**METHODS**

*Study population. –* Snake River steelhead populations are summer-run (Busby et al. 1996); adults enter freshwater from late summer through early fall and overwinter in rivers prior to spawning in the spring. Snake River steelhead spawn in tributaries ranging from 622 to nearly 1,500 km from the Pacific Ocean, with some at elevations exceeding 2,000 m, from mid-March to early June. After spawning, many steelhead (kelts) leave tributaries and attempt to return to the Pacific Ocean. Downstream migrating kelts are largely female (Keefer et al. 2008), as males tend to remain on the spawning grounds to seek out additional spawning opportunities. Some kelts return to tributaries as repeat spawners. Repeat spawning occurs either 1 year (consecutive spawners) or 2 or more years (skip spawners) after first spawning.

Prior to repeat spawning, kelts undergo reconditioning, which involves physiological recovery, accumulation of energy stores, and re-growth of the gonad. Snake River steelhead may undergo reconditioning in the wild, or in captivity, following capture by the Kelt Reconditioning Program (KRP). The captive reconditioning process was previously described (Hatch et al. 2013, Pierce et al. 2017, Jenkins et al. 2018). Briefly, kelts are maintained outdoors in tanks of flow-through river water, fed krill and pellets, and treated for disease and parasites. Kelts are sampled in late summer to determine reproductive readiness (Pierce et al. 2017, Jenkins et al. 2020). Kelts determined to be ready to spawn in the upcoming season, including consecutive spawners (collected ~ 3-6 months prior) and skip spawners (collected ~18 months prior), are released in the fall to migrate upstream and spawn with the natural run. A few additional fish are released, including fish determined to have borderline reproductive readiness, fish that have spent one winter in captivity and still not reached reproductive readiness, and fish with unknown reproductive readiness due to sampling issues.

*Data collection. –*

*Pre-spawn dataset*: Data from pre-spawn steelhead were collected during upstream migration through Lower Granite Dam (LGR, 695 km from the Pacific Ocean), the final dam before Snake River steelhead disperse to spawning tributaries. The LGR adult fish trap is operational 24 h/day, and samples systematically 4 times/h (see Steinhorst et al. 2017 for additional details). Biological samples were collected as previously described (Copeland et al. 2019). Briefly, fish were PIT-tagged, measured for fork length, and scale and tissue samples were collected. The pre-spawn dataset included fish that would spawn in 2016-2021 (Spawn Years 2016-2021), with data collection beginning July 15 of the previous calendar year (2015-2020). PIT-tagging is used to monitor upstream movement, run timing, and abundance to detection locations throughout the basin and subsequent downstream migrations to and through LGR and the Snake and Columbia rivers hydrosystem, possibly including repeat spawning migrations. Genetic sex and genetic stock of origin were determined by analysis of tissue samples (Ackerman et al. 2014, Steele et al. 2017), and age and spawning history were determined utilizing analysis of scale samples (Wright et al. 2015; Copeland et al. 2018 and described in Copeland et al. 2019). The pre-spawn sample was restricted to natural-origin, first-time spawning, female steelhead. Unclipped hatchery fish, fish mis-identified as females, and known repeat spawners were excluded from the pre-spawn dataset, as well as from the post-spawn and repeat spawner datasets (described below). After sampling, fish were returned to the LGR fish ladder to continue their upstream migration.

*Post-spawn dataset*: After spawning, downstream migrating kelts can pass through LGR by several routes: through the turbines, locks, spill, or the juvenile bypass system (JBS). PIT-arrays detect downstream migrating kelts at the JBS as well as at the spillway detector (Axel et al. 2024), which began operating in 2020. The post-spawn dataset was amassed by collection of data and samples from kelts that passed through the JBS. These fish were mechanically separated from juvenile salmonids and diverted into collection tanks for biological sampling and potential collection by the KRP. Biological sampling of kelts has previously been described (Hatch et al. 2013, Pierce et al. 2017). Briefly, kelts were scanned for pre-existing PIT tags and either collected for captive reconditioning or returned to the Snake River below LGR. Collection was restricted to natural-origin, female steelhead. At the time of encounter, sex was determined visually, and natural origin was determined based on the presence of an intact adipose fin. Kelts that were collected received a PIT-tag if one was not present.

*Repeat spawner dataset*: The repeat spawner (RS) dataset was amassed from PIT-tag detections of steelhead migrating upstream through a series of PIT-tag antennas within the LGR adult fish ladder during a second spawning migration. Two types of RS identified by PIT tags made up the RS dataset – those that were reconditioned in captivity (Reconditioned RS) and those that were not reconditioned in captivity and thus presumably reconditioned in the wild (Natural RS). Natural RS had to have been tagged at LGR prior to spawning and then detected at LGR in a subsequent spawn year. An estimate of total repeat spawners for each year was derived from this sample as previously described (Copeland et al. 2019). A Reconditioned RS had to be released by the KRP and detected the same spawn year. Reconditioned RS were of two types: fish with an existing tag from the pre-spawn dataset, and fish tagged at collection by the KRP or with an existing tag not from the pre-spawn dataset.

*Data analysis. –* To determine which fish in the pre-spawn dataset were detected migrating downstream after spawning through LGR, the Columbia Basin PIT Tag Information System (PTAGIS, www.ptagis.org) was queried with a list of tags of fish that were tagged pre-spawn at LGR. Fish that were detected at the LGR Juvenile Bypass (2016-2021) or the Spillway Detector (2020, 2021) during the spring (March 18-June 30) immediately following the summer-fall-winter during which they were tagged were identified. The number of detected fish for each year was divided by a kelt detection efficiency estimate calculated for each year (described below) to produce an estimate of the number of fish migrating downstream through LGR. This new number was divided by the total tagged for that year, producing an estimate of the percentage of downstream migrating fish for each year.

