## ARTICLE

# Patterns of Iteroparity in Wild Snake River Steelhead

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### Abstract

Some anadromous salmonids are iteroparous (repeat spawners); however, postspawn individuals are often not considered in management plans because of the lack of long-term studies of this life history. The balance of factors affecting survival between spawns and fecundity of repeat spawners should determine the percentage of iteroparous individuals in a population. Steelhead *Oncorhynchus mykiss* are capable of iteroparity, but Snake River populations in the interior Columbia River basin in the Pacific Northwest have the lowest iteroparity rates. Managers are interested in augmenting the incidence of iteroparity as a conservation measure. However, there is little information about repeat-spawning steelhead to guide and evaluate management. In this study, we elucidated patterns and characteristics of repeat-spawning steelhead in the Snake River basin. Repeat spawners were overwhelmingly female and were found in all 10 stocks. Most iteroparous fish first spawned after 1 year in the ocean (51.4%) and skipped a year between spawns (55.4%). Growth between spawns declined for longer, older steelhead. Survival from the first spawning migration to postspawn emigration increased during the study. However, survival in the Columbia River estuary and Pacific Ocean declined such that overall survival to second spawn varied little. Small females were most likely to survive to a second spawning migration. We hypothesized that iteroparity in Snake River steelhead was constrained by the energetic costs of the spawning migration (distance, elevation, timing, dam passage) combined with a lack of timely postspawn recovery. Hence, survival to second spawning migration is low for Snake River steelhead and most postspawn steelhead needed a full year to recover. Management programs intended to augment the incidence of iteroparity should account for (1) factors that increase stress and metabolic demand on spawning and postspawn fish and (2) factors that increase the time it takes for emigrating kelts to effectively refuel and recover.

Some species of anadromous salmonids can potentially have multiple reproductive events over the course of their lifetime; however, postspawn individuals are often not considered in management plans for anadromous salmonids because of the lack of long-term studies of this life history (Halttunen 2011). Iteroparous individuals (repeat

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spawners) may have higher per capita reproductive value than first-time spawners and are important to population dynamics and conservation (Seamons and Quinn 2010; Halttunen 2011). Furthermore, iteroparity provides extra population resilience for anadromous salmonids (Moore et al. 2014). However, anthropogenic changes to the environment may select for or against repeat spawning (Scott and Gill 2008), and thus iteroparity has become an important topic in anadromous salmonid management and research.

Several factors likely affect patterns of iteroparity in anadromous salmonids. Iteroparity largely benefits females because they can produce more and larger eggs for the second spawning event after additional growth between spawns (Quinn et al. 2011). However, energetic investment in spawning increases with size, while the ability to recover decreases (Jonsson et al. 1991; Fleming and Reynolds 2004), implying an optimal size for successful repeat spawners. Long migrations constrain iteroparity in anadromous salmonids (Fleming and Reynolds 2004), suggesting further energetic restrictions for some populations. Timing into the ocean is important for smolt survival (Haeseker et al. 2012), so we might expect the same for emigrating postspawn steelhead. In general, the balance of factors affecting survival between spawns and the fecundity of repeat spawners should determine the percentage of iteroparous individuals in a population (Christie et al. 2018).

Steelhead *Oncorhynchus mykiss* have the most diverse life history repertoire of the Pacific salmonids (genus *Oncorhynchus*; Quinn 2005). Unlike most other anadromous members of the genus, steelhead are capable of iteroparity, although infrequently in some populations. Despite their diversity of life histories, many steelhead populations in the Pacific Northwest are at critically low levels. Most summer-run steelhead in the Columbia River basin are from the Snake River basin, but Snake River steelhead populations have perhaps the lowest iteroparity rates recorded for steelhead (mean = 0.69% during 2002–2004; Keefer et al. 2008). Snake River steelhead migrate farther and to higher elevations than any other group of steelhead (Busby et al. 1996), which may constrain iteroparity. Steelhead managers are interested in increasing the incidence of iteroparity to conserve steelhead populations (Narum et al. 2008; Hatch et al. 2013). However, little information exists on natural patterns of iteroparity for Snake River steelhead to guide and evaluate management of this life history.

In this study, we addressed three objectives: (1) describe important characteristics of repeat spawners (life history, sex ratio, and growth between spawns), (2) estimate survival from the first spawning migration to the second spawning migration, and (3) investigate important influences on survival to second spawn. We expected to find that survival advantages accrue to females, to fish exhibiting optimal lengths and postspawn emigration dates, and to stocks lower in elevation and closer to the ocean.

## METHODS

*Study population.—* Snake River steelhead are a group of summer-run, stream-maturing populations (Busby et al. 1996). Adult fish return from the ocean in late summer and early fall to migrate up the main-stem Columbia and Snake rivers until winter, when they seek low-velocity, deeper habitats. As temperatures warm in the spring, steelhead resume upstream migration and enter spawning tributaries. The first major spawning tributary is the Tucannon River on the lower Snake River, 622 km from the Pacific Ocean, whereas the upper tributaries of the Salmon River are almost 1,500 km from the ocean (Figure 1). Stream elevations range from 105 m above sea level at the mouth of the Snake River to well over 2,000 m in the headwaters of the Salmon River. Depending on elevation, Snake River steelhead spawn from March to early June. The kelts (postspawn steelhead) then reverse course and attempt to migrate downriver to the Pacific Ocean. Adults may return to spawn the year following the first spawn (consecutive spawners) and others may return more than 1 year after the first spawn (skip spawners).

