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ARTICLE

Comparing standard- and reduced-size passive integrated transponder (PIT) tags for monitoring juvenile wild spring Chinook Salmon

Jesse J. Lamb | Benjamin P. Sandford | Steven G. Smith | Gordon A. Axel

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, Fish Ecology Division, Seattle, Washington, USA

Correspondence
Jesse J. Lamb
Email: jesse.j.lamb@noaa.gov

Abstract

Objectives: Annual migration monitoring can help to discern patterns and environmental factors that impact growth, survival, and movement timing in small fish. Mark–recapture methods form the basis for such monitoring, and the standard 12-mm passive integrated transponder (PIT) tag has emerged as an essential tool for studies of juvenile salmonids. A smaller, 9-mm PIT tag now provides the potential to conduct mark–recapture studies on smaller fish. We evaluated relative performance of the 9-mm tag, which is similar in design to its 12-mm predecessor.

Methods: For this comparison, we tagged and released approximately 8400 wild spring Chinook Salmon *Oncorhynchus tshawytscha* parr in Valley Creek, Idaho, from 2011 to 2013. Tag-size cohorts were of similar average body size and were tagged in equal numbers. We estimated survival and detection probability for each cohort over two river segments.

Results: In both segments, survival varied among years, but we observed no significant differences between tag-size groups. At Valley Creek, average detection rates of fish with 9-mm tags were a little less than one-half the rates of fish with 12-mm tags and were significantly lower in all 3 years. At Lower Granite Dam, detection rates were again lower for 9-mm tags, but the differences were much smaller (3%–12%) and were not statistically significant.

Conclusion: We found that 9-mm tags can be as effective as 12-mm tags and may allow for better inference to smaller (<55-mm) non-tagged fish. However, the lower detection rates of the 9-mm tags could lead to less precise estimates, and site-specific detection rates should be considered for studies that rely on these tags.

KEYWORDS

Chinook Salmon, migration, monitoring, PIT tag, Snake River, technology

INTRODUCTION

Fishery managers often rely on tagging studies to obtain data on the movement and survival of individual fish and fish stocks. The passive integrated transponder (PIT) is a widely used tagging technology that is favored for its ability to provide reliable, individual-specific data on tagged fish, including where fish were collected, tagged, and released as well as their subsequent migration history, timing, and survival. Like any conventional tagging or marking method, PIT tagging involves handling and often requires electrofishing, both of which may pose health risks to juvenile fish (Sharber et al. 1994; Dalbey et al. 1996; Nielsen 1998).

In addition to handling stress, tags may introduce a continuous size or mass burden to which the migrating juvenile fish would otherwise not be subject. Because of this burden, tagging may not be feasible for very small fish. Technology has continually attempted to develop the smallest tag possible to further reduce tag burden and allow for the tagging of smaller and younger juveniles. However, to make tags smaller, manufacturers must often use components that potentially affect tag performance.

For three decades, the PIT tag has been a central tool for research and monitoring of Pacific salmonids *Oncorhynchus* spp. and other species in the Columbia River basin. These tags are typically implanted by injection into the body cavity, and on average they measure 12.0 mm in length × 2.1 mm in diameter. They can be used to mark fish as small as 55 mm fork length (FL), with minimal effects on the behavior, swimming capability, or growth of the tagged fish (Prentice et al. 1994; Tiffan et al. 2015). These tags remain readable in the body cavity for at least 10 years (Skov et al. 2020), making them ideal for studies of anadromous fish that are tagged as juveniles and monitored as they return to their natal streams to spawn several years later.

At least 1–2 million hatchery-reared and wild juvenile salmon are PIT-tagged in the Columbia River basin annually (Pacific States Marine Fisheries Commission 2023). Fish are tagged both as migrating and premigrating juveniles and as adults returning to a hatchery or natal stream. Monitoring sites for PIT-tagged fish include instream antenna arrays in natal streams or rivers, juvenile bypass systems and adult ladders at hydroelectric dams (Muir et al. 2001), and a specialized trawl that tows a detection system in the estuary (Ledgerwood et al. 2004; Holcombe et al. 2020). Tags are also monitored annually from the abandoned roosting and nesting colonies of piscivorous birds (Evans et al. 2019).

