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A Bayesian multidirectional, multistate model to resolve the migration pathways of adult Steelhead within the Columbia River Basin

Markus Min

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Contents

Introduction	2
Methods	4
Modeling overview	4
Accessing PIT tag data	4
Processing PIT tag data into detections at various sites	5
Turning detections at different sites into state visits	6
The model in stan	6
Results	8
Middle Columbia River Steelhead	8
Upper Columbia River Steelhead	15
Snake River Basin Steelhead	18
Discussion	24
Current limitations and next steps	24
Detection probabilties in tributaries	24
Detection probabilities in downstream passage routes	24
Final fates	25
Adding additional covariates	25
References	26

Introduction

Most populations of Steelhead (anadromous *Oncorhynchus mykiss*) in the Columbia River Basin, including all that are found above Bonneville Dam, are listed under the Endangered Species Act. The five Columbia River Basin distinct population segments (DPSs) were first listed in the late 1990s, and are all currently listed as threatened. Despite their protected status and continued recovery efforts, counts of returning Steelhead to Bonneville Dam are currently lower than they were at the time of listing, and recently completed 5-year reviews for Columbia River Steelhead reaffirmed their status as threatened.

One element of the life history of Columbia River Basin Steelhead that may make them more vulnerable to anthropogenic modifications of the Columbia River is their adult migration. Relative to other salmonids, Steelhead from the Columbia River Basin spend longer in freshwater as adults. Essentially all populations of Steelhead in the Columbia River Basin are stream-maturing (Busby et al. 1996), meaning that these fish enter freshwater in a sexually immature state and then spend up to a year in freshwater prior to spawning. Also known as summer Steelhead, these fish enter freshwater between May and October and spawn the following spring, typically between March and May (Busby et al. 1996). Between their entry into freshwater and arrival at spawning grounds, Columbia River Steelhead exhibit considerable variability in their migration patterns. Virtually all interior Columbia River Steelhead overwinter in freshwater; the majority of individuals are known to overwinter in tributaries, but up to 20% of individuals in a given year have been observed to overwinter within the hydrosystem (Keefer et al. 2008). Additionally, as individuals migrate upstream toward natal tributaries, the majority of individuals have been observed to temporarily stage in nonnatal tributaries downstream of their natal tributary (High et al. 2006). This behavior increases with increasing mainstem river temperature, indicating the use of these colder waters as coldwater refugia (High et al. 2006). These highly variable movement patterns and increased duration in freshwater make Steelhead more vulnerable to the hazards faced in freshwater.

Descending dams, also known as fallback (Boggs et al. 2004), is another common behavior observed in Steelhead, with about 20% of Steelhead observed to fall back over at at least one mainstem dam (Boggs et al. 2004). This behavior can occur as individuals are migrating upstream to natal tributaries, but can also occur once individuals have ascended mainstem dams upstream of natal tributaries (a behavior known as overshoot), in which case this fallback is called post-overshoot fallback and is necessary for individuals to return to natal tributaries. Overshoot and fallback are consequential for the ability of individuals to successfully spawn, and therefore are consequential for the persistence of ESA-listed populations. Individuals that fall back during their upstream migration have been observed to have lower escapement rates (rates of successful spawning) to tributaries or hatcheries (Bjornn et al. 2000; Keefer et al. 2005). Furthermore, migration success to natal tributaries decreases with overshooting rates (Richins and Skalski 2018), and many overshooting fish are observed to stray to tributaries upstream of the overshoot dam. The decreased migration success with overshoot and fallback is likely due to the hazardous nature of downstream passage for adults, which is often limited to the powerhouse during the primary months that Steelhead are overwintering (Khan et al. 2013). Mortality rates for Steelhead passing downstream at dams are highly variable, but recent estimates of 48-hour survival at McNary Dam indicate around 10% mortality for individuals passing through turbines and 3% mortality for individuals passing through the spillway (Normandeau Associates 2014). Mortality in downstream passage routes is implicated by low survival rates of Steelhead kelts, which decrease with increasing number of dams that must be navigated as they move downstream to the ocean, with mortality rates of 84-96% for kelts released at Lower Granite Dam, 38-40% at McNary Dam, and

20-37% at John Day Dam (Wertheimer and Evans 2005).

Because of the association between overshoot and fallback and decreased migration success, previous studies have investigated the influence of various factors on these rates. Rates of overshoot have been shown to vary considerably among populations, but have a positive relationship with increasing mainstem water temperature and hatchery rearing upstream of the natal tributary (Richins and Skalski 2018). In spring-summer Chinook, fallback rates have a positive relationship with river discharge (Boggs et al. 2004). However, these previous studies have looked at these various factors only in isolation and for specific movements. In this study, we developed a multistate model that is capable of modeling the entire adult Steelhead migration, from first detection at Bonneville Dam to arrival in natal tributaries. The data used in this model were passive integrated transponder (PIT) tag detection histories. This modeling framework accommodates the effect of multiple categorical and continuous covariates at movement probabilities at each step within the migration. By examining how Steelhead movement probabilities, particularly those of conservation concern, such as overshoot, fallback, homing, and straying, vary by population and are influenced by various factors, this modeling framework will improve our understanding of how both environmental and anthropogenically influenced conditions affect how Steelhead move within the Columbia River and its tributaries.



Methods

Modeling overview

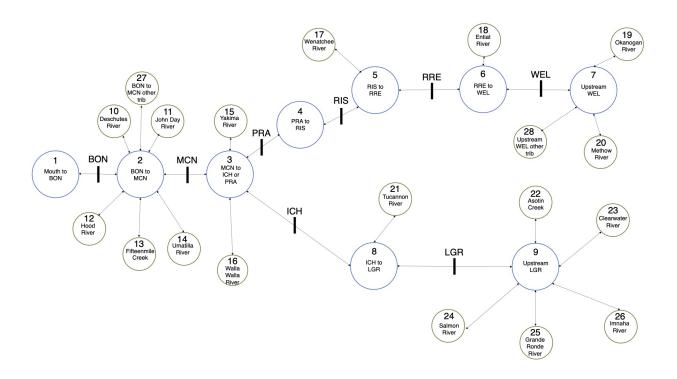


Figure 1: The model schematic.

In our model, the Columbia River and its tributaries are modeled as a series of connected states, with states defined as either reaches of the mainstem Columbia or Snake River between dams with PIT tag detection capabilities in the adult ladders or tributaries with PIT tag detectors. Fig. 1 shows all of the states in our model; movements over some dams (e.g., The Dalles or John Day Dams) were not explicitly modeled due to these dams not having PIT tag detection capabilities for the duration of our study period.

Accessing PIT tag data

PIT tag data was accessed through the Columbia Basin PIT Tag Information System (PTAGIS). Only known-origin individuals (based on known release sites) were included in this dataset. To ensure that only individuals marked as juveniles were kept in the dataset, all individuals that were greater than 350 mm

at time of marking were removed from the dataset. To select returning adults, only individuals that were seen in the adult fishways at Bonneville Dam were selected. To ensure that there was enough data for each population included in this dataset, only populations (defined as tributaries in which PIT-tagged juveniles were released) that had at least 250 individuals distributed across 8 run years were kept. Additionally, only populations with instream PIT tag detections sites in their natal tributaries were kept; if sufficient instream detection sites only became available during the later part of our study period, only individuals from those years were kept. Run years were separated by June 1 of each year, and run year 2005/2006 (beginning on June 1, 2005) was selected as the first year in our dataset. In total, populations from 17 natal tributaries met this criteria; 11 tributaries of the Columbia (Deschutes River, John Day River, Hood River, Fifteenmile Creek, Umatilla River, Yakima River, Walla Walla River, Wenatchee River, Entiat River, Okanogan River, and Methow River) and six tributaries of the Snake (Tucannon River, Asotin Creek, Clearwater River, Salmon River, Grande Ronde River, and Imnaha River). Once the tag codes were identified for each of these tributary populations, a complete tag history report was run in PTAGIS for all of the tag codes in our dataset.

Processing PIT tag data into detections at various sites

In order to convert detections of fish at individual PIT tag antennas into a history of movements between different reaches of the Columbia, Snake, and their tributaries, the first step with the PIT tag data from PTAGIS was to interpret detections at different PIT tag antennas. For instream tributary detection sites, as well as mainstem sites in between dams, no processing was required, and these detections were interpreted as the fish being in that associated state. For detection sites at dams, additional processing was required to interpret detections.

The first step in interpreting detections at dams was to identify the multiple passage routes associated with each dam. In many cases, multiple passage routes were grouped together into a single interrogation site, and assigning antennas to these different passage routes was necessary to interpret how fish were utilizing these passage routes. For example, antennas at Ice Harbor Dam are all grouped together in PTAGIS as "Ice Harbor Dam (combined)", when these antennas are actually in three different passage routes: the North Shore Ladder, the South Shore Ladder, and the Juvenile Bypass System.

