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Sea-to-sea survival of late-run adult steelhead (*Oncorhynchus mykiss*) from the Columbia and Snake rivers

Matthew L. Keefer^{1*}, Michael A. Jepson¹, Tami S. Clabough¹, Eric L. Johnson^{1,2}, Shawn R. Narum³, Jon E. Hess⁴, and Christopher C. Caudill¹

¹Department of Fish and Wildlife Sciences
College of Natural Resources
University of Idaho, Moscow, Idaho 83844-1136, USA

²Current address: Eagle Fish Genetics Lab
Idaho Department of Fish and Game
1800 Trout Rd.
Eagle, Idaho 83616

³Columbia River Inter-Tribal Fish Commission
3059F National Fish Hatchery Rd.
Hagerman, Idaho 83332

⁴Columbia River Inter-Tribal Fish Commission
700 NE Multnomah St., Suite 1200
Portland, Oregon 97232

*Corresponding author (mkeefe@uidaho.edu)
Co-Authors: mjepson@uidaho.edu, tamic@uidaho.edu, eric.johnson@idfg.idaho.gov,
nars@critfc.org, hesj@critfc.org, caudill@uidaho.edu,

Abstract

We used biotelemetry and genetic stock identification to assess sea-to-sea survival and run composition of 1212 late-migrating adult steelhead (anadromous *Oncorhynchus mykiss*) through the Columbia River and Snake River migratory corridors. The late-run was predominated by steelhead from Idaho's Clearwater and Salmon rivers that must pass eight large hydroelectric dams during both pre-spawn and post-spawn migrations. In two years (2013 and 2014), pre-spawn survival to Snake River tributaries (>500 km) was 0.48–0.67 for the most abundant populations and was higher for females and 1-sea fish. Annual survival from Snake River tributary entry to post-spawn kelt status was 0.14–0.17, with higher survival for females and those without hatchery fin clips. Kelt outmigration survival was 0.31–0.39 past four Snake River dams and 0.13–0.20 past all eight dams and was highest for smaller kelts. Full-cycle adult freshwater survival (sea-to-sea) including 16 dam passage events was 0.01–0.02. Younger steelhead and those without fin clips survived at the highest rates. This study uniquely partitioned mortality across prespawn, reproductive, and kelt life history stages and informs management strategies for this conservation-priority metapopulation.

Keywords: genetic stock identification; iteroparity; kelt; life history; parentage-based tagging

Introduction

Preservation of genetic and life history diversity are becoming increasingly important objectives in fish conservation and management programs. In the United States, the Endangered Species Act (ESA) has essentially codified tenets like reproductive isolation, degree of genetic divergence, and adaptive distinctiveness into species conservation planning (Moritz 1994;

Waples 1995; Crandall et al. 2000). Application of these criteria is commonly used in the management of Pacific salmonids (*Oncorhynchus* spp), a genus with exceptional conspecific and intraspecific diversity (Groot and Margolis 1991; Waples 1991; Quinn 2005). *Oncorhynchus mykiss* is often considered the most phenotypically diverse species in the genus, with a continuum of life history types ranging from freshwater resident (i.e., rainbow trout) to fully anadromous (i.e., steelhead) (Behnke 1992; Courter et al. 2013; Kendall et al. 2015). There are dozens of genetic and life history variants at the anadromous end of the *O. mykiss* spectrum, with differences in freshwater and ocean rearing duration, age at maturity, timing of migrations, and the timing and frequency of reproduction (Busby et al. 1996; Moore et al. 2014; Hodge et al. 2016). This variation is thought to ultimately reflect life history tradeoffs in the allocation of reproductive effort among populations and functions to buffer populations against environmental variability (Moore et al. 2014).

The conservation of life history variation is an integral component of many management frameworks, and this study was motivated by a mandate to protect and restore steelhead that inhabit the large (~278,500 km²) Snake River basin in Idaho, Oregon, and Washington (USA). The river historically sustained many genetically and phenotypically distinct steelhead populations, but overharvest, construction of impassable dams, hatchery practices, habitat impacts, and hydroelectric development along the Columbia and Snake River migration corridors resulted in steelhead population declines and extinctions (Nehlsen et al. 1991; Gustafson et al. 2007). The remaining Snake River steelhead populations were listed as threatened under the ESA in 1997 (National Marine Fisheries Service 1997) and that status was reaffirmed in 2006 and 2014. Current Snake River steelhead management and conservation plans are complex and recognize population structure at multiple tiers. The aggregate Snake River population is

managed as a ‘distinct population segment’ with six ‘major population groups’ (NOAA Fisheries 2016); there is further nesting in some schema, with multiple genetic reporting groups that encompass >60 genetically distinct wild populations and ~6 hatchery populations (e.g., Nielsen et al. 2009; Campbell et al. 2012; Matala et al. 2014). Notably, all Snake River steelhead are considered summer-run (i.e., stream-maturing), but there are multiple life history pathways with differing smolt age, migration phenology, and age and size at maturity (Busby et al. 1996; Brannon et al. 2004; Copeland et al. 2017). Within the Snake River steelhead population complex, conservation priorities include maintaining a phenotype (‘B-run’) with relatively long ocean rearing (i.e., 2- or 3-sea), late summer and fall adult migration timing, relatively large body size, and older mean age. The B-run phenotype historically spawned in portions of the Clearwater, Middle Fork Salmon, and South Fork Salmon rivers (Busby et al. 1996; Brannon et al. 2004). However, access to large portions of B-run spawning habitat was partially or completely blocked by dam construction on the Clearwater River (Lewiston Dam, built in the 1920s, removed in 1973) and the North Fork Clearwater River (Dworshak Dam, completed 1973). NOAA-Fisheries has issued several biological opinions that include directives to increase the survival, productivity, and abundance of Snake River B-run steelhead (e.g., NOAA Fisheries 2008). Efforts to protect B-run steelhead have included harvest restrictions along the Columbia River and Snake River migration corridors, improvements to adult fishways at main stem dams, and actions to increase outmigration survival of post-spawn kelts.

Recent genetic analyses have elucidated complex patterns of sea age and body size for multiple steelhead stocks (Campbell et al. 2012; Hess et al. 2016; Matala et al. 2016) that were not recognized previously. Adult age, fork length, and geographic distribution criteria do not cleanly separate B-run fish from some other Snake River populations (Copeland et al. 2017).