*Data collection.—* We collected data on the composition of prespawn steelhead as they migrated upstream past Lower Granite Dam on the Snake River, 695 km from the Pacific Ocean (Figure 1). Adults returning to spawn in tributaries of the Snake River must ascend fish ladders at eight dams during their migration. Lower Granite Dam is the final dam encountered before Snake River steelhead disperse to spawn, with the exception of those spawning in the Tucannon River. Samples were collected at a trap located on the Lower Granite Dam adult fish ladder (Steinhorst et al. 2017). The trap is operational 24 h/d, and a trap gate opens 4 times/h such that a daily systematic sample (by time) is taken from the fish ascending the fish ladder.

We collected biological data, scale samples, and tissue samples from all wild steelhead trapped. Scale samples provided age information. Tissue samples provided genetic and sex data. In the Snake River basin, most hatchery-origin steelhead have a clipped adipose fin; however, those released to supplement wild populations typically have intact adipose fins so that they are not subject to harvest in mark-selective sport fisheries. Unclipped hatchery fish were identified by parentage determined genetically (Steele et al. 2013). Fork length was measured to the nearest whole centimeter. Eight to twelve scales per fish were collected from the area immediately posterior to the dorsal fin and above the lateral line by scraping with a knife. A small portion of the anal fin was removed for genetic analysis. All fish were
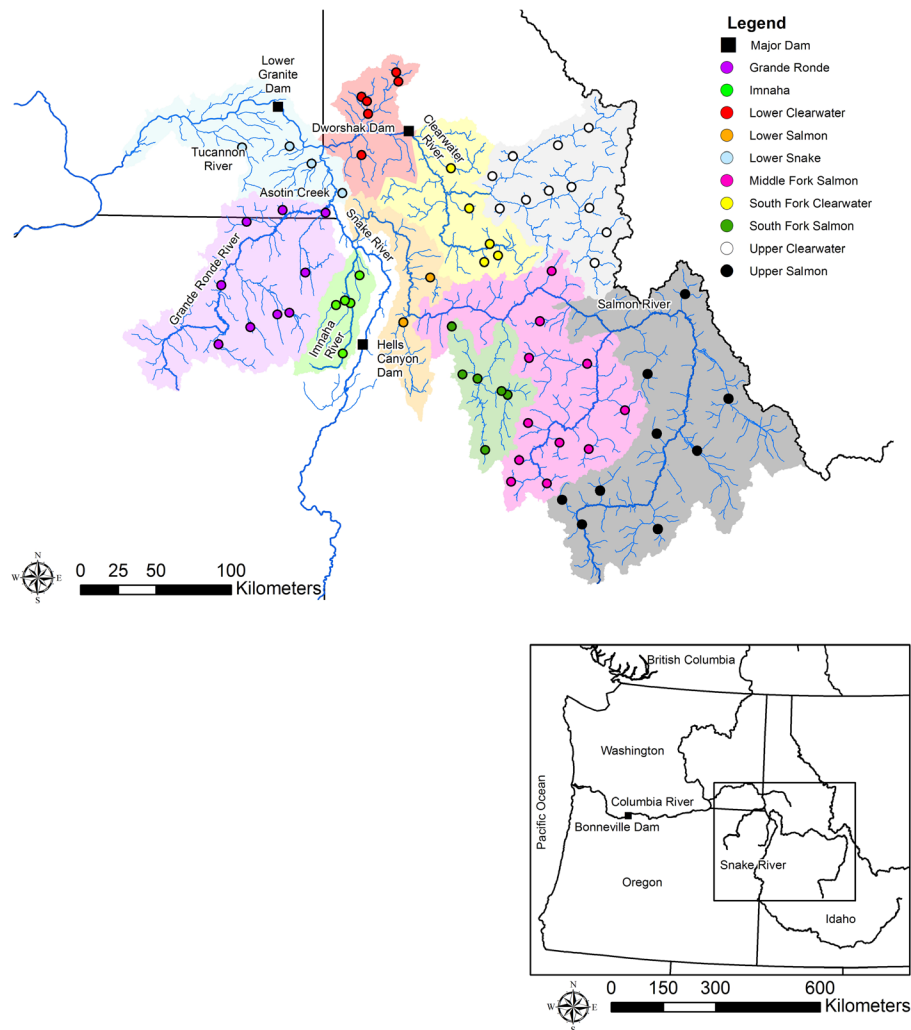
FIGURE 1. Map of the portion of the Snake River basin accessible to steelhead, showing major dams and locations where tissue samples were collected (colored circles) to determine the stock of origin (Ackerman et al. 2014). The areas for the 10 different stocks of origin are shown with the colored circles and the corresponding color-coded shading. The inset shows the position of the Snake River in the Columbia River basin in the Pacific Northwest.

scanned for a passive integrated transponder (PIT) tag. A PIT tag was injected into the pelvic girdle musculature if one was not present. Steinhorst et al. (2017) provide additional details about the program and adult trap operations at Lower Granite Dam. Repeat spawners collected in the systematic sample of upstream-migrating steelhead were identified by scale analysis. Data were aggregated by the year in which the fish would spawn (e.g., spawn year [SY] 2010 includes fish collected during summer–fall 2009 and spring 2010).

We supplemented the number of repeat spawners collected in the systematic sample by using detections of PIT tags implanted in wild adult steelhead in previous years, which we refer to as the targeted sample. Some tagged individuals on their second spawning migration were identified based on PIT tag detection and were shunted into the trap (Tenney et al. 2017) to provide samples from known repeat spawners for a validation study (Copeland et al. 2018). We used age and length data generated from this targeted sample to determine important characteristics of repeat spawners. Further, a third data set, detections of PIT-tagged fish at dams in the Columbia and Snake rivers, was used to estimate survival from first spawning migration to kelting and second spawning migration.