The second step was to identify, when possible, entrance and exit antennas within each upstream passage route. Entrance and exit antennas were only distinguished when either two distinct groupings of antennas existed in separate parts of the same passage route, or in the case of Bonneville Dam, when there are enough consecutive weirs with PIT tag detection antennas to separate these weirs into entrance and exit antennas. By distinguishing entrance and exit antennas, we were able to identify when fish detections in adult fishways were not ascents, but were rather aborted ascent attempts or descents. When fish were only seen at entrance antennas, this was noted to be an aborted ascension attempt. When fish were first seen at the exit antennas at an adult fish ladder and last seen at the entrance antennas of the same fish ladder, this was noted to be a descent through the ladder. If a fish was first seen at the entrance antennas and last seen at the exit antennas, this was noted to be an ascent. Entrance and exit antennas were identified at all adult fishways except for McNary Dam Washington Shore Ladder (prior to March 2006), Priest Rapids Dam, Rock Island Dam, Rocky Reach Dam, Wells Dam (prior to 2013), and Ice Harbor Dam.

An additional step was to identify antennas in adult fish facilities/traps at ladders. For most dams, detections in the adult fish facility were treated the same as detections in other parts of the adult ladder, as trapping did not take place and thus fish were not removed. However, in the case of Wells Dam, fish that were trapped were removed and either moved to the hatchery or trucked off-site. As such, any terminal detections in the trap at Wells Dam were treated as trapping events.

Once the antennas had been appropriately assigned, a 48 hour threshold was utilized to distinguish separate visits to a site. However, in some passage routes, due to fish being observed in the same route for days at a time, no time threshold was utilized, and instead the sequence of antennas was used to distinguish separate visits to a site. For example, because individual fish were observed not exiting the Washington shore passage

route at Bonneville Dam for upwards of 100 days, new visits to this site were only distinguished as new visits to the entrance antennas, regardless of time between detections at other antennas in the passage route.

Turning detections at different sites into state visits

With antennas appropriately assigned to different passage routes and the sequence of antenna detections used at the adult fishways to interpret directionality, the output from the previous script was used as input into the next script, which converted a history of detections at sites into a history of movements between states, as defined in Figure 1. For instream detection sites in either the mainstem or the tributaries, detections at these sites were interpreted as the fish being in the appropriate state. For detections at sites in the fish passage routes at dams, the directionality of movement, as assigned in the previous script, was used to inform transitions between states. Ascents at dams indicated a transition from the downstream state to the upstream state; descents at dams (either through the juvenile bypass system or through descents through the ladder) indicated a transition from the upstream state to the downstream state. Aborted ascension attempts were noted, but interpreted as no transition from the current state.

Until the installation of the PIT tag antennas in the spillway at Lower Granite Dam in 2020, PIT tag detection capabilities at dams have been limited to the adult fish ladders and the juvenile bypass system. As such, PIT tag antennas have historically been unable to directly monitor fallback at dams, unless an individual subsequently reascends the dam (Boggs et al. 2004). With the installation of instream antennas in natal tributaries, fallback to home has been monitored (Richins and Skalski 2018) by noting when individuals entered natal tributaries downstream of a dam that was previously ascended. In this study, we monitored fallback to the greatest extent possible with the current configuration of PIT tag antennas by using our knowledge of the connections between states in our model to note when downstream movements must have occurred. For example, consecutive ascents at the same dam indicated a fallback event between these ascensions, and detections at sites downstream of a dam that was previously ascended indicated a fallback event between these two detections. In this way, we included fallback that occurred on the mainstem downstream of the natal tributary (similar to (Boggs et al. 2004)), fallback to home (similar to (Richins and Skalski 2018)), and other fallback movements, such as fallback upstream of the natal tributary that did not end in homing.

Once we determined a history of movement between states, we then subset this movement history to eliminate any movement that occurred as a juvenile or as a kelt in order to isolate only the portion of the adult migration prior to reaching spawning areas. Juvenile history was identified as any detections within 90 days of release or on or before June 15 of the release year. Kelt movement was identified as any downstream movement occurring between March and July (following spawning). Repeat spawners were also identified in the dataset based on detections at the Bonneville adult ladders occurring at least 180 days after they were initially seen at Bonneville. For the purposes of our analysis, repeat spawners were treated as new fish when they returned to Bonneville.

The model in stan

The history of state transitions for each in the dual PIT-tagged fish, as well as the information on that fish's natal origin, were the inputs for the multistate model. The multistate model was implemented in a Bayesian framework in Stan (Carpenter et al. 2017). The multistate model is constructed as a series of states, defined as either reaches of the mainstem Columbia or Snake Rivers between dams with active PIT tag antennas for the duration of our study period or tributaries that flow into the Columbia or Snake Rivers (Fig. 1). All fish in our model begin when they are first detected as adults in the fish ladders at Bonneville Dam. At each state in our model, each fish is assigned a probability of moving to any of the states connected to the current states, or into the absorbing loss category, which a fish enters once the detection history ends. Each of these probabilities is evaluated through a multinomial logit, with the loss probability calculated as 1 - the sum of the other probabilities, enforcing a constraint that all movement probabilities have to sum to 1.

Due to the computational requirements of evaluating the detection histories of over 60,000 individual fish, the model was fit to three different datasets, corresponding to the three Steelhead DPSs found exclusively upstream of Bonneville Dam: the Middle Columbia DPS, the Upper Columbia DPS, and the Snake River Basin DPS. To reduce the number of parameters in the model, an effect of natal origin was only included for state transitions into or out of states within the DPS boundaries, whereas for states outside of the DPS, all origins shared a common movement probability. This model structure allowed different natal origins to differentiate as they neared natal tributaries.

All code is available at https://github.com/markusmin/steelhead.

Results

A total of 662 different movement probabilities, based on the combination of state transition and origin/DPS, were estimated by the model (Tables 1-6). The model schematic in Fig. 1 is necessary to interpret the ecological significance of these movement probabilities, in terms of which movements constitute the probabilities of certain movements, such as overshoot, fallback, homing, or straying. Furthermore, each movement probability represents only the probability of an individual making that movement conditional on it already being in the "from" state. Due to poor detection probabilities in tributaries and in downstream passage routes, only overshoot probabilities (which have near 100% detection probability) are discussed in the Results; see Current Limitations for a discussion of these issues and future directions to address them. Overshoot probabilities, or the probability of ascending the dam upstream of the natal tributary in the model schematic (Fig. 1), varied considerably by natal origin.

Middle Columbia River Steelhead

Of the natal tributaries downstream of McNary Dam, John Day River and Umatilla River Steelhead each had a high mean probability of overshooting McNary Dam (46.4% and 33.8%, respectively; Table 2), while Deschutes River and Fifteenmile Creek Steelhead had a low mean probability (0.7% and 9%, respectively; Table 2). Conditional on overshooting McNary Dam, John Day River and Umatilla River Steelhead had an approximately 20% chance of additionally overshooting Ice Harbor Dam on the Snake River, but only a very low probability of overshooting Priest Rapids Dam on the Columbia River (Table 2). For Yakima River and Walla Walla River Steelhead, whose natal tributaries are upstream of McNary Dam, Yakima River Steelhead were more likely to overshoot Priest Rapids Dam (13.8% mean probability) than Ice Harbor Dam (3.5% mean probability) whereas Wallla Walla River Steelhead were much more likely to overshoot Ice Harbor Dam (57.4% mean probability) than Priest Rapids Dam (2% mean probability) (Table 2).

Table 1: Movement probabilities for Middle Columbia Steelhead, outside of the DPS boundaries.

from	to	mean	q5	q95
mainstem, RIS to RRE	mainstem, PRA to RIS	0.384	0.328	0.443
mainstem, RIS to RRE	mainstem, RRE to WEL	0.390	0.330	0.446
mainstem, RIS to RRE	Wenatchee River	0.041	0.013	0.080
mainstem, RIS to RRE	loss	0.185	0.133	0.252
mainstem, RRE to WEL	mainstem, RIS to RRE	0.304	0.189	0.426
mainstem, RRE to WEL	mainstem, upstream of WEL	0.428	0.319	0.551
mainstem, RRE to WEL	Entiat River	0.021	0.001	0.067
mainstem, RRE to WEL	loss	0.247	0.136	0.373
mainstem, upstream of WEL	mainstem, RRE to WEL	0.437	0.272	0.581
mainstem, upstream of WEL	Okanogan River	0.044	0.003	0.152
mainstem, upstream of WEL	Methow River	0.130	0.034	0.260
mainstem, upstream of WEL	loss	0.388	0.232	0.545

Table 1: Movement probabilities for Middle Columbia Steelhead, outside of the DPS boundaries. (continued)

from	to	mean	q5	q95
mainstem, upstream of LGR	mainstem, ICH to LGR	0.380	0.359	0.403
mainstem, upstream of LGR	Asotin Creek	0.012	0.007	0.018
mainstem, upstream of LGR	Clearwater River	0.018	0.011	0.026
mainstem, upstream of LGR	Salmon River	0.002	0.000	0.005
mainstem, upstream of LGR	Grande Ronde River	0.016	0.010	0.023
mainstem, upstream of LGR	Imnaha River	0.003	0.001	0.007
mainstem, upstream of LGR	loss	0.569	0.543	0.590
Wenatchee River	mainstem, RIS to RRE	0.511	0.168	0.864
Wenatchee River	loss	0.489	0.136	0.832
Entiat River	mainstem, RRE to WEL	0.069	0.000	0.522
Entiat River	loss	0.931	0.478	1.000
Okanogan River	mainstem, upstream of WEL	0.087	0.000	0.618
Okanogan River	loss	0.913	0.382	1.000
Methow River	mainstem, upstream of WEL	0.661	0.240	0.962
Methow River	loss	0.339	0.038	0.760
Tucannon River	mainstem, ICH to LGR	0.096	0.067	0.127
Tucannon River	loss	0.904	0.873	0.933
Asotin Creek	mainstem, upstream of LGR	0.010	0.000	0.049
Asotin Creek	loss	0.990	0.951	1.000
Clearwater River	mainstem, upstream of LGR	0.068	0.002	0.224
Clearwater River	loss	0.932	0.776	0.998
Salmon River	mainstem, upstream of LGR	0.039	0.000	0.287
Salmon River	loss	0.961	0.713	1.000
Grande Ronde River	mainstem, upstream of LGR	0.007	0.000	0.037
Grande Ronde River	loss	0.993	0.963	1.000
Imnaha River	mainstem, upstream of LGR	0.028	0.000	0.180
Imnaha River	loss	0.972	0.820	1.000

