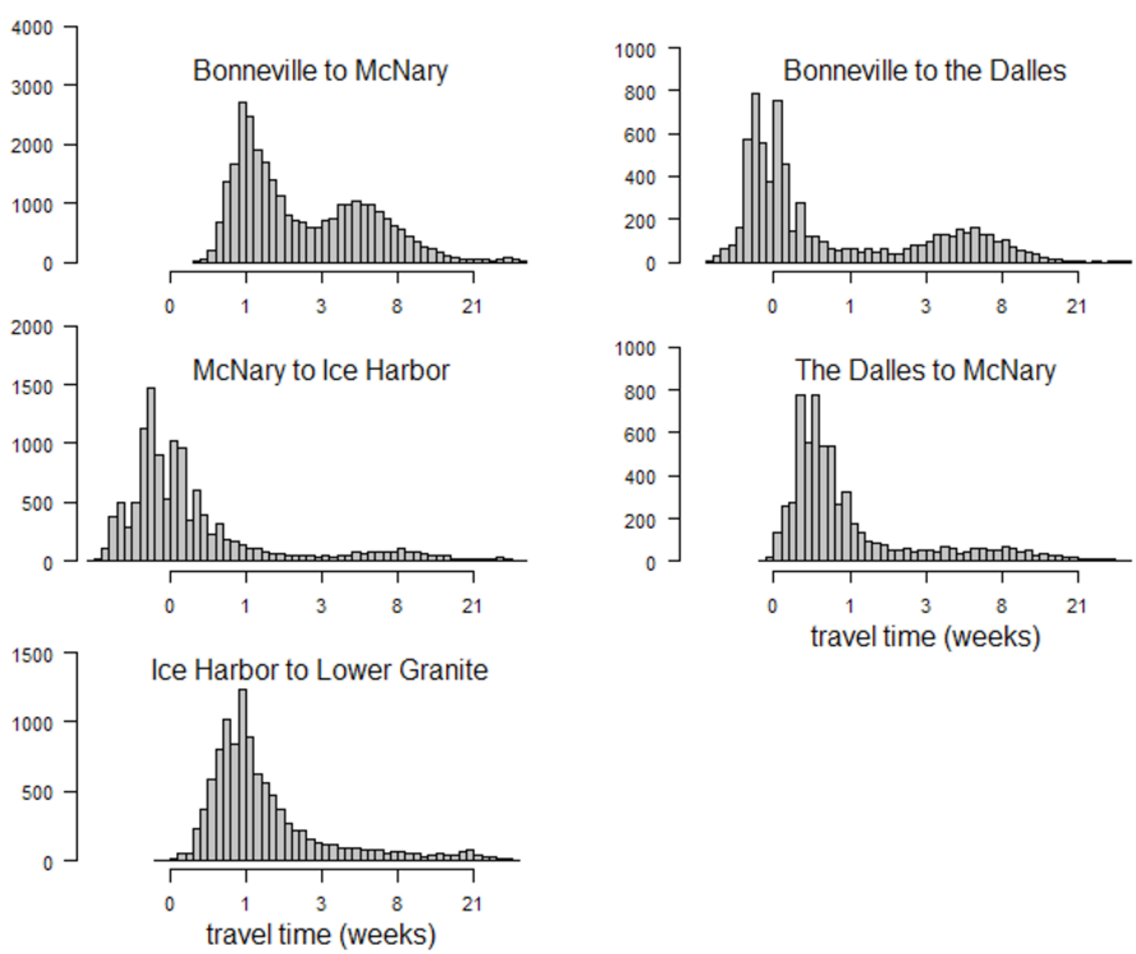


Figure B-1. Histograms of travel time (in weeks) over reaches in the Columbia and Snake Rivers for Snake River steelhead. X-axis is on a log scale.