Ages were assigned based on scale examination (Copeland et al. 2017, 2018). Scales were cleaned and mounted between two glass slides. Images of samples were then digitized with a LeicaDM4000B microscope and a LeicaDFC425 camera using a 1.25× objective. For this study, we used postsmolt ages (i.e., within the ocean-growth region of the scale). Ocean annuli were identified as bands

exhibiting narrowing circuli spacing and cutting over. Spawn checks were identified based on the appearance of a ragged scar mark within the ocean-growth region of the scale (Copeland et al. 2018). Following European age notation, an ocean-age-1 consecutive spawner was denoted as 1S while an ocean-age-2 skip spawner is denoted as 2S1.

Tissue samples were analyzed to determine sex and the stock of origin (Ackerman et al. 2014). A 57–62% subsample was genotyped for SY 2010–2012, but >99% were genotyped for SY 2013–2015. Steelhead adults were screened at 187 single nucleotide polymorphisms and with a sex-specific allelic discrimination assay. Only individuals that genotyped successfully at >90% of single nucleotide polymorphisms were used for analysis. Fish identified as hatchery origin by parentage analysis (Steele et al. 2013) were excluded from further analyses. Stock of origin was determined using individual assignment. Ackerman et al. (2014) defined 10 stocks used for assignments at Lower Granite Dam (Figure 1).

*Data analysis.*— We used all individuals from the systematic and targeted samples to describe the life history characteristics of repeat-spawning steelhead from the Snake River basin for SY 2010–2017. Three characteristics were summarized for repeat spawners in each stock: proportion of females, proportion of fish that were in the ocean for 2 years before their first spawning migration, and proportion of skip spawners. We identified 100 individuals from the targeted sample that had also been sampled during their first spawning migration. For those individuals, we investigated growth in fork length between spawning migrations as a function of length at first spawn using linear regression. Because skip spawners have more opportunity for growth, we included the interaction between length with spawner type (e.g., consecutive versus skip spawner) in the regression model.

Lastly, we investigated survival from Lower Granite Dam to the ocean and return to Lower Granite Dam on the second spawning migration using detections of tags placed in wild steelhead at Lower Granite Dam on their first spawning migration during SY 2010–2015. Note that for most fish, this period includes survival through the winter before spawning. We queried the PIT Tag Information System (www.ptagis.org) for detections of tagged fish emigrating as kelts at any dam in the Snake and Columbia rivers and as returning spawners migrating upstream past Bonneville Dam and Lower Granite Dam (Figure 1). Kelt detections were defined as detections in the juvenile bypass systems at main-stem dams or at the surface bypass flume at Bonneville Dam between April 1 and July 15 during the year of first spawn. Detections of repeat spawners were defined as detections in the adult ladders at Bonneville Dam and Lower Granite Dam from July 1 of the year of first spawn (the earliest we might expect to see

consecutive spawners returning) to April 30 two years later (the latest we might expect to see skip spawners returning).

Complete detection histories of all individuals identified as potential kelts or repeat spawners were scrutinized. Because some steelhead overwinter in the main-stem rivers (e.g., Snake and Columbia rivers) and resume their spawning migration in the spring (Copeland et al. 2017), we examined records to verify that prospective kelts were not moving upstream, and further, we removed detections within 7 d of tagging at the Lower Granite Dam adult trap. Any kelt detections at Bonneville Dam were considered definitive. We summarized kelt and repeat-spawner detections by year of first spawn.

We used data on tagged fish to validate sex ratio and percentage of skip spawners determined from the combined systematic and targeted samples described previously and to show annual variation in those values. Proportion of repeat spawners returning as consecutive or skip spawners was based on the date of detection at Bonneville Dam relative to the year of first spawn. Proportion of females was based on detected fish that were genotyped.

We estimated survival at three stages using the detection histories described earlier and combined those estimates into total survival from first to second spawning migration. For this analysis, there were two key assumptions: (1) detection efficiencies of upstream-migrating fish in the Bonneville and Lower Granite fish ladders nearly approached 100% (Tenney et al. 2017) and (2) survival in the estuary and ocean of fish detected as kelts was equivalent to that of those that entered the estuary but were not detected migrating downstream. There were five inputs: number of tags placed during the first spawning migration ($T_i$, where $i$ is the spawn year), detections of these tags as kelts at Bonneville Dam ($K_i$), detections at Bonneville Dam on the second spawning migration ($R_{Bi}$), number of detections of repeat spawners at Bonneville Dam that were previously detected as a kelt at Bonneville Dam ($R_{BKi}$), and detections of repeat spawners at Lower Granite Dam ($R_{Li}$). Survival from the first spawning migration to kelt emigration over Bonneville Dam is $K_i$ expanded to account for tagged kelts that were not detected by treating detections of repeat spawners as recaptures in a mark–recapture framework. To reduce biases caused by low numbers of recaptures we add 1 to $K_i$ and $R_{BKi}$. Thus, survival from first spawning migration to kelt emigration ($S_{Ki}$) is

$$S_{Ki} = \frac{R_{Bi} \times (K_i + 1)}{\frac{R_{BKi} + 1}{T_i}}.$$

Survival from kelt emigration to initiation of the second spawning migration at Bonneville Dam ($S_{KRi}$) is

$$S_{KRi} = \frac{R_{Bi}}{\frac{R_{Bi} \times (K_i + 1)}{R_{BKi} + 1}}.$$

Survival from initiation of the second spawning migration at Bonneville Dam to return to the Snake River at Lower Granite Dam ($S_{BLi}$) is

$$S_{BLi} = \frac{R_{Li}}{R_{Bi}}.$$

Finally, survival from first spawning migration to second spawning migration ($S_{Ti}$) is the product of the three components:

$$S_{Ti} = S_{Ki} \times S_{KRi} \times S_{BLi}.$$

We tested for the influence of selected important characteristics on survival using a mixed-model regression on the logit of binary detection history (0 = tagged fish not detected, 1 = detected). Because the primary interest was in persistent differences, year was included as a random factor on the intercept. We tested for the fixed effects of sex, stock, and initial length on survival to second spawning migration. Lengths were centered and standardized by standard deviation. We also hypothesized there may be an optimal length for survival and therefore included a quadratic term with the main effect. We did not test for interactions among the main effects to keep studywise error low because of the extra parameters needed versus the low number of repeat spawners detected.