Table 2: Movement probabilities for Middle Columbia Steelhead by natal origin, inside the DPS boundaries.

origin	from	to	mean	q5	q95
Deschutes River	mainstem, mouth to BON	mainstem, BON to MCN	0.916	0.795	0.989
Fifteenmile Creek	mainstem, mouth to BON	mainstem, BON to MCN	0.994	0.957	1.000
John Day River	mainstem, mouth to BON	mainstem, BON to MCN	0.962	0.914	0.994
Umatilla River	mainstem, mouth to BON	mainstem, BON to MCN	0.958	0.900	0.994
Yakima River	mainstem, mouth to BON	mainstem, BON to MCN	0.996	0.985	1.000
Walla Walla River	mainstem, mouth to BON	mainstem, BON to MCN	0.972	0.943	0.994
Deschutes River	mainstem, mouth to BON	loss	0.084	0.011	0.205
Fifteenmile Creek	mainstem, mouth to BON	loss	0.006	0.000	0.043
John Day River	mainstem, mouth to BON	loss	0.038	0.006	0.086
Umatilla River	mainstem, mouth to BON	loss	0.042	0.006	0.100
Yakima River	mainstem, mouth to BON	loss	0.004	0.000	0.015
Walla Walla River	mainstem, mouth to BON	loss	0.028	0.006	0.057
Deschutes River Fifteenmile Creek John Day River	mainstem, BON to MCN mainstem, BON to MCN mainstem, BON to MCN	mainstem, mouth to BON mainstem, mouth to BON mainstem, mouth to BON	0.016 0.011 0.008	0.010 0.005 0.006	0.023 0.020 0.012

Table 2: Movement probabilities for Middle Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Umatilla River	mainstem, BON to MCN	mainstem, mouth to BON	0.008	0.006	0.011
Yakima River	mainstem, BON to MCN	mainstem, mouth to BON	0.007	0.003	0.011
Walla Walla River	mainstem, BON to MCN	mainstem, mouth to BON	0.016	0.013	0.019
Deschutes River	mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.007	0.003	0.012
Fifteenmile Creek	mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.090	0.075	0.109
John Day River	mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.464	0.452	0.476
Umatilla River	mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.338	0.323	0.352
Yakima River	mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.759	0.731	0.787
Walla Walla River	mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.781	0.768	0.793
Deschutes River	mainstem, BON to MCN	Deschutes River	0.366	0.342	0.389
Fifteenmile Creek	mainstem, BON to MCN	Deschutes River	0.136	0.112	0.167
John Day River	mainstem, BON to MCN	Deschutes River	0.041	0.036	0.045
Umatilla River	mainstem, BON to MCN	Deschutes River	0.062	0.055	0.070
Yakima River	mainstem, BON to MCN	Deschutes River	0.059	0.045	0.073
Walla Walla River	mainstem, BON to MCN	Deschutes River	0.027	0.024	0.032
Deschutes River	mainstem, BON to MCN	John Day River	0.001	0.000	0.003
Fifteenmile Creek	mainstem, BON to MCN	John Day River	0.006	0.002	0.012
John Day River	mainstem, BON to MCN	John Day River	0.238	0.227	0.248
Umatilla River	mainstem, BON to MCN	John Day River	0.000	0.000	0.001
Yakima River	mainstem, BON to MCN	John Day River	0.000	0.000	0.001
Walla Walla River	mainstem, BON to MCN	John Day River	0.000	0.000	0.000
Deschutes River	mainstem, BON to MCN	Hood River	0.003	0.001	0.006
Fifteenmile Creek	mainstem, BON to MCN	Hood River	0.000	0.000	0.001
John Day River	mainstem, BON to MCN	Hood River	0.001	0.000	0.001
Umatilla River	mainstem, BON to MCN	Hood River	0.003	0.001	0.005
Yakima River	mainstem, BON to MCN	Hood River	0.000	0.000	0.001
Walla Walla River	mainstem, BON to MCN	Hood River	0.000	0.000	0.000
Deschutes River	mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
Fifteenmile Creek	mainstem, BON to MCN	Fifteenmile Creek	0.218	0.190	0.248
John Day River	mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
Umatilla River	mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
Yakima River	mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
Walla Walla River	mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
Deschutes River	mainstem, BON to MCN	Umatilla River	0.000	0.000	0.000
Fifteenmile Creek	mainstem, BON to MCN	Umatilla River	0.002	0.000	0.005
John Day River	mainstem, BON to MCN	Umatilla River	0.018	0.014	0.022
Umatilla River	mainstem, BON to MCN	Umatilla River	0.307	0.294	0.321
Yakima River	mainstem, BON to MCN	Umatilla River	0.000	0.000	0.001
Walla Walla River	mainstem, BON to MCN	Umatilla River	0.000	0.000	0.000
Deschutes River	mainstem, BON to MCN	BON to MCN other tributaries	0.001	0.000	0.002
Fifteenmile Creek	mainstem, BON to MCN	BON to MCN other tributaries	0.026	0.017	0.037
John Day River	mainstem, BON to MCN	BON to MCN other tributaries	0.001	0.001	0.002
Umatilla River	mainstem, BON to MCN	BON to MCN other tributaries	0.003	0.002	0.005
Yakima River	mainstem, BON to MCN	BON to MCN other tributaries	0.001	0.000	0.004
Walla Walla River	mainstem, BON to MCN	BON to MCN other tributaries	0.000	0.000	0.001
Deschutes River	mainstem, BON to MCN	loss	0.607	0.582	0.629
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Table 2: Movement probabilities for Middle Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, BON to MCN mainstem, BON to MCN mainstem, BON to MCN mainstem, BON to MCN mainstem, BON to MCN	loss loss loss loss	0.511 0.228 0.279 0.173 0.176	0.477 0.219 0.265 0.149 0.165	0.541 0.238 0.295 0.194 0.188
Deschutes River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.394	0.145	0.671
Fifteenmile Creek		mainstem, BON to MCN	0.472	0.347	0.599
John Day River		mainstem, BON to MCN	0.508	0.489	0.528
Umatilla River		mainstem, BON to MCN	0.478	0.453	0.501
Yakima River		mainstem, BON to MCN	0.010	0.005	0.017
Walla Walla River		mainstem, BON to MCN	0.045	0.039	0.051
Deschutes River	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.008	0.000	0.034
Fifteenmile Creek		mainstem, PRA to RIS	0.001	0.000	0.008
John Day River		mainstem, PRA to RIS	0.014	0.010	0.019
Umatilla River		mainstem, PRA to RIS	0.021	0.014	0.029
Yakima River		mainstem, PRA to RIS	0.138	0.116	0.162
Walla Walla River		mainstem, PRA to RIS	0.020	0.017	0.024
Deschutes River	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.236	0.055	0.478
Fifteenmile Creek		mainstem, ICH to LGR	0.120	0.059	0.199
John Day River		mainstem, ICH to LGR	0.212	0.199	0.225
Umatilla River		mainstem, ICH to LGR	0.192	0.168	0.212
Yakima River		mainstem, ICH to LGR	0.035	0.025	0.048
Walla Walla River		mainstem, ICH to LGR	0.574	0.558	0.590
Deschutes River	mainstem, MCN to ICH or PRA	Yakima River	0.007	0.000	0.039
Fifteenmile Creek		Yakima River	0.001	0.000	0.007
John Day River		Yakima River	0.001	0.000	0.002
Umatilla River		Yakima River	0.002	0.000	0.005
Yakima River		Yakima River	0.761	0.735	0.791
Walla Walla River		Yakima River	0.001	0.000	0.001
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, MCN to ICH or PRA	Walla Walla River	0.010 0.020 0.005 0.008 0.000 0.279	0.000 0.002 0.003 0.004 0.000 0.264	0.052 0.053 0.008 0.013 0.001 0.293
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, MCN to ICH or PRA	loss loss loss loss	0.344 0.384 0.259 0.300 0.055 0.081	0.107 0.262 0.242 0.277 0.041 0.073	0.608 0.492 0.274 0.324 0.071 0.089
Deschutes River	mainstem, PRA to RIS	mainstem, MCN to ICH or PRA	0.517	0.000	1.000
Fifteenmile Creek	mainstem, PRA to RIS		0.508	0.000	1.000
John Day River	mainstem, PRA to RIS		0.509	0.365	0.656
Umatilla River	mainstem, PRA to RIS		0.552	0.342	0.713
Yakima River	mainstem, PRA to RIS		0.603	0.523	0.684