Fork length has been used as a proxy for distinguishing A- and B-run (≥ 78 cm) steelhead for managing fisheries in the Columbia River basin, however, this criterion does not associate to geographic population or life history type as well as previously thought, highlighting a need to more precisely determine population-level life history composition and patterns of survival.

Partitioning steelhead mortality among various freshwater migration stages is challenging due to the geographic and temporal scope of their adult migrations. To reach natal sites, most Snake River steelhead migrate upstream ~1000 rkm to > 2000 rkm and must pass eight hydroelectric dams and reservoirs. In a dramatic example of migration prior to maturation (*sensu* Quinn et al. 2016), late-run steelhead enter the Columbia River in summer and fall, five to ten months prior to spawning. A portion (~20%) of the late run temporarily uses cool, non-natal tributaries (Keefer et al. 2009) and ~25% to ~45% overwinter in Columbia and Snake River reservoirs (Keefer et al. 2008a). The remaining premature fish overwinter in high-order tributaries before moving to lower-order natal spawning sites in spring. A mix of harvest and natural mortality occurs during each of these migration stages (Keefer et al. 2005, 2008a), with additional mortality during and immediately following spawning (e.g., Seamons and Quinn 2010). Thousands of wild- and hatchery-origin steelhead that spawn in Snake River tributaries initiate downstream kelt migrations each year (Evans et al. 2004). These potentially iteroparous individuals are highly valued in recovery planning for their demographic and genetic contributions (Narum et al. 2008), but kelts currently have very low outmigration survival due to energetic exhaustion (Penney et al. 2016) and the hazards of downstream passage through reservoirs and past dams (Wertheimer and Evans 2005; Colotelo et al. 2014).

Effective management of B-run Snake River steelhead requires better information on the stock and phenotypic composition of the run and details on stage-specific and cumulative

mortality. In this study, we evaluated the following hypotheses about adult survival: (i) mortality would be highest in spawning and kelt stages because of high reproductive effort and harvest during the spawning stage and declining physical condition of kelts; (ii) prespawn migration survival through the impounded migration corridor would vary with presumed origin and age at migration, with lower survival expected for hatchery-origin and older fish; (iii) steelhead survival in spawning tributaries would be lower for hatchery-origin, male, and older fish; and (iv) kelt outmigration survival would be low across trait groups, but especially for late-timed outmigrants, males, and older fish. Lower survival for hatchery-origin fish was expected because harvest was more extensive for hatchery steelhead across stages and because hatcheries collect adults for broodstock. Lower survival for older steelhead was expected given the tendency for preferential harvest of large fish (e.g., Hard et al. 2008), their higher post-spawn mortality (e.g., Crespi and Teo 2002; Matala et al. 2016), and because injury and mortality rates during downstream dam passage typically increase with fish size (Keefer et al. 2008b; Nyqvist et al. 2016). Lastly, we expected lower survival for males than females in spawning areas and during kelt outmigration because reproductive competition, post-spawn emaciation, and post-spawn mortality all tend to be higher for males (Jonsson et al. 1990; Fleming and Reynolds 2004; Ohms et al. 2014) resulting in female-skewed sex ratios for kelt steelhead (Narum et al. 2008; Matala et al. 2016).

Methods

Steelhead collection and tagging

Adult steelhead were trapped at the adult fish facility at Bonneville Dam (river kilometre ~235). The dam is located near the upper limit of tidal influence on the Columbia River and is

the first dam that upstream migrants encounter after leaving the Pacific Ocean. Steelhead were collected in 2013 and 2014 during the late-run, defined by managers as fish passing after the 25th of August each year. Protocols for steelhead trapping, anesthetization, handling, and intragastric insertion of radio transmitters were described by Keefer et al. (2005) and Caudill et al. (2014). Briefly, steelhead passing through the trap facility were diverted without handling into a tank of ~18mL•L⁻¹ solution of AQUI-S-20E (Aquatactics, Kirkland, Washington). Fish were selected in the order that they entered the trap each day (i.e., random with respect to passage sequence), but those with passive integrated transponder (PIT) tags from juvenile tagging programs were excluded to minimize potential handling effects on other research projects (~3% of returning adults). Each fish received a 3-volt, digitally-encoded radio transmitter that was 16 mm×46 mm and had a mass of 4 g in air (Model MCFT2-3A, Lotek Wireless, Newmarket, Ontario); manufacturer-reported tag life was 315 d and therefore extended through kelt migrations. A uniquely-coded, full-duplex PIT tag was inserted into the abdominal cavity as a secondary tag.

While anesthetized, steelhead were weighed (nearest 10 g), measured for fork length (nearest 0.5 cm), and inspected for hatchery fin clips, injuries, and other marks. A caudal fin tissue punch was collected for genetic analyses (details below). Fish recovered from anesthesia in a ~2275 L transport tank with oxygenated river water. They were then trucked ~8 km downstream from Bonneville Dam and released from sites on both sides of the Columbia River. An important limitation to sampling was caused by high water temperatures in late August and early September (see Fig. 2) which precluded collecting and handling fish over concerns of temperature-related stress.

Radiotelemetry and PIT-tag monitoring

More than 100 fixed-site radiotelemetry receivers, some with multiple antennas, were deployed at four lower Columbia River and four lower Snake River dams, in reservoirs, and in major tributaries (Fig 1). At dams, most antennas were underwater coaxial cable antennas used to monitor passage through fishways. Aerial Yagi antennas were used in dam tailraces, in reservoirs, and in tributaries. Detection efficiency at most sites has historically been >95% and antenna redundancy inside dam fishways increased dam-wide fish detection efficiency to near 100%. Missed detections were typically associated with transmitter loss or failure or receiver power outages. A reward (\$25 USD) was paid for transmitters returned from tribal and recreational fisheries to help estimate minimum harvest rates. Cooperating agencies also returned transmitters from steelhead recaptured at hatchery traps and weirs.