This exercise was completed for three interrelated data sets: from tagging to detection at Bonneville Dam as a repeat spawner, from tagging to detection as a kelt at a main-stem dam, and from kelt detection at Bonneville Dam to detection at Bonneville Dam as a repeat spawner. For fish detected as kelts at Bonneville Dam, we also tested the effect of Julian date of kelt emigration as a main effect with a potential optimal date (day of year, squared). Dates were centered and standardized by standard deviation.

Models were implemented in R (R Core Team 2016) using the lme4 package (Bates et al. 2016). We examined the fully saturated model for survival from tagging to detection at Bonneville Dam to assess model performance. The residual deviance was less than the degrees of freedom, so we judged that the data were not overdispersed and model performance was good. Fixed effects in all analyses were considered significant at $\alpha = 0.05$.

Parameter estimates were back-transformed or plotted for interpretation. For categorical variables (sex and stock), the odds ratio compared to the base case was determined by exponentiating the coefficient estimate. The reference cases were females for sex and Grande Ronde for stock. Because the continuous predictor variables (length and date of kelt emigration) had nonlinear effects, we present the values at which highest survival is predicted and compare predictions in terms of the odds ratio between the 25th and 75th percentiles. These predictions are also plotted along with the predictions from the 5th to the 95th percentiles to relate model predictions to the actual distributions of the data.

## RESULTS

We collected 262 repeat-spawning steelhead during normal trap operations and an additional 106 targeted samples. Only five samples failed to genotype, and there was representation from all genetic stocks (Table 1). Most repeat spawners in these samples originated from the Grande Ronde River, Upper Salmon River, and Lower Snake River genetic stocks. Similarly, we were able to assign sex to 96% of sampled fish. Repeat spawners were overwhelmingly female (92.7%). Most life histories fell into four categories: consecutive and skip spawners that first spawned after 1 year in the ocean (15.2% and 35.0%, respectively) and consecutive and skip spawners that had first spawned after 2 years in the ocean (28.6% and 19.8%, respectively). Three individuals were on their third spawning migration and one individual had skipped 2 years between spawning events; these four had first spawned after 1 year in the ocean. One fish had first spawned after 3 years in the ocean and was on a consecutive-spawning migration.

Length increased less between spawns for older, larger steelhead (Figure 2). Growth declined with length faster for skip spawners and the 95% confidence intervals about the slope estimates did not overlap between categories (skip spawners = 0.33 ± 0.10, consecutive spawners = –0.15 ± 0.08). Interestingly, both regressions predict zero growth at similar fork lengths (88.3 and 84.5 cm, respectively).

Of the 23,709 wild adult steelhead systematically tagged during SY 2010–2015, 3,172 (13.4%) were detected as kelts. Of those kelts, 295 (9.3%) were detected on a repeat-spawning migration, resulting in an overall estimated iteroparity rate of 1.2% for tagged individuals for the duration of the study. The number of kelt detections was surprisingly similar among years, indicating that conversion from spawner to kelt above Lower Granite Dam varied little among years. However, the number of kelts detected at Bonneville Dam varied among years by a factor of three. There were seven repeat spawners that were detected only at Lower Granite Dam, two of which were from a hatchery-based kelt reconditioning program (Andrew Pierce, Columbia River Inter Tribal Fish Commission, personal communication). Thus, five individuals showed evidence of naturally recovering in freshwater

TABLE 1. Numbers of repeat-spawning steelhead by life history type and stock as determined by scale patterns from the systematic and supplemented samples taken at Lower Granite Dam.

| Genetic stock | Life history type | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1S[a] | 1S1[a] | 1S1S | 1S1S1 | 1S2 | 1SS1 | 2S[b] | 2S1[a] | 3S |
| Grande Ronde | 19 | 45 | | 1 | | | 25 | 19 | |
| Imnaha | 5 | 16 | | | | | 8 | 6 | |
| Lower Clearwater | 6 | 5 | | | | 1 | 12 | 8 | |
| Lower Salmon | 1 | 4 | | | | | 5 | 2 | |
| Lower Snake | 13 | 23 | 1 | | | | 10 | 6 | 1 |
| Middle Fork Salmon | 2 | 8 | | | | | 10 | 5 | |
| South Fork Clearwater | 1 | 1 | | | | | 5 | 5 | |
| South Fork Salmon | | 3 | | | | | 6 | 4 | |
| Upper Clearwater | | 1 | | | 1 | | 3 | 7 | |
| Upper Salmon | 8 | 21 | | | | | 20 | 10 | |