Table 2: Movement probabilities for Middle Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Walla Walla River	mainstem, PRA to RIS	mainstem, MCN to ICH or PRA	0.525	0.443	0.603
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, PRA to RIS mainstem, PRA to RIS	mainstem, RIS to RRE	0.380 0.388 0.387 0.352 0.312 0.374	0.000 0.000 0.264 0.228 0.242 0.307	0.829 0.832 0.498 0.519 0.383 0.449
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, PRA to RIS mainstem, PRA to RIS	loss loss loss loss	0.103 0.105 0.104 0.095 0.084 0.101	0.000 0.000 0.066 0.057 0.057 0.071	0.262 0.261 0.145 0.146 0.112 0.141
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, ICH to LGR mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.236 0.306 0.277 0.325 0.556 0.259	0.010 0.102 0.243 0.273 0.390 0.244	0.544 0.560 0.314 0.376 0.735 0.276
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, ICH to LGR mainstem, ICH to LGR	mainstem, upstream of LGR	0.357 0.325 0.338 0.316 0.208 0.347	0.212 0.205 0.317 0.288 0.122 0.329	0.461 0.416 0.362 0.342 0.290 0.365
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, ICH to LGR mainstem, ICH to LGR	Tucannon River Tucannon River Tucannon River Tucannon River Tucannon River Tucannon River	0.114 0.104 0.108 0.101 0.066 0.111	0.067 0.066 0.097 0.089 0.039 0.102	0.154 0.139 0.120 0.115 0.094 0.120
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	mainstem, ICH to LGR mainstem, ICH to LGR	loss loss loss loss	0.292 0.265 0.276 0.258 0.169 0.283	0.175 0.169 0.260 0.235 0.105 0.271	0.376 0.345 0.296 0.283 0.234 0.299
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	Deschutes River Deschutes River Deschutes River Deschutes River Deschutes River Deschutes River	mainstem, BON to MCN mainstem, BON to MCN	0.003 0.248 0.642 0.486 0.950 0.808	0.000 0.173 0.582 0.413 0.889 0.744	0.008 0.330 0.692 0.549 0.990 0.861
Deschutes River Fifteenmile Creek John Day River	Deschutes River Deschutes River Deschutes River	loss loss	0.997 0.752 0.358	0.992 0.670 0.308	1.000 0.827 0.418

Table 2: Movement probabilities for Middle Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Umatilla River	Deschutes River	loss	0.514	0.451	0.587
Yakima River	Deschutes River	loss	0.050	0.010	0.111
Walla Walla River	Deschutes River	loss	0.192	0.139	0.256
Deschutes River	John Day River	mainstem, BON to MCN	0.032	0.000	0.157
Fifteenmile Creek	John Day River	mainstem, BON to MCN	0.014	0.000	0.064
John Day River	John Day River	mainstem, BON to MCN	0.001	0.000	0.003
Umatilla River Yakima River	John Day River	mainstem, BON to MCN	$0.031 \\ 0.223$	0.000 0.000	0.251 1.000
Walla Walla River	John Day River John Day River	mainstem, BON to MCN mainstem, BON to MCN	0.223 0.520	0.000	1.000
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Deschutes River Fifteenmile Creek	John Day River John Day River	loss loss	$0.968 \\ 0.986$	0.843 0.936	1.000 1.000
John Day River	John Day River	loss	0.980 0.999	0.930 0.997	1.000
Umatilla River	John Day River	loss	0.969	0.749	1.000
Yakima River	John Day River	loss	0.777	0.000	1.000
Walla Walla River	John Day River	loss	0.480	0.000	1.000
Deschutes River	Hood River	mainstem, BON to MCN	0.369	0.026	0.793
Fifteenmile Creek	Hood River	mainstem, BON to MCN	0.652	0.000	1.000
John Day River	Hood River	mainstem, BON to MCN	0.953	0.688	1.000
Umatilla River	Hood River	mainstem, BON to MCN	0.993	0.957	1.000
Yakima River	Hood River	mainstem, BON to MCN	0.665	0.000	1.000
Walla Walla River	Hood River	mainstem, BON to MCN	0.407	0.000	1.000
Deschutes River	Hood River	loss	0.631	0.207	0.974
Fifteenmile Creek	Hood River	loss	0.348	0.000	1.000
John Day River	Hood River	loss	0.047	0.000	0.312
Umatilla River	Hood River	loss	0.007	0.000	0.043
Yakima River Walla Walla River	Hood River Hood River	loss loss	$0.335 \\ 0.593$	0.000 0.000	1.000 1.000
Deschutes River Fifteenmile Creek	Fifteenmile Creek Fifteenmile Creek	mainstem, BON to MCN	0.278	0.000	1.000
John Day River	Fifteenmile Creek	mainstem, BON to MCN mainstem, BON to MCN	$0.001 \\ 0.257$	0.000 0.000	0.005 1.000
Umatilla River	Fifteenmile Creek	mainstem, BON to MCN	0.257 0.279	0.000	1.000
Yakima River	Fifteenmile Creek	mainstem, BON to MCN	0.242	0.000	1.000
Walla Walla River	Fifteenmile Creek	mainstem, BON to MCN	0.517	0.000	1.000
Deschutes River	Fifteenmile Creek	loss	0.722	0.000	1.000
Fifteenmile Creek	Fifteenmile Creek	loss	0.999	0.995	1.000
John Day River	Fifteenmile Creek	loss	0.743	0.000	1.000
Umatilla River	Fifteenmile Creek	loss	0.721	0.000	1.000
Yakima River	Fifteenmile Creek	loss	0.758	0.000	1.000
Walla Walla River	Fifteenmile Creek	loss	0.483	0.000	1.000
Deschutes River	Umatilla River	mainstem, BON to MCN	0.354	0.000	1.000
Fifteenmile Creek	Umatilla River	mainstem, BON to MCN	0.047	0.000	0.309
John Day River	Umatilla River	mainstem, BON to MCN	0.068	0.027	0.117
Umatilla River	Umatilla River	mainstem, BON to MCN	0.001	0.000	0.004
Yakima River Walla Walla River	Umatilla River Umatilla River	mainstem, BON to MCN	0.332	0.000	1.000
		mainstem, BON to MCN	0.460	0.000	1.000
Deschutes River	Umatilla River	loss	0.646	0.000	1.000

Table 2: Movement probabilities for Middle Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	———— q95
Fifteenmile Creek John Day River Umatilla River Yakima River	Umatilla River Umatilla River Umatilla River Umatilla River	loss loss loss	0.953 0.932 0.999 0.668	0.691 0.883 0.996 0.000	1.000 0.973 1.000 1.000
Walla Walla River	Umatilla River	loss	0.540	0.000	1.000
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	Yakima River Yakima River Yakima River Yakima River Yakima River Yakima River	mainstem, MCN to ICH or PRA	$\begin{array}{c} 0.166 \\ 0.190 \\ 0.016 \\ 0.020 \\ 0.004 \\ 0.532 \end{array}$	0.000 0.000 0.000 0.000 0.001 0.054	1.000 1.000 0.060 0.085 0.009 0.973
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	Yakima River Yakima River Yakima River Yakima River Yakima River Yakima River	loss loss loss loss loss	0.834 0.810 0.984 0.980 0.996 0.468	0.000 0.000 0.940 0.915 0.991 0.027	1.000 1.000 1.000 1.000 0.999 0.946
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	Walla Walla River	mainstem, MCN to ICH or PRA	0.402 0.074 0.391 0.565 0.405 0.011	0.000 0.000 0.152 0.272 0.000 0.006	1.000 0.475 0.669 0.852 1.000 0.017
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	Walla Walla River	loss loss loss loss loss	0.598 0.926 0.609 0.435 0.595 0.989	0.000 0.525 0.331 0.148 0.000 0.983	1.000 1.000 0.848 0.728 1.000 0.994
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	BON to MCN other tributaries BON to MCN other tributaries	mainstem, BON to MCN mainstem, BON to MCN	0.058 0.145 0.215 0.697 0.035 0.977	0.000 0.030 0.018 0.368 0.000 0.851	0.400 0.319 0.570 0.927 0.179 1.000
Deschutes River Fifteenmile Creek John Day River Umatilla River Yakima River Walla Walla River	BON to MCN other tributaries BON to MCN other tributaries	loss loss loss loss	0.942 0.855 0.785 0.303 0.965 0.023	0.600 0.681 0.430 0.073 0.821 0.000	1.000 0.970 0.982 0.632 1.000 0.149

Upper Columbia River Steelhead

Wenatchee River Steelhead, whose natal tributary is between Rock Island Dam and Rocky Reach Dam, had a 58.3% (90% CI 57%-59.6%) probability of overshooting Rocky Reach Dam. Entiat River Steelhead, whose natal tribuatry is between Rocky Reach Dam and Wells Dam, had a 36.3% (90% CI 33%-39.5%) probability of overshooting Wells Dam. Because no dam with PIT tag detectors in the adult fishways exists above Wells Dam, overshoot probabilities on the Columbia River could not be calculated for Okanogan River or Methow River Steelhead. Overshoot probabilities at Ice Harbor Dam for all four Upper Columbia River origins were exceedingly low (0-0.1%).