Upstream dam passage by steelhead was also monitored using PIT-tag detection antennas located inside adult fishways at Bonneville, The Dalles, McNary, Ice Harbor, and Lower Granite dams in both years and at Lower Monumental and Little Goose dams (2014 only). Antennas inside juvenile bypass systems (e.g., Axel et al. 2005) were used to detect downstream dam passage by steelhead kelts at all dams except The Dalles Dam. Additional PIT antennas were located at Columbia River dams upstream from the Columbia River–Snake River confluence and at >200 sites inside Columbia and Snake River tributaries, including instream arrays (e.g., Connolly et al. 2008) and at many hatchery-operated traps and weirs. Detection data for the PIT-tagged steelhead in our study were archived in the Columbia River PIT-tag Information System (PTAGIS) maintained by the Pacific States Marine Fisheries Commission.

Genetic assignments

Two methods were used for genetic mixed stock analyses to assign stock-of-origin. Parental baselines from Snake River hatchery broodstocks were used to assign fish from those hatchery programs, an approach called parentage-based tagging (PBT). Parentage assignments for the tagged steelhead used 95 single nucleotide polymorphism (SNP) loci and a baseline of genotypes to identify hatchery-origin parents (e.g., Steele et al. 2013). Assignment accuracy for PBT approaches 100% and therefore provides precise origin and age information (Steele et al. 2013), but the method was limited to steelhead with genotyped parents from Snake River basin hatcheries. To identify fish not assigned by PBT (wild fish and hatchery fish without parents in the PBT baseline), individuals were assigned to likely reporting groups (or genetic stocks) that have been determined based on genetic divergence at 180 SNP loci (e.g., Matala et al. 2014; Hess et al. 2016). Hereafter, we refer to this approach as genetic assignment to ‘reporting groups’. Fourteen Columbia and Snake River reporting groups (Table 1) were used as the SNP-based genetic baseline (Campbell et al. 2012; Hess et al. 2016) and genetic assignment was made for each tagged steelhead using ONCOR v1.0 (available at <http://www.montana.edu/kalinowski>), which estimates a probability of assignment using the method of Rannala and Mountain (1997).

In addition to the SNP loci, all genetic samples were screened with the Y-chromosome – specific assay *OmyY1_2SEXY*, which is associated with the *OmyY1* locus (Brunelli et al. 2008) and differentiates sex in *O. mykiss*. In previous tests, the *OmyY1_2SEXY* assay matched phenotypic sex in 99.6% of ~5,000 Snake River steelhead (Steele et al. 2015). The *OmyY1_2SEXY* assay failed to genotype or provided ambiguous results for a small portion of samples and these fish were considered as unknown sex.

Survival estimation

The combined radiotelemetry and PIT-tag detection data were used to construct migration histories for each steelhead. Detection efficiency approached 100% during upstream migration due to extensive redundancy in the radiotelemetry monitoring array and high (>95%) detection efficiency at the PIT-tag interrogation sites inside adult fishways. Detection efficiency was <100% during downstream kelt outmigration because there were far fewer detection locations and kelts could pass unmonitored routes (i.e., dam spillways and turbines). We used the Cormack-Jolly-Seber live recaptures option in Program MARK (White and Burnham 1999) to estimate kelt detection efficiency at dams. Detection probability ranged from 0.500 to 1.000 per dam assuming independence among detections and was 0.824 (95% ci = 0.731-0.890) assuming constant detection probability across the first seven dams kelts encountered. Non-detection of kelts or seasonal changes in detection efficiency would tend to result in underestimation of survival. Kelt detection efficiency could not be estimated at Bonneville Dam as there was very limited downstream monitoring.

We calculated point estimates of migration survival past each main stem dam for upstream-migrating prespawn adults and for post-spawn kelts during downstream migration. Missed detections at dams were inferred when plausible detections were collected either upstream (prespawn adults) or downstream (kelts) from the missed site. The survival estimates were likely precise and unbiased for the upstream migration given large sample sizes and the high detection probabilities during upstream migration described above. Survival estimates for kelt outmigration were likely underestimates due to much lower sample sizes (see Results) and lower detection probability; these estimates should be considered minima. An additional potential bias was likely for kelts that exited spawning tributaries, but passed monitoring sites undetected. Thus, survival in tributaries and kelt survival may have been slightly underestimated.

Point estimates of cumulative survival were calculated between important life history transitions (Fig. 1), from: (1) the start of upstream migration at Bonneville Dam; (2) entry into Snake River spawning areas upstream from Lower Granite reservoir (i.e., ‘potential spawners’); (3) re-entry into Lower Granite reservoir in spring after presumed spawning (i.e., ‘likely kelts’), and (4) downstream kelt passage at Ice Harbor Dam and Bonneville Dam.

A series of multiple logistic regression models was used to evaluate effects of covariates on steelhead survival during prespawn upstream migration, in spawning tributaries, and during kelt outmigration. Predictor variables included steelhead traits (reporting group, sex, fin clip presence [an indicator of hatchery origin], estimated age, fork length) as well as migration year and either release date (prespawn adults) or kelt migration timing. Kelt timing was classified as either early (≤ 24 April) or late (> 24 April) based on the median date of first detection in Lower Granite reservoir or downstream at a main stem dam. We created several *a priori* model sets ($n = 15$ to 17 models for each stage) that included single covariates, pairs of traits (e.g., migration year and date, sex and fin clip, etc.), and a mixture of timing and trait variables (Table S3). The candidate models were compared using information-theoretic techniques, ranked using Akaike’s information criterion (AIC), and evaluated with respect to ΔAIC , the change in AIC relative to the most parsimonious model (Buckland et al. 1997; Burnham and Anderson 2002). No interaction terms were considered.

There were two important sources of uncertainty in the model comparisons. First, some steelhead were missing covariate data including individual assignment to reporting group, sex, and ocean age, due to incomplete or ambiguous genetic information. Fish with missing covariates were excluded from some models. Second, some steelhead from the mixed-stock MGILCS reporting group (Table 1) were of non-Snake River origin based on final detection

inside other tributaries (e.g., Deschutes River, John Day River, Walla Walla River, etc.). The MGILCS fish had lower apparent survival in the model comparison for upstream migration, which used Lower Granite reservoir as the upstream endpoint. Steelhead assigned to MGILCS with likely origin outside the Snake River (based on tributary entry) were excluded from summaries of spawning ground and kelt outmigration survival.