The quantity of detections is increasing as novel monitoring technologies are developed, such as the multi-array spillway detection system at Lower Granite Dam and the prototype fin array system deployed from a stationary barge (Axel et al. 2021). The PIT tag is unique among available tag technologies in that it allows an individual fish to be tracked throughout its lifetime. For this reason, PIT tag data have revolutionized the life cycle modeling that is used to assess population-level impacts, such as extinction risk (National Marine Fisheries Service 2020).

Researchers at the U.S. National Marine Fisheries Service have used PIT tag technology to monitor the migration of wild spring Snake River Chinook Salmon *O. tshawytscha* smolts since 1989 (Achord et al. 1996). Contributing to this long-term effort, our research group annually collects, PIT-tags, and releases salmon parr in up to 15 streams in the Salmon River basin, Idaho (Figure 1). A portion of the tagged individuals are subsequently detected at monitoring sites as they move downstream.

Impact statement

Fish tagging technology has evolved with a goal of having minimal tag burden on study fish. However, use of tags that are smaller than the standard size may result in performance tradeoffs and therefore requires careful consideration to address specific research inquiries effectively.

The Columbia River PIT Tag Information System (PTAGIS) is a centralized database that serves as the repository for basinwide data on PIT tagging as well as subsequent detections or recoveries. The PTAGIS database is maintained by the Pacific States Marine Fisheries Commission (www.ptagis.org).

In 2011, a tag smaller than the standard 12-mm PIT tag was made available for field research to provide fisheries scientists with an improved tool for use in smaller fish. The ability to tag small fish is especially important when studying wild populations: a significant portion of each parr population is small enough to warrant concern about possible tag effects, even with a 12-mm tag. The 9-mm PIT tag offers the potential to track movements of fish as small as 55 mm FL at the time of collection and tagging. Monitoring systems installed throughout the Columbia River basin were designed to detect the 12-mm PIT tag, and performance of this tag is relatively well understood. While existing monitoring systems are also capable of detecting the smaller, 9-mm tag, no field study has yet been conducted to specifically evaluate the relative performance of 9- versus 12-mm tags instream or over an extended river distance (e.g., Valley Creek to Lower Granite Dam [740 km]; Figure 1). Tiffan et al. (2021) studied subyearling Chinook Salmon with 8-, 9-, and 12-mm PIT tags to assess differential growth and survival over a relatively short distance within the Snake River.

The purpose of our study was to model effects and interactions of three variables—tag size, year, and tag length—to answer the following questions:

- Was there a tag size effect on survival, growth, or detection rates at an instream array and/or a main-stem dam?
- Was the tag size effect consistent among years?
- Did the probability of detection, the probability of survival, or the tag effect depend on fish size?