Table 3: Movement probabilities for Upper Columbia Steelhead, outside of the DPS boundaries.

from	to	mean	q 5	q95
mainstem, mouth to BON	mainstem, BON to MCN	0.976	0.960	0.990
mainstem, mouth to BON	loss	0.024	0.010	0.040
mainstem, BON to MCN	mainstem, mouth to BON	0.012	0.010	0.013
mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.749	0.744	0.754
mainstem, BON to MCN	Deschutes River	0.013	0.012	0.014
mainstem, BON to MCN	John Day River	0.000	0.000	0.000
mainstem, BON to MCN	Hood River	0.000	0.000	0.000
mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
mainstem, BON to MCN	Umatilla River	0.000	0.000	0.000
mainstem, BON to MCN	BON to MCN other tributaries	0.000	0.000	0.000
mainstem, BON to MCN	loss	0.226	0.221	0.231
mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.096	0.003	0.248
mainstem, ICH to LGR	mainstem, upstream of LGR	0.890	0.727	0.990
mainstem, ICH to LGR	Tucannon River	0.004	0.000	0.017
mainstem, ICH to LGR	loss	0.009	0.000	0.042
mainstem, upstream of LGR	mainstem, ICH to LGR	0.330	0.124	0.558
mainstem, upstream of LGR	Asotin Creek	0.009	0.000	0.034
mainstem, upstream of LGR	Clearwater River	0.109	0.007	0.340
mainstem, upstream of LGR	Salmon River	0.009	0.000	0.047
mainstem, upstream of LGR	Grande Ronde River	0.009	0.000	0.062
mainstem, upstream of LGR	Imnaha River	0.010	0.000	0.061
mainstem, upstream of LGR	loss	0.525	0.259	0.790
Deschutes River	mainstem, BON to MCN	0.872	0.830	0.908
Deschutes River	loss	0.128	0.092	0.170
Hood River	mainstem, BON to MCN	0.956	0.741	1.000
Hood River	loss	0.044	0.000	0.259
Clearwater River	mainstem, upstream of LGR	0.070	0.000	0.458
Clearwater River	loss	0.930	0.542	1.000

Table 4: Movement probabilities for Upper Columbia Steelhead by natal origin, inside the DPS boundaries.

origin	from	to	mean	q5	q95
Wenatchee River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.010	0.008	0.012
Entiat River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.007	0.004	0.011
Okanogan River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.011	0.008	0.015
Methow River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.009	0.008	0.012

Table 4: Movement probabilities for Upper Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Wenatchee River	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.980	0.977	0.984
Entiat River		mainstem, PRA to RIS	0.985	0.978	0.992
Okanogan River		mainstem, PRA to RIS	0.978	0.972	0.984
Methow River		mainstem, PRA to RIS	0.981	0.978	0.984
Wenatchee River	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.001	0.000	0.001
Entiat River		mainstem, ICH to LGR	0.000	0.000	0.001
Okanogan River		mainstem, ICH to LGR	0.001	0.000	0.001
Methow River		mainstem, ICH to LGR	0.001	0.000	0.001
Wenatchee River	mainstem, MCN to ICH or PRA	Yakima River	0.000	0.000	0.000
Entiat River		Yakima River	0.000	0.000	0.000
Okanogan River		Yakima River	0.000	0.000	0.000
Methow River		Yakima River	0.000	0.000	0.000
Wenatchee River	mainstem, MCN to ICH or PRA	Walla Walla River	0.000	0.000	0.000
Entiat River		Walla Walla River	0.000	0.000	0.000
Okanogan River		Walla Walla River	0.000	0.000	0.000
Methow River		Walla Walla River	0.000	0.000	0.000
Wenatchee River Entiat River Okanogan River Methow River	mainstem, MCN to ICH or PRA	loss loss loss	0.009 0.007 0.010 0.009	0.007 0.004 0.007 0.007	0.011 0.011 0.013 0.010
Wenatchee River	mainstem, PRA to RIS	mainstem, MCN to ICH or PRA	0.015	0.012	0.018
Entiat River	mainstem, PRA to RIS		0.020	0.010	0.033
Okanogan River	mainstem, PRA to RIS		0.016	0.011	0.023
Methow River	mainstem, PRA to RIS		0.012	0.010	0.014
Wenatchee River	mainstem, PRA to RIS	mainstem, RIS to RRE	0.951	0.944	0.957
Entiat River	mainstem, PRA to RIS	mainstem, RIS to RRE	0.966	0.950	0.979
Okanogan River	mainstem, PRA to RIS	mainstem, RIS to RRE	0.969	0.960	0.977
Methow River	mainstem, PRA to RIS	mainstem, RIS to RRE	0.963	0.959	0.966
Wenatchee River Entiat River Okanogan River Methow River	mainstem, PRA to RIS mainstem, PRA to RIS mainstem, PRA to RIS mainstem, PRA to RIS	loss loss loss	0.035 0.014 0.014 0.026	0.030 0.006 0.009 0.023	0.040 0.024 0.022 0.029
Wenatchee River	mainstem, RIS to RRE	mainstem, PRA to RIS	0.013	0.010	0.016
Entiat River	mainstem, RIS to RRE	mainstem, PRA to RIS	0.009	0.004	0.018
Okanogan River	mainstem, RIS to RRE	mainstem, PRA to RIS	0.004	0.001	0.008
Methow River	mainstem, RIS to RRE	mainstem, PRA to RIS	0.010	0.008	0.012
Wenatchee River	mainstem, RIS to RRE	mainstem, RRE to WEL	0.583	0.570	0.596
Entiat River	mainstem, RIS to RRE	mainstem, RRE to WEL	0.981	0.968	0.990
Okanogan River	mainstem, RIS to RRE	mainstem, RRE to WEL	0.973	0.964	0.982
Methow River	mainstem, RIS to RRE	mainstem, RRE to WEL	0.954	0.949	0.958
Wenatchee River	mainstem, RIS to RRE	Wenatchee River	0.319	0.307	0.331
Entiat River	mainstem, RIS to RRE	Wenatchee River	0.007	0.002	0.015
Okanogan River	mainstem, RIS to RRE	Wenatchee River	0.002	0.000	0.005
Methow River	mainstem, RIS to RRE	Wenatchee River	0.002	0.001	0.003

Table 4: Movement probabilities for Upper Columbia Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Wenatchee River Entiat River Okanogan River Methow River	mainstem, RIS to RRE mainstem, RIS to RRE mainstem, RIS to RRE mainstem, RIS to RRE	loss loss loss	0.085 0.003 0.020 0.034	0.078 0.000 0.012 0.030	0.092 0.008 0.027 0.038
Wenatchee River	mainstem, RRE to WEL	mainstem, RIS to RRE	0.228	0.213	0.243
Entiat River	mainstem, RRE to WEL	mainstem, RIS to RRE	0.027	0.016	0.039
Okanogan River	mainstem, RRE to WEL	mainstem, RIS to RRE	0.002	0.001	0.005
Methow River	mainstem, RRE to WEL	mainstem, RIS to RRE	0.006	0.004	0.008
Wenatchee River	mainstem, RRE to WEL	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	0.564	0.548	0.579
Entiat River	mainstem, RRE to WEL		0.362	0.330	0.395
Okanogan River	mainstem, RRE to WEL		0.978	0.969	0.985
Methow River	mainstem, RRE to WEL		0.930	0.924	0.935
Wenatchee River	mainstem, RRE to WEL	Entiat River	0.032	0.027	0.037 0.623 0.001 0.000
Entiat River	mainstem, RRE to WEL	Entiat River	0.585	0.552	
Okanogan River	mainstem, RRE to WEL	Entiat River	0.000	0.000	
Methow River	mainstem, RRE to WEL	Entiat River	0.000	0.000	
Wenatchee River Entiat River Okanogan River Methow River	mainstem, RRE to WEL mainstem, RRE to WEL mainstem, RRE to WEL mainstem, RRE to WEL	loss loss loss	0.175 0.027 0.020 0.064	0.166 0.016 0.013 0.059	0.188 0.038 0.028 0.069
Wenatchee River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	mainstem, RRE to WEL	0.205	0.192	0.219
Entiat River		mainstem, RRE to WEL	0.618	0.571	0.666
Okanogan River		mainstem, RRE to WEL	0.022	0.015	0.031
Methow River		mainstem, RRE to WEL	0.029	0.026	0.032
Wenatchee River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	Okanogan River	0.002	0.000	0.004
Entiat River		Okanogan River	0.005	0.001	0.014
Okanogan River		Okanogan River	0.667	0.639	0.692
Methow River		Okanogan River	0.025	0.021	0.028
Wenatchee River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	Methow River	0.124	0.109	0.140
Entiat River		Methow River	0.202	0.163	0.245
Okanogan River		Methow River	0.050	0.039	0.064
Methow River		Methow River	0.232	0.223	0.243
Wenatchee River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	Upstream WEL other tributaries	0.003	0.001	0.006
Entiat River		Upstream WEL other tributaries	0.004	0.000	0.014
Okanogan River		Upstream WEL other tributaries	0.002	0.000	0.005
Methow River		Upstream WEL other tributaries	0.000	0.000	0.001
Wenatchee River Entiat River Okanogan River Methow River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	loss loss loss	0.666 0.171 0.259 0.714	0.644 0.129 0.232 0.703	0.687 0.211 0.281 0.724
Wenatchee River	Wenatchee River	mainstem, RIS to RRE	0.043	0.034	0.052
Entiat River	Wenatchee River	mainstem, RIS to RRE	0.977	0.856	1.000
Okanogan River	Wenatchee River	mainstem, RIS to RRE	0.963	0.803	1.000
Methow River	Wenatchee River	mainstem, RIS to RRE	0.905	0.742	0.986