Results

Sample summary

We collected and double-tagged 620 (2013) and 592 (2014) adult late-run steelhead at Bonneville Dam from early or mid-September through 15 October (Fig. 2). The samples were 0.18%–0.27% of the total steelhead count in each year ($n = 231\,417$ – $322\,134$) and 0.27%–0.97% of the total late-run count ($n = 64\,121$ – $127\,712$).

Large majorities ($n = 576$ – 591 , 95%–97%) of the tagged samples were genetically assigned to one of 12 reporting groups (Table 2, Fig. 3). The largest percentages assigned to the SFCLWR group (57%–59% of those released), followed by the UPSALM (17%–18%) and MGILCS (11%–15%) groups. Fewer fish were assigned to the UPCLWR (3–5%), SFSALM (~1%), and MFSALM (~1%) groups in the Snake River basin and to groups definitively outside the Snake River (LOWCOL, SKAMAN, WILLAM, KICKR, YAKIMA, or UPPCOL; 1%–2% in total).

Snake River origin was assigned by PBT for $n = 423$ – 459 steelhead (71%–74% of those released) to ten Snake River hatchery stocks nested within the SFCLWR, UPSALM, and MGILCS reporting groups (Tables S1 and S2). Snake River origin was probable for another 11%–16% that assigned to the SFCLWR, UPCLWR, SFSALM, MFSALM, or UPSALM

reporting groups, but with no PBT match. There was less certainty about the origin of 7%–9% of the samples assigned to the MGILCS group with no PBT match and for the 3%–5% of samples with no PBT match or reporting group assignment. Two-thirds (66%–68%) of the tagged steelhead had adipose-clips in both years (Fig. 3). Notably, 18% of PBT-assigned fish had no adipose-clips despite near-certain hatchery origin based on assignment to specific broodstock parents.

Genotypic sex was assigned for all but two fish with genetic samples, and 47 steelhead with no genetic data were designated unknown sex. Sex ratios (M:F) differed between years at 56:44 in 2013 and 37:63 in 2014 ($n = 1,165$, $\chi^2 = 41.2$, $P < 0.001$). Likely ocean age was available for 883 steelhead with PBT assignments: 243 (28%) were 1-sea, 631 (71%) were 2-sea, and 9 (1%) were 3-sea; fish not assigned by PBT were designated unknown age. Hereafter, 2- and 3-sea fish were combined for analyses. The 1-sea:2-sea ratios differed by year at 39:61 in 2013 and 15:85 in 2014 ($\chi^2 = 64.9$, $P < 0.001$). Sex $\times$ sea age composition differed within year: males made up 76% of 1-sea and 43% of 2-sea fish in 2013 ($\chi^2 = 48.1$, $P < 0.001$) and were 69% of 1-sea and 31% of 2-sea fish in 2014 ($\chi^2 = 32.9$, $P < 0.001$).

On average, steelhead tagged in 2014 were longer (mean = 75.5 cm, SD = 9.4, range = 52.5 cm to 95.0 cm) than those tagged in 2013 (mean = 71.1 cm, SD = 10.4, range = 52.5 cm to 95.0 cm) (ANOVA $F = 58.7$, $P < 0.001$). Furthermore, females were shorter than males by 3 cm to 5 cm, on average, within the 1-sea (ANOVA $F = 17.1$, $P < 0.001$, $n = 242$) and 2-sea (ANOVA $F = 123.3$, $P < 0.001$, $n = 636$) sub-samples (years combined).

Upriver migration survival

Survival from release downstream from Bonneville Dam to exit from the Lower Granite reservoir was 0.566 for the full sample of 620 steelhead in 2013 and 0.586 for the 592 in 2014 (Table 2, Fig. 4). During this migration stage, 7% of radio transmitters were returned from main stem fisheries, another 1.3% was returned with no information (presumed main stem harvest); additional Snake River-assigned fish were reported harvested in lower Columbia River tributaries. Survival estimates for the most abundant Snake River reporting groups were 0.611–0.652 (SFCLWR, $n = 351$ – 352), 0.479–0.653 (UPSALM, $n = 98$ – 121), and 0.588–0.667 (UPCLWR, $n = 17$ – 30). The mixed-origin MGILCS group had lower apparent survival (0.315–0.397, $n = 68$ – 92) past Lower Granite reservoir, but at least 29% of the MGILCS fish entered Columbia River tributaries other than the Snake River (i.e., they were likely successful migrants from other locations, for a minimum survival to presumed natal tributaries of ~ 0.65).

Adipose-clipped steelhead had higher survival from Bonneville Dam past Lower Granite reservoir (0.600–0.606, $n = 401$ – 407) than steelhead without clips (0.505–0.545, $n = 191$ – 212) (Fig. 3). However, this was partially an artifact of the relatively low proportion of adipose-clipped steelhead in the MGILCS reporting group, many of which were wild-origin fish from the John Day River, a middle Columbia River tributary. Female survival (0.559–0.646, $n = 263$ – 362) was higher than male survival (0.469–0.553, $n = 211$ – 329), though the difference was slight in 2013. Survival was higher, on average, for 1-sea (0.603–0.683, $n = 63$ – 180) than 2-sea (0.606–0.611, $n = 280$ – 360) steelhead, and both age classes had higher survival than the unknown-age group (0.450–0.509, $n = 160$ – 169) again reflecting, in part, the mixed-origin, unknown-age of the MGILCS fish.

A total of 1147 steelhead were included in the upstream migration survival models (Table S3), and 65 were excluded because they were likely from sites outside the Snake River or had

missing covariate data. The most parsimonious model included reporting group ($df = 4$, $\chi^2 = 36.7$, $P < 0.001$), sex ($df = 2$, $\chi^2 = 15.1$, $P < 0.001$), and sea age ($df = 2$, $\chi^2 = 15.1$, $P < 0.001$). Among reporting groups, survival was lower for the MGILCS group (odds ratio = 0.320, 95% CI = 0.209–0.491) and the UPSALM group (odds = 0.620, 95% CI = 0.438–0.878), with SFCLWR as the reference group. Confidence intervals included 1.000 for the UPCLWR group and for the combined SFSALM and MFSALM fish. Males had lower survival than females (odds = 0.608, 95% CI = 0.471–0.785) and the 95% CI included 1.000 for the comparison of unknown sex fish and females. Lastly, 2-sea steelhead had lower survival than 1-sea fish (odds = 0.565, 95% CI = 0.393–0.813) and unknown age steelhead also had lower survival than 1-sea fish (odds = 0.459, 95% CI = 0.302–0.699).