[a] A single fish of this type did not genotype.
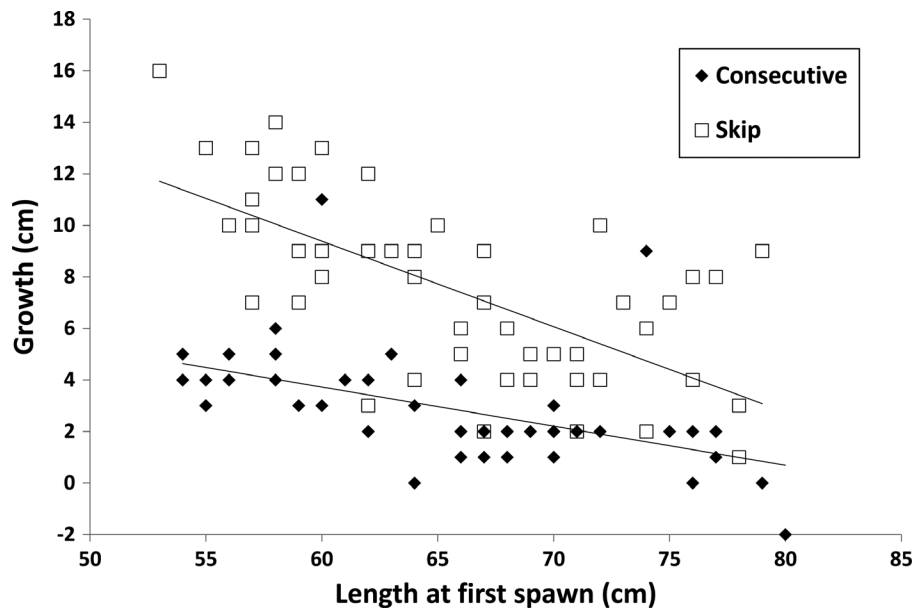[b] Two fish of this type did not genotype.



FIGURE 2. Comparison of growth in length between spawns against fork length at first spawn for repeat-spawning Snake River steelhead. Regression lines are shown separately for consecutive spawners ($R^2 = 0.26$, $y = -0.15x + 12.8$; $n = 45$) and skip spawners ($R^2 = 0.45$, $y = -0.33x + 29.3$; $n = 55$).

between spawns. All seven were excluded from survival calculations.

The probability of a spawning steelhead surviving from their first spawning migration to repeating that journey changed little during the study period, but the components of that probability varied (Table 2). Survival from migrating upstream past Lower Granite Dam to emigration as a kelt downstream to Bonneville Dam increased during the study. However, survival in the Columbia River estuary and ocean declined. Survival of repeat spawners migrating

upstream within the Columbia and Snake rivers (from Bonneville Dam to Lower Granite Dam) also varied. However, the end result was that components of survival largely offset themselves such that overall survival varied little. The exception was SY 2015, when survival in freshwater and the ocean declined together and total survival was the lowest we estimated.

Tagged steelhead later detected as repeat spawners varied annually in sex ratio and proportion of skip spawners (Table 2). Fish detected as repeat spawners were

TABLE 2. Survival, numbers of tags, and selected characteristics of tagged, spawning steelhead by year of first spawn. Survival is from first spawn to kelt emigration at Bonneville Dam ($S_k$), from emigration to return on a second spawning migration ($S_{kr}$), from return back to Lower Granite Dam ($S_{BL}$), and total survival from first to second spawning migration ($S_T$). The numbers of tags were those placed at Lower Granite Dam during the first spawning migration and the number subsequently detected at Lower Granite Dam on a second spawning migration. Characteristics are proportions of repeat spawners that were female or that skipped a year between spawns.

| Parameter | Year of first spawn | | | | | |
| | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 |
|---|---|---|---|---|---|---|
| $S_k$ | 0.127 | 0.096 | 0.278 | 0.316 | 0.437 | 0.198 |
| $S_{kr}$ | 0.104 | 0.139 | 0.073 | 0.035 | 0.027 | 0.018 |
| $S_{BL}$ | 0.788 | 0.746 | 0.643 | 0.737 | 0.707 | 0.818 |
| $S_T$ | 0.010 | 0.010 | 0.013 | 0.008 | 0.008 | 0.003 |
| Tags placed | 4,025 | 4,691 | 4,153 | 3,394 | 3,459 | 3,988 |
| Tags detected | 41 | 47 | 54 | 28 | 29 | 12 |
| Females | 0.929 | 0.765 | 0.878 | 0.949 | 0.885 | 0.929 |
| Skip spawner | 0.558 | 0.651 | 0.690 | 0.921 | 0.300 | 0.545 |

TABLE 3. Parameter estimates of three mixed models relating the fixed effects of length, sex, and stock to survival from first spawn to detection as a repeat spawner at Bonneville Dam. The effect of sex is males compared with females; the effect of stock is Grande Ronde compared with other stocks. The year of first spawn was included in models as a random effect on the model intercept. Significant values are in bold italics.

| Parameter | Estimate | Z-score | P-value |
|---|---|---|---|
| **Effect of length** | | | |
| *Length* | *−0.466* | *−6.16* | *<0.001* |
| *Length$^2$* | *−0.200* | *−2.79* | *0.005* |
| **Effect of sex** | | | |
| *Male* | *−1.277* | *−6.26* | *<0.001* |
| **Effect of stock** | | | |
| Imnaha | 0.111 | 0.42 | 0.67 |
| Lower Clearwater | 0.379 | 1.59 | 0.11 |
| Lower Salmon | 0.051 | 0.16 | 0.88 |
| Lower Snake | 0.051 | 0.22 | 0.82 |
| Middle Fork Salmon | −0.337 | −1.11 | 0.27 |
| South Fork Clearwater | −0.578 | −1.59 | 0.11 |
| *South Fork Salmon* | *−1.092* | *−2.11* | *0.04* |
| *Upper Clearwater* | *−0.875* | *−2.17* | *0.03* |
| Upper Salmon | −0.063 | −0.29 | 0.77 |

predominately female, but the proportion varied by spawn year from 76.5% to 94.9% (median = 90.7%). Similarly, most repeat spawners were detected after a full year in the ocean, skipping a year between spawns (median = 60.4%), but this metric was most extreme for SY 2013 and SY 2014. Thus, these results corroborate the systematic and targeted sample results but show annual variation.