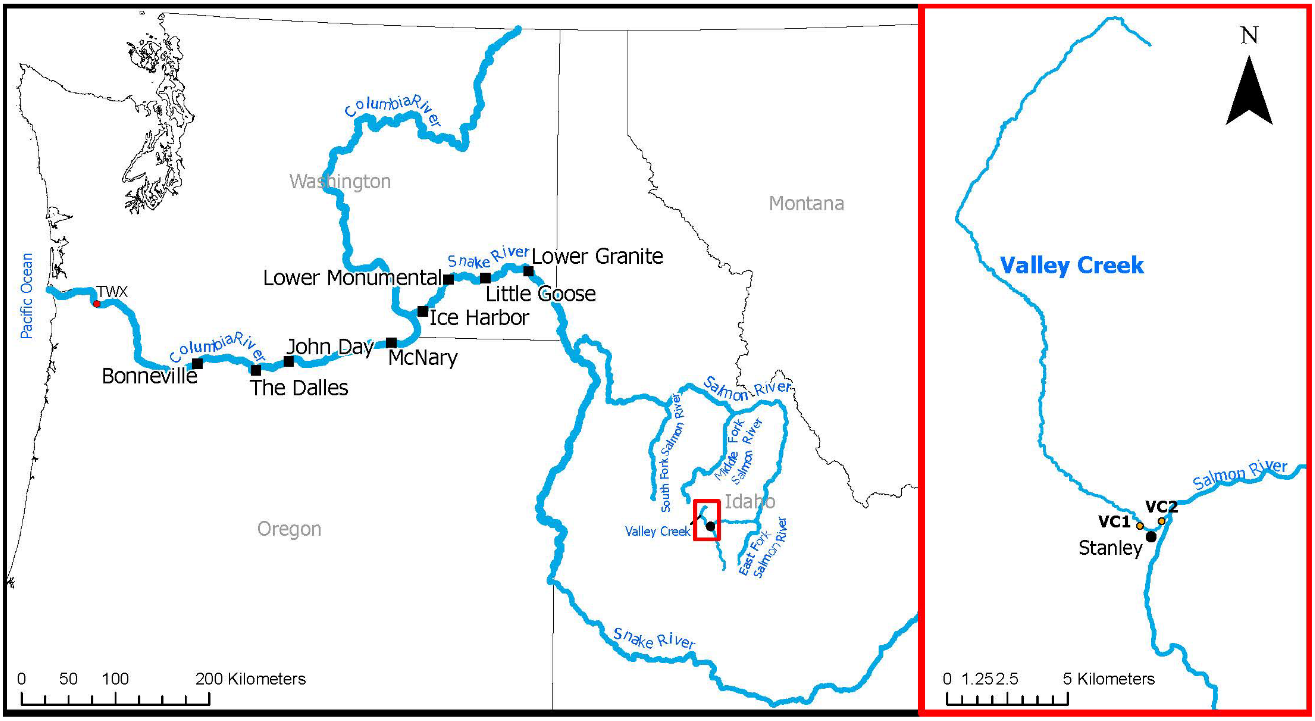

FIGURE 1 Map of the Columbia–Snake River system, showing the locations of dams (black squares), the Columbia River estuary towed array (TWX), and the study area (red rectangle). Inset shows the Valley Creek study area in the upper Salmon River basin, central Idaho, situated 740 river kilometers upstream from Lower Granite Dam. Detection data from both instream monitoring systems (VC1 and VC2) were combined for analyses.

- Was the relationship between tag effect and fish size consistent among years?

Here, we examine effects on growth, migration timing, and survival of juvenile Chinook Salmon that were tagged as parr in Valley Creek, Idaho, and monitored during their 740-km emigration to Lower Granite Dam on the Snake River.

METHODS

Study area

Valley Creek is a tributary of the Salmon River, which flows into the Snake River and then into the Columbia River (Figure 1). The mouth of Valley Creek is located at the base of the Sawtooth Mountains in central Idaho, 740 river kilometers (rkm) from Lower Granite Dam on the Snake River and 1434 rkm from the Pacific Ocean. Flowing east for approximately 60 km before entering the Salmon River near the town of Stanley, the stream provides ideal habitat for spawning and rearing of wild Chinook Salmon. The Chinook Salmon that spawn in Valley Creek are part of an evolutionarily significant unit that is listed as threatened under the U.S. Endangered Species Act (ESA) of 1973 (Endangered and Threatened Species 1992).

Study design and tagging protocol

During July and August of 2011–2013, we captured wild spring Chinook Salmon parr in Valley Creek by using either backpack electrofishers (Smith-Root Models 12 and LR-20B) or a modified beach seine in accordance with scientific collection permits (i.e., ESA and the State of Idaho). Backpack electrofishing was conducted by experienced fish biologists with specialized training in safe capture, handling, and tagging techniques. Conductivity of the stream was measured daily before electrofishing, and backpack units were adjusted accordingly to minimize injury to sampled fish. When parr densities were sufficient (2011 and 2013), we collected fish using the seine technique described by Achord et al. (1996). Once captured, fish were placed in an 18.9-L (5-gal) bucket fitted with an oxygenation system, where they were held until they were transported to a tagging station. Any mortality due to electrofishing, seining, or direct handling of the fish prior to tagging was reported as collection mortality.