Survival in Snake River spawning areas

In total, 351 (2013) and 347 (2014) tagged steelhead entered possible spawning areas upstream from Lower Granite reservoir (Table 2). Of the fish that reached tributaries, about 18.2% of transmitters were returned from tributary fisheries and 13.6% were returned from hatchery facilities. Minimum survival of the 698 fish to kelt detection in the Lower Granite reservoir or at a downstream dam was 0.137 (2013) and 0.170 (2014). Adipose-clipped steelhead had lower survival (0.098–0.128, $n = 243$ –244) than those without clips (0.224–0.269, $n = 104$ –107). Males had lower survival (0.051–0.071, $n = 99$ –182) than females (0.222–0.238, $n = 147$ –234). Survival for the most abundant reporting groups was 0.144–0.153 (SFCLWR, $n = 215$ –229), 0.109–0.121 (UPSALM, $n = 58$ –64), 0.241–0.333 (MGILCS, $n = 27$ –29), and 0.100–0.250 (UPCLWR, $n = 10$ –20).

Of the 698 steelhead that entered spawning areas upstream from Lower Granite reservoir, 660 (95%) had complete covariate data and individual assignments to Snake River groups. The most parsimonious model for steelhead survival from Lower Granite reservoir exit to kelt status included fin clip ($df = 1$, $\chi^2 = 18.2$, $P < 0.001$, $n = 660$) and sex ($df = 1$, $\chi^2 = 27.4$, $P < 0.001$). Adipose-clipped steelhead had lower survival than unclipped fish (odds = 0.382, 95% CI = 0.245–0.594) and males had much lower survival than females (odds = 0.236, 95% CI = 0.137–0.405).

Kelt outmigration survival through reservoirs and past dams

In total, 48 (spring 2014) and 59 (spring 2015) presumed kelts were detected in Lower Granite reservoir or at dams further downstream. First detection dates of kelts ranged from late March to mid-May in both years (*median* = 20 April and 25 April). These fish were 8%–10% of the total samples of late-run steelhead released below Bonneville Dam and 14%–17% of the potential spawners upstream from Lower Granite reservoir. A majority (62%) was from the SFCLWR reporting group, most (81%) were females, and age composition was 17% 1-sea, 51% 2-sea, and 34% unknown age.

Minimum survival for the presumed kelts from the head of Lower Granite reservoir to Ice Harbor Dam was 0.313 (spring 2014) and 0.390 (spring 2015) and was 0.125 and 0.203, respectively, to Bonneville Dam (Table 2, Fig. 5). Sample sizes were small for most trait groups within year. With both years combined, minimum kelt survival to Bonneville Dam was 0.091 (SFCLWR, $n = 66$), 0.357 (UPSALM, $n = 14$), 0.145 (adipose-clipped, $n = 55$), 0.192 (unclipped, $n = 52$), 0.278 (male, $n = 18$), 0.149 (female, $n = 87$), 0.250 (1-sea, $n = 16$), 0.073 (2-sea, $n = 55$), and 0.278 (unk-sea, $n = 36$).

Of the 107 presumed kelts, 103 (96%) had complete covariate data and individual assignments to Snake River reporting groups. Initial models indicated quasi-complete data separation due to three kelts from the SFSALM and MFSALM groups; these fish were excluded from the model comparison (i.e., final model $n = 100$). The most parsimonious model for kelt survival to Ice Harbor Dam was the age-only model, with lower survival for 2-sea versus 1-sea fish ($df = 2$, 10.82, $P = 0.005$, odds 0.233, 95% CI = 0.070–0.770); there was no difference between unknown- and 1-sea fish. The best model for survival to Bonneville Dam was the length-only model ($df = 1$, $\chi^2 = 5.92$, $P = 0.015$), where survival declined as steelhead length increased (odds = 0.932, 95% CI = 0.880–0.986).

Bonneville-to-Bonneville survival

Eighteen Snake River kelts were detected at or downstream from Bonneville Dam. Bonneville-to-Bonneville survival models had quasi-complete data separation and so we instead compared proportions among the primary trait groups and excluded fish from probable non-Snake River sites and with missing covariate data ($n = 1,143$ – $1,147$ per comparison). Survival was higher for unclipped (0.027) than adipose-clipped steelhead (0.010) (Pearson's $\chi^2 = 4.5$, $P = 0.033$) and was higher for unknown-age fish (0.038) than for 1-sea (0.017) and 2-sea (0.006) fish ($\chi^2 = 11.9$, $P = 0.003$), at least partially reflecting differences between wild- and hatchery-origin fish. Survival also differed among reporting groups, at 0.025 (MGILCS), 0.009 (SFCLWR), 0.021 (UPCLWR), 0.023 (UPSALM), and 0.100 (SFSALM+MFSALM) ($\chi^2 = 13.2$, $P = 0.010$). Survival did not differ in 2013-2014 (0.010) versus 2014-2015 (0.021) ($\chi^2 = 2.3$, $P = 0.133$) or for females (0.021) versus males (0.009) ($\chi^2 = 2.6$, $P = 0.106$).

Discussion

Mortality patterns across freshwater stages

This study uniquely partitioned the freshwater mortality of late-run Snake River steelhead over their long-distance migration and temporally-protracted adult life history stages. Approximately 1% to 2% of Snake River-assigned steelhead survived from pre-spawn collection at Bonneville Dam to kelt detection at Bonneville Dam the following year, a sequence that serves as a proxy for sea-to-sea survival. Among fish genetically assigned to Snake River reporting groups (i.e., to SFCLWR, UPCLWR, UPSALM, SFSALM, or MFSALM), estimated additive mortality across groups was: ~38% mortality during upstream migration through the impounded migration corridor, ~53% mortality in Snake River tributaries through the spawning period, and ~8% mortality during kelt outmigration through reservoirs and past dams. Stage-specific mortality estimates across years and Snake River reporting groups were relatively lower during upstream migration (~38%) than during the reproductive stage (~85% mortality among steelhead that reached spawning tributaries) and during kelt outmigration (~84% mortality among steelhead detected initiating kelt outmigration), confirming our first hypothesis.