All five characteristics investigated had significant effects on survival from first spawning migration to second spawning migration (Table 3). The model of survival as a function of length with a quadratic term was better than a simple linear model, so only those results are shown (Figure 3A). Small fish survived better such that the 15th percentile length (57 cm) had the highest predicted survival and the 25th percentile length (60 cm) survived 2.1 times better than the 75th percentile length (74 cm). Females survived at a 3.6 times higher rate than males (Table 3). Two stocks survived at significantly lower rates than the reference stock; Grande Ronde fish survived 3.0 and 2.4 times higher than the South Fork Salmon and Upper Clearwater stocks, respectively. Survival differences between the Grande Ronde and other stocks were not statistically significant ($P > 0.1$).

Results for survival from the first spawning migration to kelt emigration were similar to results for survival from first spawning migration to second spawning migration (Table 4; Figure 3B). Small fish survived better such that the 7th percentile length (55 cm) had the highest predicted survival and the 25th percentile length (60 cm) survived 1.3 times higher than the 75th percentile length (74 cm). Females survived at a 2.6 times higher rate than males (Table 4). Two stocks survived at significantly lower rates

than the reference stock ($P < 0.001$); Grande Ronde fish survived 1.8 and 1.6 times higher than the South Fork Clearwater and Upper Clearwater stocks, respectively.

Length and date of kelt emigration had significant effects on survival from kelt emigration to return as a repeat spawner; sex and stock did not significantly affect survival (Table 5). Small fish survived better such that the 25th percentile length (58 cm) had the highest predicted survival, which was 1.8 times higher than the 75th percentile length (72 cm; Figure 3C). Note that only fish that survived to kelt emigration at Bonneville Dam were used in this analysis; therefore, length percentiles given here are different from those above. Further, early emigrating kelts survived better such that fish emigrating on the 13th percentile date (May 2) had the highest predicted survival and individuals emigrating on the 25th percentile date (May 9) survived 1.7 times better than those emigrating on the 75th percentile date (June 1; Figure 4).

## DISCUSSION

Iteroparous steelhead in the Snake River basin exhibit a wide range of life history patterns. In this paper, we examined an extensive representative sampling of repeat spawners supplemented with targeted samples that helped detect low-incidence life histories, including some not previously observed. While the exact mechanisms that prompt each life history variation were not addressed here, this study provides compelling evidence that
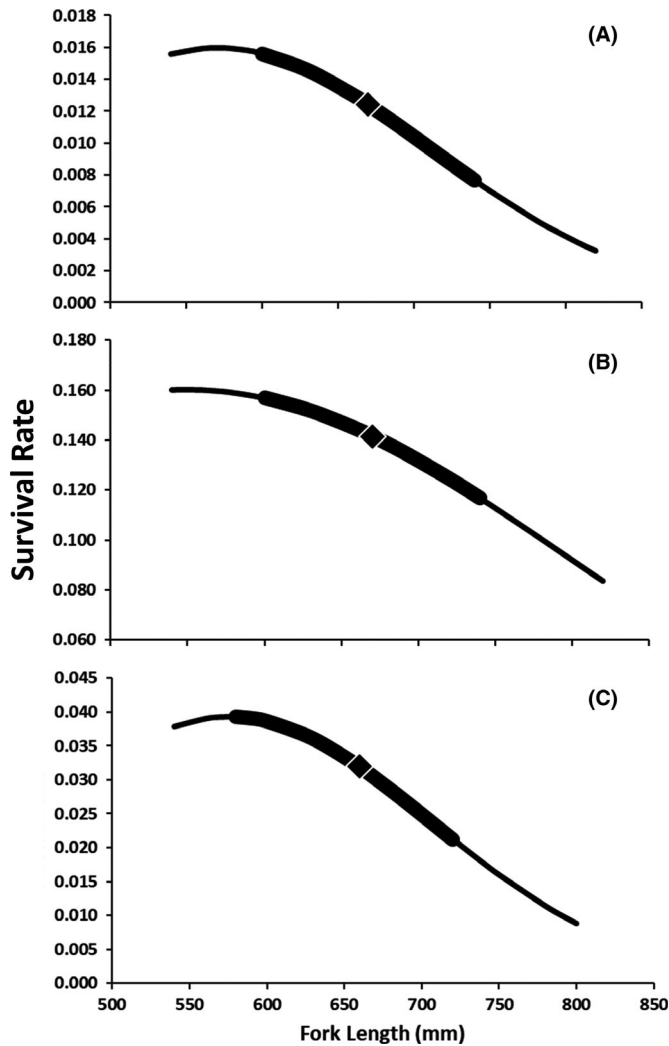
FIGURE 3. Predictions of survival at a range of fork lengths **(A)** from first to second spawning migration, **(B)** from first spawning migration to kelt emigration, and **(C)** from kelt emigration to second spawning migration. The thin line shows predictions from the 5th to 95th percentile lengths, the thick line shows predictions between the quartiles, and the diamond is the prediction at the median length.

TABLE 4. Parameter estimates of three mixed models relating the fixed effects of length, sex, and stock to survival from first spawn to detection as a kelt in the Snake or Columbia rivers. The effect of sex is males compared with females. The effect of stock is Grande Ronde compared with other stocks. The year of first spawn was included in models as a random effect on the model intercept. Significant values are in bold italics.

| Parameter | Estimate | Z-score | P-value |
|---|---|---|---|
| **Effect of length** | | | |
| *Length* | *−0.220* | *−10.58* | *<0.001* |
| *Length²* | *−0.078* | *−4.03* | *<0.001* |
| **Effect of sex** | | | |
| *Male* | *−0.943* | *−17.69* | *<0.001* |
| **Effect of stock** | | | |
| Imnaha | 0.001 | 0.02 | 0.99 |
| Lower Clearwater | −0.062 | −0.72 | 0.47 |
| Lower Salmon | 0.098 | 0.93 | 0.35 |
| Lower Snake | 0.006 | 0.09 | 0.93 |
| Middle Fork Salmon | 0.155 | 1.86 | 0.06 |
| *South Fork Clearwater* | *−0.568* | *−5.04* | *<0.001* |
| South Fork Salmon | 0.079 | 0.76 | 0.45 |
| *Upper Clearwater* | *−0.443* | *−4.34* | *<0.001* |
| Upper Salmon | 0.051 | 0.74 | 0.46 |