Prior to tagging, fish were anesthetized using tricaine methanesulfonate (MS-222), and the fish were PIT-tagged using sterilized, preloaded, single-use needles designed to be used with a handheld implanter (MK10; Biomark). This system ensured safe handling and minimized stress and potential injury during the tagging process (Lamb et al. 2013). All tagging was performed at a single station. Each implanter was loaded in an alternating pattern with a stainless-steel needle containing either a 12-mm tag or a 9-mm tag. Tags were implanted into randomly selected fish to minimize the chance of fish size bias in the tag comparison by ensuring that equal numbers were implanted with tags of each size across the fish size distribution of each sample. Fish were excluded if they were smaller than 55 mm FL, had been previously tagged, were obviously injured, or had matured precociously. All fish exposed to the anesthetic were allowed to recover until they exhibited normal swimming behavior and then were released. After all suitable fish had been tagged or permit limits had been reached, any remaining fish were released without tagging or additional handling.

Study fish were implanted with either standard 12-mm tags of the type used throughout the Columbia River basin or the newer 9-mm tag (TX1400SST-PL and TX49011B9-PL; Biomark). The 12- and 9-mm tags averaged 12.34 and 9.05 mm, respectively, in length and 0.105 and 0.080 g, respectively, in weight; both tags were 2.04 mm in diameter (Axel et al. 2017). Both tag types operated on a resonant frequency of 134.2 kHz but differed in bandwidth, modulation percentage, and turn-on voltage. Bandwidth (kHz) refers to the range of electromagnetic frequencies above and below the resonant frequency at which the tag signal response is most effective. Modulation percentage is a measurement of amplitude differences between the modulated and unmodulated carrier signal in the presence of a tag. Turn-on voltage (mV) is the amount of energy that is necessary to activate the tag. Tags with a lower turn-on voltage require less energy and therefore may be activated and detected at greater distances from an antenna. Data regarding bandwidth, modulation percentage, and turn-on voltage were collected by the Pacific States Marine Fisheries Commission using an automated PIT tag test system that provides researchers with information on expected tag performance (Table S1 available in the Supplemental Material in the online version of this article). These data were not specific to the individual tags used in our study; rather, they were based on random subsamples collected from among all manufactured tags that were used in projects funded by the Bonneville Power Administration during 2011–2013.

After tagging, we measured and recorded FL (mm) for all fish, and weight (g) was recorded for 33, 79, and 48% of the tagged collection in 2011, 2012, and 2013, respectively. Logistical constraints precluded recording the weights of all fish, most commonly due to scale malfunction or excessive wind; however, nearly identical percentages of fish were weighed from each tag-size cohort. To compare weight between tag-size cohorts in each year, we adjusted the recorded weight of each fish by subtracting the weight of its tag (0.105 g for 12-mm tags and 0.08 g for 9-mm tags). For fish with both FL and weight measurements, we used the adjusted weight to calculate Fulton's condition factor (Fulton's K) as $10^5 \times \text{weight}/\text{length}^3$ (Nash et al. 2006).

Prior to release, all fish regardless of tag size were mixed and held in the stream within a pass-through enclosure that provided a continual supply of fresh water. After recovery from handling and tagging, fish were released into the reach from which they had been collected. To evaluate potential short-term mortality or tag loss, 10% of each cohort was held for 24 h. After holding, fish were observed in the enclosure, and any visible shed tags or dead fish were removed and recorded before release of the remaining live fish.

Once released, fish were tracked to their arrival as smolts at Lower Granite Dam in the following spring and summer (2012–2014; Figure 1). Based on the locations of PIT tag monitoring systems, we divided this overall distance into two segments: (1) a small stream segment spanning the point of release to our monitoring systems near the mouth of Valley Creek (4–7 km) and (2) a much larger river segment extending from the Valley Creek monitoring systems to Lower Granite Dam on the Snake River (740 km). For each tag-size cohort that was released in each year, we estimated survival probability, detection probability at monitoring systems, mean growth, and passage distribution timing at Lower Granite Dam. We tested for differences in these metrics between tag-size cohorts and investigated whether any tag effects were dependent on fish size or migration year.