Improved understanding of when and where adult steelhead mortality occurs, and how patterns differ among the many demographic groups, should help managers tasked with the conservation and recovery of late-run Snake River populations, including the B-run phenotype. Reducing the ~38% mortality during upstream migration, for example, may have a more direct effect on population growth rates than reducing the ~8% of total mortality that occurred during kelt outmigration. Alternately, if restoration of genetic and life history diversity is prioritized, then management actions that reduce kelt mortality will warrant additional resources. The

relationships among stock-of-origin, individual traits, and stage-specific mortality highlight the complex management challenges for the Snake River metapopulation.

Upstream migration survival

More than a third of the putative Snake River steelhead did not survive upstream migration past eight dams and eight reservoirs. The unsuccessful group included known harvested fish (i.e., main stem harvest reported to us: ~8%) and strays that were harvested or last detected in non-natal lower Columbia River tributaries (~3–7% of the SFCLWR, UPCLWR, UPSALM, SFSALM, and MFSALM reporting groups). Harvest of steelhead strays that temporarily use cool-water tributaries along the migration route can be a substantial portion of total harvest in this system (e.g., Keefer et al. 2009). Predation, mortality associated with fallback at dams (Keefer et al. 2005), and harvest not reported to us likely accounted for some of the remaining unsuccessful upstream migrants. Our combined harvest estimate from main stem fisheries (~8%) and non-natal tributary fisheries (<7%) was lower than some independent estimates of B-run harvest in the lower Columbia reach, which are near 20% in some years (unpublished data from the US v OR Technical Advisory Committee [TAC]). However, methodological differences make direct comparison of harvest estimates difficult. For example, in our study area, tribal gillnet fisheries are assessed differently than recreational fisheries. Furthermore, the TAC estimates use a B-run index stock based solely on steelhead size (≥ 78 cm), whereas the radiotelemetry estimates were for the aggregate late-run fish, including those <78 cm. Continued assessment of harvest estimation methods is recommended.

Support was mixed for our trait-based upstream migration hypotheses. As expected, steelhead survival to Snake River spawning tributaries varied among reporting groups and was

higher for younger than for older fish. Contrary to expectations, survival was higher for adipose-clipped fish than for unclipped fish, though this was related in part to sample demographics. More specifically, the geographic imprecision of the MGILCS reporting group and uncertainty associated with the unknown-sex and unknown-age MGILCS fish complicated interpretation of model results for this stage. In each year, well over half of the MGILCS steelhead did not have parentage data and consequently may have originated from Columbia River tributaries other than the Snake River (Hess et al. 2016). More than half of the MGILCS fish also did not have adipose clips and the lower survival for unclipped fish in the full models was at least partially an artifact of natal origin rather than elevated mortality relative to adipose-clipped fish. When we excluded all fish in the MGILCS group from upstream survival models, the results indicated that reporting group, sex, and age covariates remained important predictors of survival, but adipose clip status did not. Future studies may resolve the stock-of-origin uncertainties as genetic baselines expand in geographic scope, accuracy, and precision. Age uncertainty could also be reduced through scale analysis, though interpretation errors are often >10% for adult steelhead scales, and are especially high for wild-origin fish (e.g., Seamons et al. 2009).

Survival in spawning tributaries

We expected high steelhead attrition in Snake River spawning tributaries due to high reproductive effort (i.e. spawning-related mortality), hatchery collection, and terminal fisheries. However, our trait-based hypotheses within the spawning stage were only partially confirmed. In line with expectations, steelhead without fin clips survived at more than twice the rate of adipose-clipped steelhead, and female survival was more than three times higher than male survival. Relatively higher male mortality is common among iteroparous salmonids, and has

been attributed to aggressive male-male competition, investment in secondary sexual traits, and the energetic costs of early arrival on spawning grounds and extensive searching for mates (Fleming 1996; Fleming and Reynolds 2004; Nyqvist et al. 2016).

Unexpectedly, sea age was not included in the most parsimonious model for the tributary survival stage, although 1-sea fish survived at more than double the rate of older fish in an age-only comparison (see Table 2). The incongruity between the age-only data and the ‘best’ model results was perhaps due to the inclusion of many unknown-age fish in the models, to the unbalanced age×sex composition of the samples, or to insufficient sample size to detect effects. Males made up 69%–76% of the 1-sea fish versus 31%–43% of the older fish, for example. Models with interaction terms (i.e., age×sex) were not in our *a priori* model set, but may have better captured the demographic complexity in the data. In any case, reproductive life history analyses strongly support a decrease in iteroparity as adult age and body size increase (Crespi and Teo 2002) and this has been demonstrated in other Snake River steelhead studies. Narum et al. (2008) and Matala et al. (2016) used genetic data to identify the origin populations of prespawn steelhead and kelts in the Snake River and then calculated the relative abundance of each group. In these studies, nominal B-run steelhead from the Clearwater and Salmon rivers were substantially under-represented in the kelt samples relative to their prespawn abundance; furthermore, smaller steelhead were more likely to survive within populations, supporting the hypothesis that large body size or age limits expression of iteroparous behaviors in these populations.

Kelt outmigration survival

Less than 10% of the total radio-tagged sample was detected as Snake River kelts and this group was strongly (~4.8:1) female-skewed. The female bias was consistent with previous studies of Snake River kelts (Narum et al. 2008; Matala et al. 2016) and studies of many other iteroparous salmonid populations (e.g., Fleming 1998; Ohms et al. 2014; Clemens 2015) and implies that males allocate a greater proportion of resources during spawning than females. Many Snake River kelts were also older fish from the SFCLWR reporting group, and the skewed demographics of the kelt sample may have limited the inferential power of downstream survival analyses. Nonetheless, our expectation that younger (and smaller) kelts would survive outmigration at higher rates than older fish was confirmed, paralleling results from previous studies of steelhead kelts (Keefer et al. 2008b; Harnish et al. 2015) and Atlantic salmon *Salmo salar* kelts (Jonsson et al. 1991; Fleming 1998; Nyqvist et al. 2016). Our hypothesis that female kelts would survive at higher rates than male kelts was not supported, perhaps due to the highly skewed sex ratio or the aforementioned age×sex interaction. We also did not find evidence for higher mortality by kelts that initiated outmigration relatively late in the spring, despite previous research showing a clear relationship between late kelt migration in the Columbia and Snake rivers and reduced probability of repeat spawning (Keefer et al. 2008b).