TABLE 5. Parameter estimates of four mixed models relating the fixed effects of length, emigration date, sex, and stock to survival from detection as a kelt at Bonneville Dam to detection as a repeat spawner at Bonneville Dam. The effect of sex is males compared with females. The effect of stock is Grande Ronde compared with other stocks. The year of first spawn was included in models as a random effect on the model intercept. Significant values are in bold italics.

| Parameter | Estimate | Z-score | P-value |
|---|---|---|---|
| **Effect of length** | | | |
| *Length* | *−0.409* | *−3.15* | *0.002* |
| Length² | −0.208 | −1.61 | 0.11 |
| **Effect of emigration date** | | | |
| *Day* | *−0.435* | *−2.69* | *0.007* |
| Day² | −0.197 | −1.46 | 0.14 |
| **Effect of sex** | | | |
| Male | −0.565 | −1.38 | 0.17 |
| **Effect of stock** | | | |
| Imnaha | −0.249 | −0.48 | 0.63 |
| Lower Clearwater | −0.170 | −0.33 | 0.74 |
| Lower Salmon | 0.379 | 0.77 | 0.44 |
| Lower Snake | 0.202 | 0.52 | 0.60 |
| Middle Fork Salmon | −1.345 | −1.79 | 0.07 |
| South Fork Clearwater | −1.107 | −1.07 | 0.28 |
| South Fork Salmon | −1.453 | −1.41 | 0.16 |
| Upper Clearwater | −1.379 | −1.34 | 0.18 |
| Upper Salmon | −0.218 | −0.55 | 0.58 |

iteroparity in Snake River steelhead is related to certain characteristics. Despite low survival rates, we found that females, smaller fish, and earlier migrating kelts survived at higher rates to the second spawning migration. We also found that certain stocks tend to produce more repeat spawners. Energetic costs and mortality risks associated with migration have a substantial effect on the frequency of iteroparity in a population (Christie et al. 2018). Low rates of iteroparity in Snake River steelhead are likely generated through energetic costs associated with the migration corridor (distance, elevation, timing, dam passage) and a lack of timely postspawn recovery due to migration distance and timing of ocean reentry.

Our results illustrate the energetic costs of the journey from the ocean to spawning streams in the Snake River basin and back again. Most Snake River steelhead
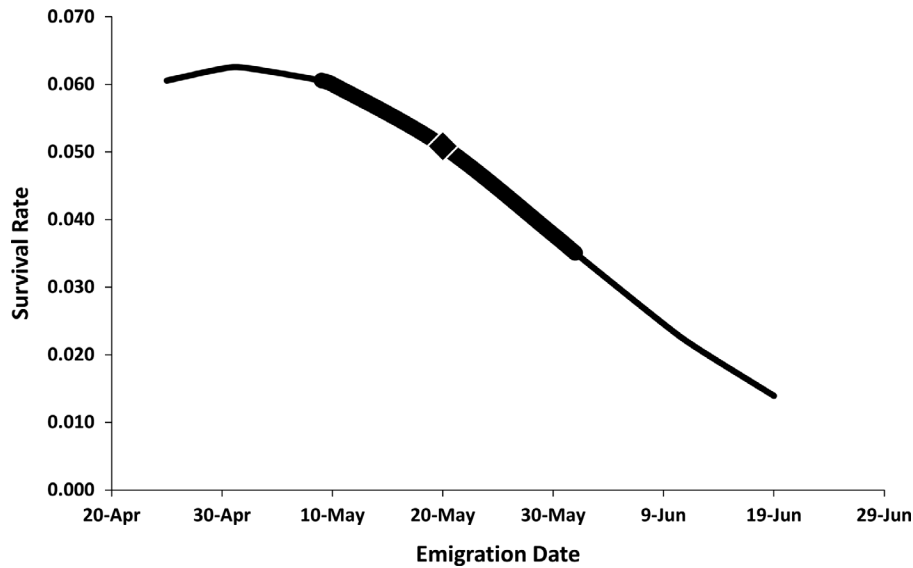
FIGURE 4. Predictions of survival from kelt emigration to second spawning migration at a range of kelt emigration dates. The thin line shows predictions from the 5th to 95th percentile emigration date, the thick line shows predictions between the quartiles, and the diamond is the prediction at the median emigration date.

skipped a year between spawns, risking additional mortality before spawning again. Skip spawning has been primarily linked to poor feeding conditions and insufficient energy accumulation (Rideout and Tomkiewicz 2011). Skip spawners take longer than consecutive spawners to regain sufficient energy and nutritional resources between spawning migrations (Jonsson et al. 1991; Haraldstad et al. 2018). Snake River steelhead deplete their lipids before kelt emigration such that postspawn physiological performance and survival may be affected (Penney and Moffitt 2015). Kelts in poor nutritional condition (low condition factor and plasma triglyceride concentrations) tend to stay in salt water longer (Bordeleau et al. 2018). For Snake River steelhead, we infer an even greater proportion of kelts were attempting a years recovery than the percentage of skip spawners indicates. In contrast, steelhead in southeastern Alaska that spend about a month in freshwater (ocean maturing, see Lohr and Bryant 1999) typically spawn in consecutive years (Love 2016). Among Columbia River basin steelhead populations, consecutive spawners were proportionally more common in populations closer to the Pacific Ocean (Hatch et al. 2013; Keefer and Caudill 2014).