Valley Creek instream monitoring

A PIT tag detection system was installed in Valley Creek during 2002 and has operated continuously since 2003 (Achord et al. 2003a, 2012). This was the first instream detection system in the Salmon River basin, allowing detections of juvenile fish near their natal rearing sites. Two instream arrays were installed approximately 1.2 km apart in Valley Creek to allow determination of fish movement directionality. This set of arrays could also be used to estimate survival from release upstream to the first instream array without waiting for detections the following spring at locations much further downstream.

The respective upstream and downstream detection arrays were located 1.6 and 0.4 km upstream from the mouth of Valley Creek and were dubbed VC1 and VC2, respectively (Figure 1). Each array spanned 85–100% of the stream width, depending on flow levels. Both systems were equipped with multiplex transceivers (FS 1001M; Biomark), which were configured to automatically interrogate, store, and transmit data to PTAGIS.

Connolly et al. (2008) described a method of estimating detection and survival probabilities using data from two consecutive detection arrays. However, past data from Valley Creek showed that detection at VC2 was not independent of detection at VC1, violating an assumption necessary for this method. Thus, for the present study, we pooled detections from the two arrays, effectively treating the two systems as a single detection site.

Interrogation at Lower Granite Dam

Study fish that were tagged as parr in late summer began their seaward migration after transitioning to the smolt stage during spring and summer of the following years. These smolts encounter eight dams on the lower Snake and Columbia rivers, seven of which are equipped with PIT tag monitoring systems. The dams with monitoring systems include Lower Granite, Little Goose, Lower Monumental, and Ice Harbor dams on the Snake River; and McNary, John Day, and Bonneville dams on the Columbia River (Figure 1). At Lower Granite Dam and other dams, fish must pass either (1) through the spillway via surface passage structures or (2) through the powerhouse via turbine intakes or the juvenile bypass system. The powerhouse of each dam is fitted with diversion screens to guide fish away from turbines and through a series of structures leading to the juvenile bypass system. During the 3 years of this study, PIT tag monitoring systems were present in the juvenile bypass facilities at all detector dams except Bonneville Dam, where tags were monitored in a specialized corner collector system.

In the juvenile bypass facilities, a series of antennas is installed on the flumes and pipes that lead fish either to collection areas or to the tailrace of the dam (Prentice et al. 1990; Marsh et al. 1999). Each antenna presents an opportunity for detection of each PIT-tagged fish that enters the juvenile bypass system. All bypass system detections are recorded automatically, along with the specific location, date, and time of detection. These data are then uploaded remotely to the PTAGIS database. We used these detection data to determine the route taken through the bypass system by each detected fish, noting whether or not the fish was ultimately routed to the tailrace to continue migration.

The final detection site from which tagged smolt data were utilized by our study was in the upper estuary of the Columbia River, approximately 150 km downstream from Bonneville Dam. In this river reach, a pair trawl fitted with a PIT tag detection antenna was used to sample tagged fish as they passed through the estuary from approximately rkm 66 to rkm 84 (Ledgerwood et al. 2004).

Data analyses

Size distribution between tag-size cohorts

To test for differences in distributions of length, weight, and fish condition between the tag-size cohorts, we conducted a two-sample, nonparametric Mann–Whitney *U*-test on paired cohorts from each tagging year (Hollander and Wolfe 1973). The null hypothesis for this test was that the two samples came from the same population. To be effective, the test does not require that the samples come from a population with specific statistical distributions (e.g., normal). For these tests, we used the stats package in the R statistical environment (R Core Team 2021).

Detection and survival probability

To estimate the probabilities of detection and survival on sequential occasions within each year, we used the Cormack–Jolly–Seber (CJS) release–recapture model (hereafter, "CJS model"; Cormack 1964; Jolly 1965; Seber 1965). The CJS model is the standard model for estimates of survival and detection probability using release–recapture data from marked individuals sampled from an unmarked population. For juvenile salmonids migrating downstream through the Snake and Columbia rivers, the CJS modeling framework has long been applied to PIT tag detection data, substituting space for time—that is, the intervals between detection "occasions" are stretches of river between detection sites that are sequential in space (Skalski et al. 1998; Smith et al. 2002). For a group of marked animals, release–recapture data consist of the set of individual detection histories for the group.