Table 4: Movement probabilities for Upper Columbia Steelhead by natal origin, inside the DPS boundaries. *(continued)*

origin	from	to	mean	q5	q95
Wenatchee River Entiat River	Wenatchee River Wenatchee River	loss	0.957 0.023	0.948 0.000	0.966 0.144
Okanogan River Methow River	Wenatchee River Wenatchee River	loss loss	$0.037 \\ 0.095$	$0.000 \\ 0.014$	0.197 0.258
Wenatchee River Entiat River Okanogan River Methow River	Entiat River Entiat River Entiat River Entiat River	mainstem, RRE to WEL mainstem, RRE to WEL mainstem, RRE to WEL mainstem, RRE to WEL	0.116 0.027 0.412 0.520	0.066 0.014 0.000 0.000	0.180 0.043 1.000 1.000
Wenatchee River Entiat River Okanogan River Methow River	Entiat River Entiat River Entiat River Entiat River	loss loss loss	0.884 0.973 0.588 0.480	0.820 0.957 0.000 0.000	0.934 0.986 1.000 1.000
Wenatchee River Entiat River Okanogan River Methow River	Okanogan River Okanogan River Okanogan River Okanogan River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	0.022 0.887 0.004 0.001	0.000 0.337 0.001 0.000	0.119 1.000 0.008 0.003
Wenatchee River Entiat River Okanogan River Methow River	Okanogan River Okanogan River Okanogan River Okanogan River	loss loss loss	0.978 0.113 0.996 0.999	0.881 0.000 0.992 0.997	1.000 0.663 0.999 1.000
Wenatchee River Entiat River Okanogan River Methow River	Methow River Methow River Methow River Methow River	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	0.128 0.615 0.023 0.007	0.095 0.480 0.001 0.004	0.165 0.731 0.070 0.011
Wenatchee River Entiat River Okanogan River Methow River	Methow River Methow River Methow River Methow River	loss loss loss	0.872 0.385 0.977 0.993	0.835 0.269 0.930 0.989	0.905 0.520 0.999 0.996
Wenatchee River Entiat River Okanogan River Methow River	Upstream WEL other tributaries Upstream WEL other tributaries Upstream WEL other tributaries Upstream WEL other tributaries	mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL mainstem, upstream of WEL	0.006 0.032 0.019 0.026	0.000 0.000 0.000 0.000	0.032 0.210 0.123 0.215
Wenatchee River Entiat River Okanogan River Methow River	Upstream WEL other tributaries Upstream WEL other tributaries Upstream WEL other tributaries Upstream WEL other tributaries	loss loss loss	0.994 0.968 0.981 0.974	0.968 0.790 0.877 0.785	1.000 1.000 1.000 1.000

Snake River Basin Steelhead

Tucannon River Steelhead are the only Snake River Steelhead population for which overshoot probabilities at the upstream dam could be calculated. Tucannon River Steelhead had a 57% (90% CI 55.8%-58.2%) probability of overshooting Lower Granite Dam. All six origins had probabilities of overshooting Priest Rapids Dam on the Columbia River between 1% and 3%.

Table 5: Movement probabilities for Snake River Basin Steelhead, outside of the DPS boundaries.

from	to	mean	q5	q95
mainstem, mouth to BON	mainstem, BON to MCN	0.980	0.973	0.986
mainstem, mouth to BON	loss	0.020	0.014	0.027
mainstem, BON to MCN	mainstem, mouth to BON	0.020	0.019	0.021
mainstem, BON to MCN	mainstem, MCN to ICH or PRA	0.746	0.742	0.749
mainstem, BON to MCN	Deschutes River	0.037	0.036	0.039
mainstem, BON to MCN	John Day River	0.004	0.003	0.004
mainstem, BON to MCN	Hood River	0.001	0.000	0.001
mainstem, BON to MCN	Fifteenmile Creek	0.000	0.000	0.000
mainstem, BON to MCN	Umatilla River	0.001	0.001	0.001
mainstem, BON to MCN	BON to MCN other tributaries	0.001	0.001	0.001
mainstem, BON to MCN	loss	0.191	0.187	0.195
mainstem, PRA to RIS	mainstem, MCN to ICH or PRA	0.468	0.437	0.502
mainstem, PRA to RIS	mainstem, RIS to RRE	0.476	0.445	0.507
mainstem, PRA to RIS	loss	0.056	0.039	0.071
mainstem, RIS to RRE	mainstem, PRA to RIS	0.378	0.336	0.413
mainstem, RIS to RRE	mainstem, RRE to WEL	0.569	0.532	0.612
mainstem, RIS to RRE	Wenatchee River	0.006	0.001	0.012
mainstem, RIS to RRE	loss	0.048	0.032	0.068
mainstem, RRE to WEL	mainstem, RIS to RRE	0.261	0.219	0.307
mainstem, RRE to WEL	mainstem, upstream of WEL	0.627	0.573	0.677
mainstem, RRE to WEL	Entiat River	0.013	0.004	0.027
mainstem, RRE to WEL	loss	0.100	0.077	0.126
mainstem, upstream of WEL	mainstem, RRE to WEL	0.306	0.248	0.375
mainstem, upstream of WEL	Okanogan River	0.110	0.071	0.159
mainstem, upstream of WEL	Methow River	0.160	0.117	0.201
mainstem, upstream of WEL	Upstream WEL other tributaries	0.006	0.000	0.017
mainstem, upstream of WEL	loss	0.418	0.362	0.480
Deschutes River	mainstem, BON to MCN	0.797	0.781	0.815
Deschutes River	loss	0.203	0.185	0.219
John Day River	mainstem, BON to MCN	0.262	0.197	0.330
John Day River	loss	0.738	0.670	0.803
Hood River	mainstem, BON to MCN	0.734	0.576	0.874
Hood River	loss	0.266	0.126	0.424
Fifteenmile Creek	mainstem, BON to MCN	0.020	0.000	0.106
Fifteenmile Creek	loss	0.980	0.894	1.000
Umatilla River	mainstem, BON to MCN	0.142	0.061	0.230
Umatilla River	loss	0.858	0.770	0.939
Yakima River	mainstem, MCN to ICH or PRA	0.355	0.152	0.541
Yakima River	loss	0.645	0.459	0.848
Walla Walla River	mainstem, MCN to ICH or PRA	0.213	0.124	0.312
Walla Walla River	loss	0.787	0.688	0.876
Wenatchee River	mainstem, RIS to RRE	0.488	0.055	0.946
Wenatchee River	loss	0.512	0.054	0.945
Entiat River	mainstem, RRE to WEL	0.029	0.000	0.150
Entiat River	loss	0.971	0.850	1.000
Okanogan River	mainstem, upstream of WEL	0.117	0.017	0.278
Okanogan River	loss	0.883	0.722	0.983
Methow River	mainstem, upstream of WEL	0.238	0.128	0.377
Methow River	loss	0.762	0.623	0.872
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Table 5: Movement probabilities for Snake River Basin Steelhead, outside of the DPS boundaries. (continued)

from	to	mean	q5	q95
BON to MCN other tributaries	mainstem, BON to MCN	0.233	0.134	0.357
BON to MCN other tributaries	loss	0.767	0.643	0.866
Upstream WEL other tributaries	mainstem, upstream of WEL	0.083	0.000	0.561
Upstream WEL other tributaries	loss	0.917	0.439	1.000

Table 6: Movement probabilities for Snake River Basin Steelhead by natal origin, inside the DPS boundaries.

origin	from	to	mean	q5	q95
Tucannon River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.074	0.068	0.079
Asotin Creek	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.058	0.047	0.069
Clearwater River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.031	0.028	0.034
Salmon River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.048	0.045	0.051
Grande Ronde	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.029	0.026	0.032
Imnaha River	mainstem, MCN to ICH or PRA	mainstem, BON to MCN	0.046	0.042	0.049
Tucannon River	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.028	0.025	0.030
Asotin Creek	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.022	0.017	0.026
Clearwater River	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.012	0.011	0.013
Salmon River	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.018	0.016	0.020
Grande Ronde	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.011	0.010	0.012
Imnaha River	mainstem, MCN to ICH or PRA	mainstem, PRA to RIS	0.017	0.016	0.019
Tucannon River	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.854	0.844	0.863
Asotin Creek	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.884	0.863	0.907
Clearwater River	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.938	0.933	0.943
Salmon River	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.905	0.900	0.910
Grande Ronde	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.943	0.938	0.947
Imnaha River	mainstem, MCN to ICH or PRA	mainstem, ICH to LGR	0.909	0.903	0.915
Tucannon River	mainstem, MCN to ICH or PRA	Yakima River	0.001	0.000	0.001
Asotin Creek	mainstem, MCN to ICH or PRA	Yakima River	0.001	0.000	0.001
Clearwater River	mainstem, MCN to ICH or PRA	Yakima River	0.000	0.000	0.000
Salmon River	mainstem, MCN to ICH or PRA	Yakima River	0.001	0.000	0.001
Grande Ronde	mainstem, MCN to ICH or PRA	Yakima River	0.000	0.000	0.000
Imnaha River	mainstem, MCN to ICH or PRA	Yakima River	0.001	0.000	0.001
Tucannon River	mainstem, MCN to ICH or PRA	Walla Walla River	0.003	0.002	0.004
Asotin Creek	mainstem, MCN to ICH or PRA	Walla Walla River	0.002	0.002	0.003
Clearwater River	mainstem, MCN to ICH or PRA	Walla Walla River	0.001	0.001	0.002
Salmon River	mainstem, MCN to ICH or PRA	Walla Walla River	0.002	0.001	0.002
Grande Ronde	mainstem, MCN to ICH or PRA	Walla Walla River	0.001	0.001	0.001
Imnaha River	mainstem, MCN to ICH or PRA	Walla Walla River	0.002	0.001	0.002
Tucannon River	mainstem, MCN to ICH or PRA	loss	0.041	0.038	0.045
Asotin Creek	mainstem, MCN to ICH or PRA	loss	0.033	0.026	0.039
Clearwater River	mainstem, MCN to ICH or PRA	loss	0.017	0.016	0.019
Salmon River	mainstem, MCN to ICH or PRA	loss	0.027	0.025	0.029
Grande Ronde	mainstem, MCN to ICH or PRA	loss	0.016	0.014	0.018
Imnaha River	mainstem, MCN to ICH or PRA	loss	0.025	0.024	0.028
Tucannon River	mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.032	0.027	0.037