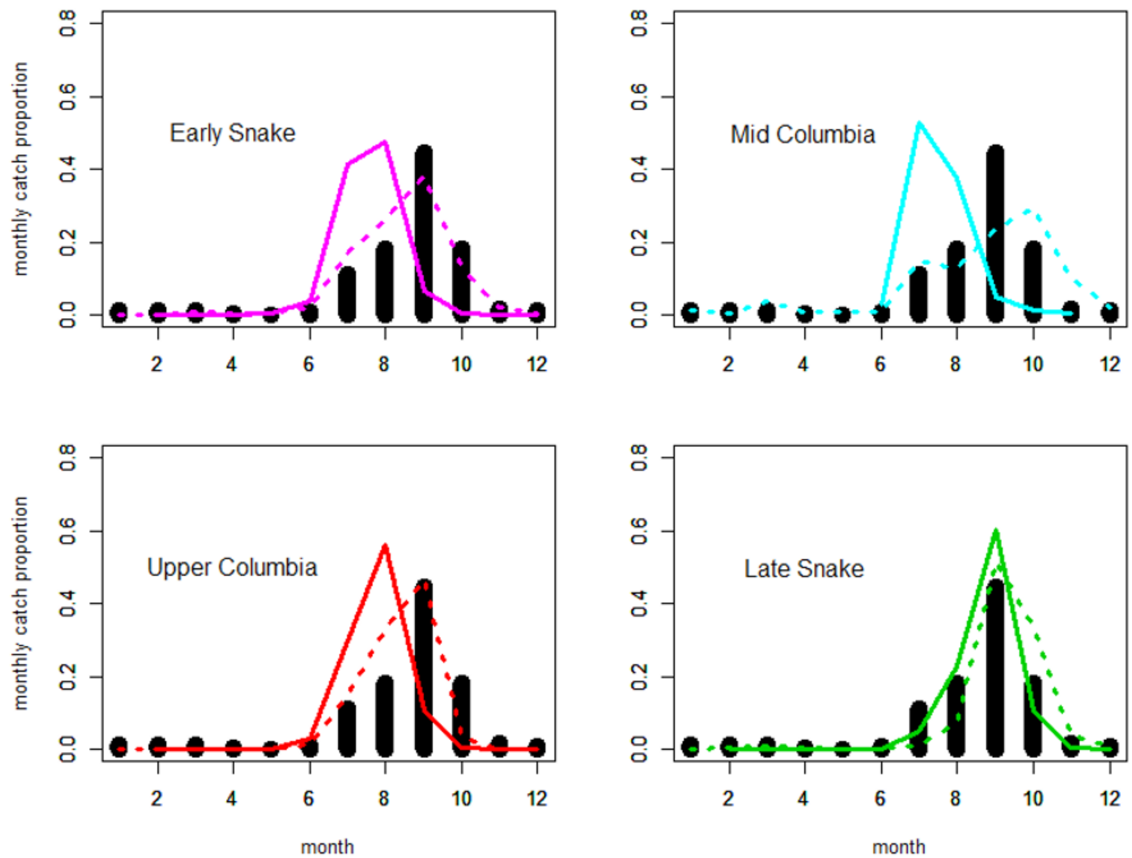


Figure B-2. Monthly average proportion of PIT-tagged steelhead arrivals at Bonneville Dam (solid lines) and McNary Dam (dotted lines), and monthly averaged catch proportions (black bars).

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163 **Jannot, J. E., K. E. Richerson, K. A. Somers, V. J. Tuttle, R. S. Shama, and J. T. McVeigh. 2021.** Pacific Halibut Bycatch in U.S. West Coast Groundfish Fisheries, 2002–19. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-163. https://doi.org/10.25923/8y03-z703

162 **Sol, S. Y., B. Anulacion, D. P. Lomax, P. Chittaro, P. Moran, G. M. Ylitalo, A. Hanson, C. Corbett, and L. L. Johnson. 2021.** Juvenile Salmon Ecology in Tidal Freshwater Wetlands in the Lower Columbia River Estuary. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-162. https://doi.org/10.25923/2bfz-ah24

161 **Clarke, M. E., E. L. Fruh, A. Powell, J. Anderson, J. C. Taylor, and C. E. Whitmire. 2020.** Autonomous Underwater Vehicle (AUV) Survey at The Footprint and Piggy Bank in the Southern California Bight, 2011. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-161. https://doi.org/10.25923/mfq8-6773

160 **Harvey, C., N. Garfield, G. Williams, N. Tolimieri, K. Andrews, K. Barnas, E. Bjorkstedt, S. Bograd, J. Borchert, C. Braby, R. Brodeur, B. Burke, J. Cope, A. Coyne, D. Demer, L. deWitt, J. Field, J. Fisher, P. Frey, T. Good, C. Grant, C. Greene, E. Hazen, D. Holland, M. Hunter, K. Jacobson, M. Jacox, J. Jahncke, C. Juhasz, I. Kaplan, S. Kasperski, S. Kim, D. Lawson, A. Leising, A. Manderson, N. Mantua, S. Melin, R. Miller, S. Moore, C. Morgan, B. Muhling, S. Munsch, K. Norman, J. Parrish, A. Phillips, R. Robertson, D. Rudnick, K. Sakuma, J. Samhouri, J. Santora, I. Schroeder, S. Siedlecki, K. Somers, B. Stanton, K. Stierhoff, W. Sydeman, A. Thompson, D. Trong, P. Warzybok, B. Wells, C. Whitmire, M. Williams, T. Williams, J. Zamon, S. Zeman, V. Zubkousky-White, and J. Zwolinski. 2020.** Ecosystem Status Report of the California Current for 2019–20: A Summary of Ecosystem Indicators Compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-160. https://doi.org/10.25923/e5rb-9f55

159 **Hartley, M. L., D. M. Schug, K. F. Wellman, B. Lane, W. T. Fairgrieve, and J. A. Luckenbach. 2020.** Sablefish Aquaculture: An Assessment of Recent Developments and Their Potential for Enhancing Profitability. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-159. https://doi.org/10.25923/cb0y-n468

158 **Richerson, K. E., J. E. Jannot, Y.-W. Lee, J. T. McVeigh, K. A. Somers, V. J. Tuttle, and S. Wang. 2020.** Observed and Estimated Bycatch of Green Sturgeon in 2002–17 U.S. West Coast Groundfish Fisheries. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-158. https://doi.org/10.25923/sn5z-w384

157 **Holland, D. S. 2020.** An Analysis of the Pacific Groundfish Trawl Individual Fishing Quota (IFQ) Quota Pound (QP) Market Through 2019. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-157. https://doi.org/10.25923/sxdw-kb49

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