Our estimate of kelt-specific mortality across trait groups and years (~84%) was similar to estimates from earlier radio and acoustic telemetry studies of mixed-origin Snake River kelts (e.g., Wertheimer and Evans 2005; Colotelo et al. 2014). High kelt mortality in the Columbia-Snake River system can be attributed in large part to exhaustion of the lipids and proteins that are metabolized to complete outmigration. Recent physiological assays of steelhead kelts collected at Lower Granite Dam and in the Clearwater River basin found that many were effectively starved, with energetic reserves comparable to levels found in dead, post-spawn Pacific salmon

(Penney and Moffitt 2014; Penney et al. 2016). Iteroparity rates also generally decline as the distance from spawning grounds to the ocean increases (Willson 1997; Keefer et al. 2008b), and it is therefore likely that most Snake River steelhead populations historically had low repeat spawning rates relative to populations spawning closer to the Pacific Ocean.

Impoundment of the lower Snake River and Columbia River has almost certainly further reduced kelt survival and iteroparity rates, because kelts migrate more slowly (and therefore with additional energetic costs) through low-velocity reservoirs than through undammed rivers (Wertheimer and Evans 2005; English et al. 2006). Dam passage also presents a variety of direct and indirect kelt mortality risks from turbine blade strikes, from contact with fish bypass infrastructure, and from passage over spillways. A number of projects have been undertaken to improve passage effectiveness and survival of kelts in the Columbia River basin, including springtime operation of surface-flow routes (e.g., Wertheimer 2007; Khan et al. 2013), kelt collection and downstream transportation (Evans et al. 2008), and kelt collection and reconditioning in hatchery facilities (Hatch et al. 2013). It remains to be seen whether these incremental changes lead to increased iteroparity in Snake River steelhead and to concomitant demographic, genetic, and fitness benefits.

Demographics of late-run steelhead

The late-run steelhead samples collected at Bonneville Dam were demographically and genetically complex, with many fish not meeting the traditional B-run size and age criteria (2- or 3-sea fish with body size >78 cm FL). For example, ~28% of the steelhead with parentage data were apparently 1-sea fish, including some from Dworshak National Fish Hatchery in the Clearwater River (a B-run facility) and some from Salmon River hatcheries with B-run

production (Tables S1 and S2). These demographic patterns were consistent with recent studies that demonstrate a non-dichotomous continuum of phenotypes in Snake River steelhead (Copeland et al. 2017) as well as complex genetic relationships among Columbia and Snake River populations (Blankenship et al. 2011; Campbell et al. 2012; Hess et al. 2016). Our genetic assignments further indicated that at least ~15% of tagged late-run steelhead were associated with putative early-run groups, including from hatcheries in the Grande Ronde River and from a mix of wild and hatchery populations from the Deschutes, John Day, and Walla Walla rivers nested in the MGILCS reporting group. Very few (~1%) of the late-run fish were from Columbia River populations upstream from the Columbia River–Snake River confluence. However, it is probable that the relative abundance of upper Columbia and MGILCS populations would have been higher had steelhead tagging started 26 August (the established separation date for the early and late runs at Bonneville Dam); temperature-related restrictions precluded some of the planned tagging each year.

Both genetic assignment methods had some limitations that affected results and interpretation. The PBT data were highly accurate and precise with respect to many Snake River hatchery-origin steelhead, but these assignments were limited to fish with available genotyped parents and therefore all wild-origin fish and those from hatcheries without baseline genotypes could not be assigned with this approach. Individual assignment to reporting groups was possible for nearly all fish, but this approach was less accurate and precise than PBT assignments (Hess et al. 2016). In particular, reporting group assignments were less geographically explicit than PBT assignments, which made some data interpretation more challenging. Uncertainty was especially high for the mixed-origin MGILCS reporting group, which included ~39 baseline populations spread across multiple mid-Columbia River and Snake River watersheds (Hess et al.

2016). Their close genetic relationships derive from a legacy of inter-basin hatchery transfers in this region (Busby et al. 1996), and to high rates of inter-basin straying and gene flow among the populations that comprise this reporting group (Keefer and Caudill 2014). Low geographic specificity and missing age data for wild steelhead and for many MGILCS fish were significant sources of uncertainty for the study’s composition objectives and for interpreting upstream migration survival estimates. Nonetheless, the integration of genetic assignments with biotelemetry greatly enhanced our ability to understand how steelhead mortality varied across demographic, phenotypic, and origin groups. These advances should inform regional conservation and management of the species.

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Table 1. Geographic locations of 14 genetic reporting groups (RG) used in genetic assignment of radio-tagged steelhead (*Oncorhynchus mykiss*) in 2013-2014. rkm = river kilometres from the Columbia River mouth.

RG code	Description	Geographic location
WCOAST	Quinault	Washington coast north of Columbia River
LOWCOL	Lower Columbia River	Primarily tributaries below Bonneville Dam
SKAMAN	Skamania	Hatchery stock with lower Columbia origin
WILLAM	Willamette River	Columbia River tributary (rkm ~163)
BWSALM	Big White Salmon River	Columbia River tributary (rkm ~270)
KLICKR	Klickitat River	Columbia River tributary (rkm ~290)
MGILCS	Mix: Deschutes River, mid-Columbia River, lower Snake River, lower Clearwater River, Grande Ronde River, Imnaha River, & lower Salmon River	Middle Columbia River and lower and middle Snake River
YAKIMA	Yakima River	Columbia River tributary (rkm ~539)
UPPCOL	Upper Columbia River: mix of Wenatchee, Methow, Entiat, & Okanogan rivers	Columbia River tributaries (rkm ≥700)
SFCLWR	South Fork Clearwater River	Clearwater River tributary (rkm ~866)
UPCLWR	Upper Clearwater River	Clearwater River (rkm ≥866)
SFSALM	South Fork Salmon River	Salmon River tributary (rkm ~1 040)
MFSALM	Middle Fork Salmon River	Salmon River tributary (rkm ~1 144)
UPSALM	Upper Salmon River	Salmon River (rkm ≥1 144)

Table 2. Point estimates of prespawn adult and post-spawn kelt steelhead (*Oncorhynchus mykiss*) survival through several segments of their freshwater migrations, by reporting group, fin clip status, sex, and ocean age. Tagged = number of prespawn adults released downstream from Bonneville Dam; potential spawner = detected at a site upstream from Lower Granite reservoir; likely kelt = detected in Lower Granite reservoir or at a main stem dam in spring following presumed spawning; kelt at IHD = presumed kelt detected at Ice Harbor Dam; kelt at BON = presumed kelt detected at Bonneville Dam.