Table 6: Movement probabilities for Snake River Basin Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q 5	q95
Asotin Creek	mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.033	0.022	0.048
Clearwater River	mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.010	0.008	0.012
Salmon River	mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.021	0.019	0.024
Grande Ronde	mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.019	0.016	0.022
Imnaha River	mainstem, ICH to LGR	mainstem, MCN to ICH or PRA	0.038	0.033	0.043
Tucannon River	mainstem, ICH to LGR	mainstem, upstream of LGR	0.570	0.558	0.582
Asotin Creek	mainstem, ICH to LGR	mainstem, upstream of LGR	0.901	0.877	0.923
Clearwater River	mainstem, ICH to LGR	mainstem, upstream of LGR	0.954	0.949	0.959
Salmon River	mainstem, ICH to LGR	mainstem, upstream of LGR	0.939	0.935	0.942
Grande Ronde	mainstem, ICH to LGR	mainstem, upstream of LGR	0.937	0.931	0.942
Imnaha River	mainstem, ICH to LGR	mainstem, upstream of LGR	0.912	0.905	0.919
Tucannon River	mainstem, ICH to LGR	Tucannon River	0.289	0.278	0.301
Asotin Creek	mainstem, ICH to LGR	Tucannon River	0.018	0.009	0.030
Clearwater River	mainstem, ICH to LGR	Tucannon River	0.001	0.001	0.002
Salmon River	mainstem, ICH to LGR	Tucannon River	0.002	0.002	0.003
Grande Ronde	mainstem, ICH to LGR	Tucannon River	0.003	0.002	0.004
Imnaha River	mainstem, ICH to LGR	Tucannon River	0.002	0.001	0.003
Tucannon River	mainstem, ICH to LGR	loss	0.109	0.100	0.118
Asotin Creek	mainstem, ICH to LGR	loss	0.048	0.033	0.066
Clearwater River	mainstem, ICH to LGR	loss	0.034	0.030	0.039
Salmon River	mainstem, ICH to LGR	loss	0.038	0.035	0.041
Grande Ronde	mainstem, ICH to LGR	loss	0.042	0.038	0.046
Imnaha River	mainstem, ICH to LGR	loss	0.049	0.043	0.055
Tucannon River	mainstem, upstream of LGR	mainstem, ICH to LGR	0.413	0.395	0.433
Asotin Creek	mainstem, upstream of LGR	mainstem, ICH to LGR	0.046	0.028	0.064
Clearwater River	mainstem, upstream of LGR	mainstem, ICH to LGR	0.018	0.015	0.021
Salmon River	mainstem, upstream of LGR	mainstem, ICH to LGR	0.020	0.017	0.022
Grande Ronde	mainstem, upstream of LGR	mainstem, ICH to LGR	0.019	0.016	0.021
Imnaha River	mainstem, upstream of LGR	mainstem, ICH to LGR	0.026	0.022	0.029
Tucannon River	mainstem, upstream of LGR	Asotin Creek	0.033	0.026	0.041
Asotin Creek	mainstem, upstream of LGR	Asotin Creek	0.689	0.644	0.727
Clearwater River	mainstem, upstream of LGR	Asotin Creek	0.000	0.000	0.000
Salmon River	mainstem, upstream of LGR	Asotin Creek	0.000	0.000	0.000
Grande Ronde	mainstem, upstream of LGR	Asotin Creek	0.002	0.001	0.003
Imnaha River	mainstem, upstream of LGR	Asotin Creek	0.002	0.000	0.000
Tucannon River	mainstem, upstream of LGR	Clearwater River	0.024	0.019	0.029
Asotin Creek	mainstem, upstream of LGR	Clearwater River	0.024 0.000	0.000	0.023 0.001
Clearwater River	mainstem, upstream of LGR	Clearwater River	0.303	0.294	0.313
Salmon River	mainstem, upstream of LGR	Clearwater River	0.000	0.294 0.000	0.313
Grande Ronde	mainstem, upstream of LGR	Clearwater River	0.000	0.000	0.000
Imnaha River	mainstem, upstream of LGR	Clearwater River	0.000	0.000	0.000
Tucannon River	mainstem, upstream of LGR	Salmon River	0.002	0.000	0.003
Asotin Creek	mainstem, upstream of LGR mainstem, upstream of LGR	Salmon River	0.002	0.000	0.003
Clearwater River	mainstem, upstream of LGR	Salmon River	0.000	0.000	0.000
Salmon River	mainstem, upstream of LGR mainstem, upstream of LGR	Salmon River Salmon River	0.000 0.279	0.000 0.270	0.000
Grande Ronde	mainstem, upstream of LGR mainstem, upstream of LGR	Salmon River	0.279 0.000	0.270 0.000	0.280 0.000
Grange Ronge	manistem, upstream of LGR	Samon River	0.000	0.000	0.000

Table 6: Movement probabilities for Snake River Basin Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q 5	q95
Imnaha River	mainstem, upstream of LGR	Salmon River	0.000	0.000	0.000
Tucannon River	mainstem, upstream of LGR	Grande Ronde River	0.007	0.004	0.010
Asotin Creek	mainstem, upstream of LGR	Grande Ronde River	0.020	0.010	0.032
Clearwater River	mainstem, upstream of LGR	Grande Ronde River	0.000	0.000	0.000
Salmon River	mainstem, upstream of LGR	Grande Ronde River	0.000	0.000	0.000
Grande Ronde	mainstem, upstream of LGR	Grande Ronde River	0.084	0.077	0.092
Imnaha River	mainstem, upstream of LGR	Grande Ronde River	0.000	0.000	0.000
Tucannon River	mainstem, upstream of LGR	Imnaha River	0.002	0.000	0.003
Asotin Creek	mainstem, upstream of LGR	Imnaha River	0.000	0.000	0.001
Clearwater River	mainstem, upstream of LGR	Imnaha River	0.000	0.000	0.000
Salmon River	mainstem, upstream of LGR	Imnaha River	0.000	0.000	0.000
Grande Ronde	mainstem, upstream of LGR	Imnaha River	0.001	0.000	0.002
Imnaha River	mainstem, upstream of LGR	Imnaha River	0.463	0.448	0.477
Tucannon River	mainstem, upstream of LGR	loss	0.520	0.500	0.537
Asotin Creek	mainstem, upstream of LGR	loss	0.245	0.211	0.288
Clearwater River	mainstem, upstream of LGR	loss	0.679	0.668	0.688
Salmon River	mainstem, upstream of LGR	loss	0.701	0.693	0.709
Grande Ronde	mainstem, upstream of LGR	loss	0.894	0.887	0.901
Imnaha River	mainstem, upstream of LGR	loss	0.512	0.497	0.526
Tucannon River	Tucannon River	mainstem, ICH to LGR	0.026	0.018	0.033
Asotin Creek	Tucannon River	mainstem, ICH to LGR	0.236	0.053	0.488
Clearwater River	Tucannon River	mainstem, ICH to LGR	0.167	0.029	0.402
Salmon River	Tucannon River	mainstem, ICH to LGR	0.358	0.195	0.518
Grande Ronde	Tucannon River	mainstem, ICH to LGR	0.142	0.026	0.309
Imnaha River	Tucannon River	mainstem, ICH to LGR	0.493	0.178	0.789
Tucannon River	Tucannon River	loss	0.974	0.967	0.982
Asotin Creek	Tucannon River	loss	0.764	0.512	0.947
Clearwater River	Tucannon River	loss	0.833	0.598	0.971
Salmon River	Tucannon River	loss	0.642	0.482	0.805
Grande Ronde	Tucannon River	loss	0.858	0.691	0.974
Imnaha River	Tucannon River	loss	0.507	0.211	0.822
Tucannon River	Asotin Creek	mainstem, upstream of LGR	0.094	0.045	0.150
Asotin Creek	Asotin Creek	mainstem, upstream of LGR	0.003	0.000	0.009
Clearwater River	Asotin Creek	mainstem, upstream of LGR	0.347	0.000	1.000
Salmon River	Asotin Creek	mainstem, upstream of LGR	0.292	0.000	1.000
Grande Ronde	Asotin Creek	mainstem, upstream of LGR	0.006	0.000	0.037
Imnaha River	Asotin Creek	mainstem, upstream of LGR	0.468	0.000	1.000
Tucannon River	Asotin Creek	loss	0.906	0.850	0.955
Asotin Creek	Asotin Creek	loss	0.997	0.991	1.000
Clearwater River	Asotin Creek	loss	0.653	0.000	1.000
Salmon River	Asotin Creek	loss	0.708	0.000	1.000
Grande Ronde	Asotin Creek	loss	0.994	0.963	1.000
Imnaha River	Asotin Creek	loss	0.534	0.000	1.000
Tucannon River	Clearwater River			0.000	0.010
Asotin Creek	Clearwater River Clearwater River	mainstem, upstream of LCR	0.002		
		mainstem, upstream of LGR	0.287	0.000	1.000
Clearwater River	Clearwater River	mainstem, upstream of LGR	0.003	0.001	0.006