Growth is an important indicator of fish performance and reproductive potential. We found that growth between spawns was less for fish that were large at first spawn. This implies that larger females did not accrue as much additional fecundity on the second spawn as would be expected for smaller fish. The potential to recover from spawning in salmonids declines with size and age such that larger fish may senesce and never reach recrudescence

(Dutil 1986). Larger kelts take longer to recover, tend to skip a year between spawns, and survive at lower rates than smaller kelts (Jonsson et al. 1991). We also found that larger fish did not survive as well. For steelhead in the Snake River basin, we speculate that the potential fitness benefits of iteroparity relative to semelparity declined with increasing length at first spawn.

Life history theory suggests that iteroparity in anadromous salmonids provides greater fitness benefits for females than for males (Fleming and Reynolds 2004). Although Snake River steelhead tend to be female biased (64% of tagged fish in this study, data not shown), the ratio is even more skewed on the second spawning migration. Sex ratios of repeat spawners in other anadromous salmonid species and in other steelhead populations tend to also be female biased (e.g., Keefer et al. 2008; Scott and Gill 2008; Christie et al. 2018; Haraldstad et al. 2018). Males may spend more time pursuing additional reproductive opportunities during the spawning season, engaging in intense and risky competition, whereas females emigrate soon after reproduction (Fleming 1998). Because earlier emigrating kelts survived better, sex-biased emigration timing resulted in an increased percentage of females in repeat spawners.

The stock effect on survival was likely related to other characteristics, such as sex and size and age composition. We expected that stocks at lower elevations and with shorter migrations would survive to second spawning migration at higher rates, but survival of the stocks farthest upstream (Upper Salmon and Middle Fork Salmon) were not significantly different from the reference stock

(Grande Ronde). We found that South Fork Salmon River and Upper Clearwater River stocks survived at a lower rate. These stocks included steelhead that were older and larger at first spawn, although they were also more female biased than other Snake River steelhead populations (Copeland et al. 2017). We concluded that, within the Snake River basin, all stocks undertake energetically costly migrations such that relative energetic costs and mortality risks are controlled more by individual traits rather than by distance and elevation. Expression of iteroparity is not uniform across the Snake River basin (Narum et al. 2008) because of the combination of traits characteristic of stocks in different parts of the basin.

Steelhead kelts must survive two critical processes before returning to freshwater again: migration downstream through the river system and recovery in the ocean. Colotelo et al. (2014) found higher downstream kelt survival from Lower Granite Dam to Bonneville Dam (37.0% in 2012 and 27.3% in 2013) after surface passage routes (specialized spillway weirs and surface flow outlets) were in place than Wertheimer and Evans (2005) found before installation (4.1% in 2001 and 15.3% in 2002). We found that survival rates from upstream passage at Lower Granite Dam to kelt emigration were more similar to the kelt survival rates observed by Colotelo et al. (2014) than those seen by Wertheimer and Evans (2005). However, those benefits were offset by poor ocean conditions during the later years of our study.

Estuary and ocean conditions have a significant effect on kelts, similar to their influence on growth and survival of emigrating smolts (e.g., Haeseker et al. 2012). Secondary productivity in salt water is important to the survival of kelts to the next spawn (Chaput and Benoît 2012). Furthermore, warm ocean conditions can increase metabolic demands with implications for survival of salmonids (Daly and Brodeur 2015). Ocean survival of kelts in our study was highest for cohorts reentering the ocean during 2010–2012. During 2013–2015, the eastern Pacific Ocean was 1–4°C warmer than average with reduced secondary productivity (Cavole et al. 2016), resulting in poor kelt survival after ocean entry. Hence, total survival rate did not change appreciably until the SY 2015 cohort because postspawn survival trends in freshwater and salt water offset each other.

We postulate two nonexclusive, potentially interacting, proximate explanations for the extreme low incidence of iteroparity in Snake River steelhead: energetic costs and timing of kelt emigration. The high incidence of skipped spawning provides evidence to support the first hypothesis. Lower survival associated with later emigration timing supports the second hypothesis. A later time of ocean reentry may also reduce the likelihood of encountering ocean conditions favorable for survival, as demonstrated for steelhead smolts (Haeseker et al. 2012). Further, experiences during emigration may influence later survival in the ocean, as they do for smolts (Haeseker et al. 2012). Late emigration timing reduces the likelihood of Snake River kelts surviving emigration to the ocean as the Snake and Columbia rivers warm and flows decrease during late spring and early summer. Low flows may force kelts through dam turbines, where mortality is high (Harnish et al. 2015). Thus, several factors may increase stress and metabolic demand on the emigrating kelts, while also increasing the time it takes for them to reach the estuary and ocean to refuel and recover.

There is scope for management to increase iteroparity in Snake River steelhead. Improved kelt survival in recent years suggests that surface passage options have helped increase iteroparity rates in the Columbia River basin (Keefer and Caudill 2014; this study). Continued improvements could result in higher percentages, particularly when improved downstream passage for kelts aligns with favorable ocean conditions. Historically, Long and Griffin (1937) observed 2% and 4% iteroparous individuals among steelhead migrating in the lower Columbia River during summer and fall, respectively, and Whitt (1954) observed 4% and 2% in 1951 and 1952, respectively, in the Clearwater River in Idaho. There are two general management strategies to increase the numbers of repeat spawning steelhead in target populations (Wertheimer and Evans 2005). Management of main-stem dams could facilitate passage of steelhead kelts back to the estuary and ocean. Alternatively, managers could collect kelts, recondition them, and release them to spawn again. Our results provide a useful framework for planning these kelt management strategies as well as providing a baseline from which to evaluate their success.

## ACKNOWLEDGMENTS

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