Group	Number of steelhead					Survival proportions			
	Tagged	Potential	Likely	Kelt at	Kelt at	B:A	C:B	D:C	E:C
		Spawner ¹	kelt	IHD	BON				
	(A)	(B)	(C)	(D)	(E)				
2013	620	351	48	15	6	0.566	0.137	0.313	0.125
2014	592	347	59	23	12	0.586	0.170	0.390	0.203
SFCLWR	703	444	66	17	6	0.632	0.149	0.258	0.091
UPCLWR	47	30	6	4	1	0.638	0.200	0.667	0.167
UPSALM	219	122	14	6	5	0.557	0.115	0.429	0.357
SFSALM	12	9	3	3	2	0.750	0.333	1.000	0.667
MFSALM	8	3	-	-	-	0.375	-	-	-
MGILCS	160	56	16	8	4	0.350	0.286	0.500	0.250
Other ²	19	1	1	-	-	0.053	1.000	-	-
None	44	33	1	-	-	0.750	0.030	-	-
Ad clip	808	487	55	19	8	0.603	0.113	0.345	0.145
No clip	403	211	52	22	10	0.524	0.246	0.423	0.192

Male	540	281	18	8	5	0.520	0.064	0.444	0.278
Female	625	381	87	29	13	0.610	0.228	0.333	0.149
Unk-sex	47	36	2	1	-	0.766	0.056	0.500	-
1-sea	243	151	16	8	4	0.621	0.106	0.500	0.250
2-,3-sea	640	389	55	11	4	0.608	0.141	0.200	0.073
Unk-sea	329	158	36	19	10	0.480	0.228	0.528	0.278

¹ Potential spawner in Snake River upstream from Lower Granite reservoir

² LOWCOL, SKAMAN, WILLAM, KLICKR, YAKIMA, UPPCOL

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Figure legends

Fig 1. Map of the Columbia and Snake rivers showing main stem dams and major tributaries mentioned in the text. Adult summer-run steelhead (*Oncorhynchus mykiss*) were collected and double-tagged (radio transmitters, PIT tags) at Bonneville Dam in 2013 and 2014 and then monitored during prespawn upstream migration and during post-spawn downstream migration by kelts.

Fig 2. Numbers of adult summer-run steelhead (*Oncorhynchus mykiss*) that were counted (solid lines) at Bonneville Dam on the Columbia River and that were collected and double-tagged (bars) with radio transmitters and PIT tags in (a) 2013 and (b) 2014. Dashed vertical lines represent the management separation date between early- and late-run summer steelhead.

Fig. 3. Treemap showing relative abundance of steelhead (*Oncorhynchus mykiss*) that were collected and radio-tagged at Bonneville Dam by genetic assignment to genetic reporting group, year (2013, $n = 620$; 2014, $n = 592$), fin clip status (Clip, None), and sea age (1 = 1-sea, 2 = 2-sea, U = unknown). Reporting groups include: South Fork Clearwater River (SFCLWR), Upper Clearwater River (UCW=UPCLWR), Upper Salmon River (UPSALM), the combined Middle Fork and South Fork Salmon River (MSF = MFSALM, SFSALM), and the mixed-stock, mid-Columbia River and Snake River group (MGILCS). The 'Other' category includes stocks from outside the Snake River (WILLAM, LOWCOL, SKAMAN, KCLICKR, YAKIMA, UPPCOL) plus steelhead with no genetic stock assignment.

801 Fig 4. Cumulative prespawn migration survival in the main stem Columbia and Snake rivers of
802 double-tagged, steelhead (*Oncorhynchus mykiss*), from release downstream from Bonneville
803 Dam on the Columbia River to pass ('Exit') the upstream end of Lower Granite Reservoir on the
804 Snake River. Estimates are for the subsets of steelhead with probable or possible Snake River
805 origin based on genetic assignments and data from both years are combined. Left panel shows
806 survival for fish with genetic assignment to reporting groups, including: SFCLWR (South Fork
807 Clearwater River), UPCLWR (upper Clearwater River), UPSALM (upper Salmon River), and
808 MGILCS (mix of mid-Columbia and Snake River stocks). Right panel shows survival for
809 steelhead with and without fin clips, for males and females, and by ocean age: 1-, 2-, and 3-sea
810 fish were classified using parentage-based tagging (PBT) and the remainder was classified as
811 unknown age (Unk-sea). X-axis labels are dam abbreviations spaced by river kilometer in
812 ascending order: BON = Bonneville, TDD = The Dalles, JDD = John Day, MCN = McNary,
813 IHD = Ice Harbor, LMD = Lower Monumental, LGD = Little Goose, LGR = Lower Granite.
814

815 Fig 5. Cumulative kelt (*Oncorhynchus mykiss*) migration survival from entry into the Lower
816 Granite reservoir (Enter) downstream past Bonneville Dam. Left panel shows survival for fish
817 with genetic assignment to reporting groups, including: SFCLWR (South Fork Clearwater
818 River), UPCLWR (upper Clearwater River), UPSALM (upper Salmon River), and MGILCS
819 (Snake River stocks only). Right panel shows survival for kelts with and without fin clips, for
820 males and females, and by ocean age: 1-, 2-, and 3-sea fish were classified using parentage-based
821 tagging (PBT) and the remainder was classified as unknown age (Unk-sea). X-axis labels are
822 dam abbreviations spaced by river kilometer in descending order: LGR = Lower Granite, LGD =

823 Little Goose, LMD = Lower Monumental, IHD = Ice Harbor, MCN = McNary, JDD = John Day,
824 TDD = The Dalles, BON = Bonneville.

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Fig 1.

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