Table 6: Movement probabilities for Snake River Basin Steelhead by natal origin, inside the DPS boundaries. (continued)

origin	from	to	mean	q5	q95
Salmon River	Clearwater River	mainstem, upstream of LGR	0.245	0.000	1.000
Grande Ronde	Clearwater River	mainstem, upstream of LGR	0.293	0.000	1.000
Imnaha River	Clearwater River	mainstem, upstream of LGR	0.513	0.000	1.000
Tucannon River	Clearwater River	loss	0.998	0.990	1.000
Asotin Creek	Clearwater River	loss	0.713	0.000	1.000
Clearwater River Salmon River	Clearwater River Clearwater River	loss loss	$0.997 \\ 0.755$	0.994 0.000	0.999 1.000
Grande Ronde	Clearwater River	loss	0.793	0.000	1.000
Imnaha River	Clearwater River	loss	0.487	0.000	1.000
Tucannon River	Salmon River	mainstem, upstream of LGR	0.020	0.000	0.085
Asotin Creek	Salmon River	mainstem, upstream of LGR	0.020 0.287	0.000	1.000
Clearwater River	Salmon River	mainstem, upstream of LGR	0.342	0.000	1.000
Salmon River	Salmon River	mainstem, upstream of LGR	0.001	0.000	0.002
Grande Ronde	Salmon River	mainstem, upstream of LGR	0.360	0.000	1.000
Imnaha River	Salmon River	mainstem, upstream of LGR	0.584	0.000	1.000
Tucannon River	Salmon River	loss	0.980	0.915	1.000
Asotin Creek	Salmon River	loss	0.713	0.000	1.000
Clearwater River	Salmon River	loss	0.658	0.000	1.000
Salmon River	Salmon River	loss	0.999	0.998	1.000
Grande Ronde	Salmon River	loss	0.640	0.000	1.000
Imnaha River	Salmon River	loss	0.416	0.000	1.000
Tucannon River	Grande Ronde River	mainstem, upstream of LGR	0.001	0.000	0.006
Asotin Creek	Grande Ronde River	mainstem, upstream of LGR	0.007	0.000	0.044
Clearwater River Salmon River	Grande Ronde River Grande Ronde River	mainstem, upstream of LGR	0.158	0.000	$1.000 \\ 0.998$
Grande Ronde	Grande Ronde River Grande Ronde River	mainstem, upstream of LGR mainstem, upstream of LGR	0.131 0.000	0.000 0.000	0.998 0.001
Imnaha River	Grande Ronde River	mainstem, upstream of LGR	0.491	0.000	1.000
Tucannon River	Grande Ronde River	loss	0.999	0.994	1.000
Asotin Creek	Grande Ronde River	loss	0.999 0.993	0.954 0.956	1.000
Clearwater River	Grande Ronde River	loss	0.842	0.000	1.000
Salmon River	Grande Ronde River	loss	0.869	0.002	1.000
Grande Ronde	Grande Ronde River	loss	1.000	0.999	1.000
Imnaha River	Grande Ronde River	loss	0.509	0.000	1.000
Tucannon River	Imnaha River	mainstem, upstream of LGR	0.020	0.000	0.119
Asotin Creek	Imnaha River	mainstem, upstream of LGR	0.383	0.000	1.000
Clearwater River	Imnaha River	mainstem, upstream of LGR	0.390	0.000	1.000
Salmon River	Imnaha River	mainstem, upstream of LGR	0.882	0.351	1.000
Grande Ronde	Imnaha River	mainstem, upstream of LGR	0.022	0.000	0.113
Imnaha River	Imnaha River	mainstem, upstream of LGR	0.001	0.000	0.002
Tucannon River	Imnaha River	loss	0.980	0.881	1.000
Asotin Creek	Imnaha River	loss	0.617	0.000	1.000
Clearwater River Salmon River	Imnaha River Imnaha River	loss	0.610	0.000	1.000
Grande Ronde	Imnana River Imnaha River	loss loss	$0.118 \\ 0.978$	$0.000 \\ 0.887$	0.649 1.000
Imnaha River	Imnaha River	loss	0.978	0.998	1.000
	minana mivoi	1000	0.333	0.000	1.000

Discussion

Current limitations and next steps

Detection probabilties in tributaries

Over the course of our study period, detection efficiencies in tributaries varied wildly as arrays were installed and decommissioned. For example, from 2010 to 2018, the number of tag detection arrays in tributaries almost tripled (Morrisett 2018). In some years of our study, the tributaries in our model had no active antennas at all (Richins 2017). However, our current model configuration does not explicitly account for detection efficiency in any state transition. The consequences of this are that movement probabilities into tributaries will be biased low, whereas loss probabilities both from the mainstem state that is connected to the tributary and any mainstem states that are overshoot states will be biased high, as missed detections in tributaries will be interpreted as loss from the state in which an individual was last detected. As a result, post-overshoot fallback to natal tributaries is also biased low, as this type of fallback is not able to be captured well due to low detection efficiencies in tributaries.

In future iterations of the model, detection probabilities in tributaries, as well as when tributaries had active arrays, will be explicitly modeled. When tributaries had multiple active arrays, detection probabilities will be calculated for the array furthest downstream (closest to the confluence with the mainstem) by examining what percentage of fish that were eventually seen at upstream arrays were also seen at the furthest downstream array. The model will account for years in which tributaries had no active arrays by removing those states from the model for movements occurring in that year.

Detection probabilities in downstream passage routes

Steelhead fallback is difficult to monitor using PIT tags because of the lack of detection capabilities in the primary downstream passage routes for Steelhead, which include spillways, the Juvenile Bypass System (JBS), navigation locks, ice/trash sluiceways, and turbines. While some passage routes, such as the JBS, the corner collector at Bonneville Dam, and as of 2020, the spillway at Lower Granite Dam, have PIT tag detection capability, the majority of downstream movements are only detected by examining the rest of the detection history. For example, Boggs et al. (2004) used consecutive detections in the same adult fish ladder to monitor rates of fallback, whereas Richins and Skalski (2018) calculated fallback to home following overshoot as detections in tributaries following detections in the adult fish ladder at a dam upstream of the tributary. Our modeling framework includes both of these ways of detecting fallback, but this is still an underestimate of total fallback. Fallback such as fallback that leads to mortality cannot be detected using PIT tags, and any time a fish is not seen after fallback (i.e., either due to a fish entering a tributary with PIT tag arrays but not being detected, entering a tributary without PIT tag arrays, spawning in the mainstem, or mortality following fallback), the fallback event will not be observed. While accounting for detection probability in tributaries in future iterations of the model should allow us to achieve a better estimate of post-overshoot fallback, the current network of PIT tag arrays is incapable of monitoring all fallback, and as such all estimates of fallback from this model will be lower bound estimates. However, the current modeling framework will give us the closest estimate of fallback possible using PIT tag data.

Final fates

The final fate of an individual fish is of central concern to the management and conservation of Steelhead. Whether an individual strayed (and to which tributary), reached its natal tributary, or died before spawning (and where) is one of the core questions that we set out to answer with this model. Final fates are not directly estimated directly as parameters in this model, but can be derived from the stepwise movement probabilities presented in Tables 1-6. This can be done either using a simulation-based approach, where a large number of simulated fish (e.g., 1,000,000) enter the model at Bonneville Dam and subsequently move through the states, with movements governed by random draws from the movement probabilities estimated in the model. It can also be calculated analytically by multiplying out the probabilities of each possible sequence of movements. It is of note that the biases for certain movements mentioned in the preceding sections will be perpetuated in any calculation of final fates, and thus some final fates (primarily associated with entering tributaries) would currently be underestimated due to detection probability issues.

Adding additional covariates

The model structure and the use of the multinomial logit to evaluate movement probabilities allows for the inclusion of both categorical and continuous covariates in the model. The next covariates that we plan to include in future iterations of the model are rear type (hatchery or wild), temperature (mainstem temperatures from dam tailraces), flow, and spill. We are also considering the addition of covariates related to juvenile experiences (barged vs. not barged, acclimated vs. not acclimated hatchery releases). The inclusion of these covariates will further our understanding of what environmental conditions (e.g., temperature or flow conditions) lead to increased probability of Steelhead choosing more dangerous migration pathways to natal tributaries, such as overshooting natal tributaries, and the inclusion of covariates that can be influenced by hydropower managers (e.g., spill or flow) or fishery managers (e.g., hatchery practices or assisted juvenile migration) would help inform how we can help Steelhead return safely to natal tributaries. Given the increased interest in assisting downstream Steelhead passage, such as via spill practices (Ham et al. 2021), the inclusion of these covariates would improve our understanding of how to help recover these populations by informing management practices.

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