[insert methods for developing detection efficiency here]

Detection probabilities (efficiencies) of PIT-tagged, post-spawn steelhead kelts at LGR were estimated using a Cormack-Jolly-Seber (CJS) mark-recapture framework (Lebreton et al. 1992). The dataset included adult steelhead trapped and PIT-tagged - if not previously tagged - at the LGR adult trap during the systematic, random sampling period and designated as *valid* (Beeken et al. 2024). Complete tag histories were retrieved from PTAGIS and processed using the PITcleanr::compress() function (See et al. 2024), which collapsed temporally clustered observations at each location to retain only essential information: PIT-tag code, observation location, and minimum and maximum observation times. For previously PIT-tagged individuals, only observations occurring after their first detection at the LGR adult trap were retained to remove any juvenile or pre-return adult detections.

To estimate detection probability at LGR, the analysis focused on adult steelhead that were detected upstream of LGR at instream PIT-tag detection systems (IPTDS) or mark-recapture-recovery (MRR) sites, indicating movement towards spawning areas. Capture histories were then constructed for each fish using three distinct detection occasions: 1) upstream detection towards spawning areas, 2) detection as a kelt at LGR (either via the juvenile bypass system or spillway antennas), and 3) any subsequent detection downstream in the lower Snake or Columbia River hydrosystem, including estuary antennas. Kelts removed from the river for reconditioning were excluded from model estimation of detection and survival rates at LGR, since they cannot be detected at downstream locations. Finally, the dataset was further refined to exclude any individuals later identified as hatchery-origin via parentage-based tagging (Steele et al. 2013) and individuals with unknown sex.

The CJS models were implemented in R using the marked::cmr() function (Laake et al. 2013; R Core Team 2024) and included fixed effects for spawn year, spawning population, and sex to account for variation in detection probability (p) and apparent survival (ϕ; the product of true survival and migration). A logit-link function was used to relate covariates to detection and survival probabilities. Candidate models included biologically plausible interaction terms (e.g., spawn year × population, population × sex) and were ranked using Akaike’s Information Criterion (AIC; Akaike 1974) to identify the most parsimonious model. The top model included spawn year as a predictor of detection probability and spawn year, spawning population (based on observations at upstream IPTDS and MRR sites during the spawning run), and sex as predictors of apparent survival.

To determine which fish in the pre-spawn dataset were encountered and collected in the post-spawn dataset, PIT-tag lists were compared, and fish in the pre-spawn dataset were identified. Percentages of fish encountered and collected as a portion of the pre-spawn dataset were calculated. The repeat spawner dataset was constructed by querying PTAGIS with lists of tags from the pre-spawn dataset and fish released by the KRP for spawn years 2016-2021. Fish detected on a repeat spawning migration through LGR were categorized as Natural or Reconditioned RS, and Reconditioned RS were partitioned into those with a tag from the pre-spawn dataset and those without. Percentages of Natural and Reconditioned fish tagged in the pre-spawn dataset and then detected on a subsequent spawning migration were calculated.

All RS were classified as either consecutive or skip spawners. Consecutive spawners were individuals detected migrating upstream through LGR one year after their initial spawn year, whereas skip spawners were detected two or more years after their initial spawning. To increase sample size, for Reconditioned RS, the total number of Reconditioned RS and numbers of consecutive and skip spawners were based on all fish released by the KRP and detected moving upstream through LGR after release, rather than just those in the pre-spawn dataset.

To determine the relative contribution of consecutive versus skip spawners in Natural and Reconditioned RS, the probability of returning as a skip spawner was assessed using a binary logistic regression analysis. Binomial response variables were defined as Consecutive Spawners = 0, and Skip Spawners = 1. The predictor variable of interest was RS Type (Natural or Reconditioned). The data were examined for a year effect. Preliminary tests revealed a year effect, and year was thus included in the final model:

Probability of Skip Spawning = year + RS Type + intercept + error

To explore variables associated with the composition of consecutive versus skip spawners in Natural and Reconditioned RS, binary logistic regression was used to determine the effects of predictors variables pre-spawn fork length (Length), Ocean Age, and repeat spawner (RS) Type (Natural and Reconditioned) on the probability of skipped spawning. We used AIC to select the best supported model. The best model according to the AIC analysis included the ocean age by type interaction and a length effect that was common to all groups:

Probability of Skip Spawning = Length + Ocean Age\* RS Type

The relative contributions of consecutive versus skip spawners were further explored utilizing genetic stock of origin and management unit designation in Natural and Reconditioned RS.

Next, the overall contributions of Natural and Reconditioned RS to the spawning run were explored. The total number of natural-origin female steelhead migrating upstream each year was estimated by multiplying the total run estimate for each year by the percent of females that were tagged at LGR adult fish trap each year. The estimate of the number of Natural RS migrating upstream each year was determined by subtracting the number of Reconditioned RS detected migrating upstream through LGR from the estimate of the total number of RS for each year. The number reported for Reconditioned RS each year is the actual number of Reconditioned RS detected migrating upstream through LGR after release.

Finally, the percent of natural-origin female steelhead collected by the KRP and then detected migrating upstream following release was calculated.