To evaluate detection and survival, we developed separate data sets for Valley Creek and for Lower Granite Dam. For Valley Creek, we constructed a set of detection histories for which the Valley Creek monitoring system was the first potential detection site. All sites downstream from Valley Creek were treated as a potential second, composite detection site. For each detection history, 1 represented detection and 0 represented nondetection at the two respective detection sites. Thus, each tagged fish realized one of four possible two-digit detection histories: 11, 10, 01, and 00. For this data set, there were three parameters of interest for each tag-size cohort in each year:

ϕ_{VC} = probability of survival from release to Valley Creek

p_{VC} = probability that a tagged fish that passed Valley Creek was detected

λ_{VC} = probability that a fish that passed Valley Creek alive was subsequently detected at least once at a site downstream

Because we combined all sites downstream from Valley Creek into a second composite detection site and because survival and detection probabilities were not separately identifiable for this composite site, the parameter λ_{VC} subsumed multiple survival and detection probabilities.

For Lower Granite Dam, we used the set of detection histories that included potential detection at or downstream from the dam, ignoring previous detection or nondetection at Valley Creek. This data set included a two-digit detection history for each fish, similar to the detection histories for Valley Creek, in which Lower Granite Dam was the first site and all sites downstream were combined into a second, composite detection site. For this data set, there were three parameters of interest for each tag-size cohort in each year:

ϕ_{GR} = probability of survival from release to Lower Granite Dam

p_{GR} = probability that a tagged fish that passed Lower Granite Dam was detected

λ_{GR} = probability that a fish that passed Lower Granite Dam alive was subsequently detected at least once at a site downstream

At Lower Granite Dam, the probability of being detected during passage was equal to the joint probability of entering and being detected in the juvenile bypass system. This is the case at most dams in our study area, as the juvenile bypass system is usually the only passage route monitored for PIT tags and evaluations over several decades have shown that very few fish that are implanted with standard 12-mm tags pass through a juvenile bypass system without being detected at least once (Axel et al. 2005). Accordingly, the probability of detecting a fish with a 12-mm PIT tag is typically considered equivalent to the probability that the fish entered the juvenile bypass system.

The standard CJS model does not incorporate effects of either cohort- or individual-level covariates. Instead, it is used to derive cohort-level estimates of survival, detection, and composite detection probabilities. These are interpreted as average probabilities across individuals that make up the cohort. We calculated these estimates for each cohort for both the Valley Creek data set and the Lower Granite Dam data set.

For each pair of tag-size cohorts within a single year, we used CJS estimates to construct asymptotic 95% confidence intervals (CIs) on the differences between the respective detection and survival probabilities. These differences provided a first check of the magnitude and potential significance of tag size effects on detection and survival probability. If fish size distributions are found to be equal between the two tag-size cohorts, then cohort-level differences in survival or detection probability can be attributed to differential effects of the tags themselves and not to inherent differences among fish in the respective cohorts.

It would have been possible to analyze detection histories that used Valley Creek and Lower Granite Dam as sequential detection sites within a single CJS model. This model would have had one parameter for survival from release to Valley Creek and one parameter for survival from Valley Creek to Lower Granite Dam. We chose to use the separate data sets to keep the covariate modeling more straightforward. Metrics for the Valley Creek to Lower Granite Dam section can be calculated as the difference between the two evaluated sections.

Model comparisons

The CJS model framework has been extended considerably to allow modeling of survival and detection probability as functions of both cohort- and individual-level covariates (e.g., Lebreton et al. 1992; Zabel and Achord 2004; Zabel et al. 2005). We used program MARK (White and Burnham 1999) to simultaneously analyze the data from all six tag-size cohorts from our 3 years of tagging, with probabilities modeled as functions of the main effects of year, tag size, and (for some probabilities) individual fish length at tagging.

Models could also include interactions among these fixed main effects. For each type of probability, we addressed the following questions:

- Was there a tag effect? (Did probabilities differ by tag size?)
- Was the tag effect consistent among years?
- Did the probability or the tag effect depend on fish size?
- Was the tag effect–fish size relationship consistent among years?

From both the Valley Creek and Lower Granite Dam data sets, we were primarily interested in results of modeling the probabilities of survival and detection. Although we did investigate models for the probability of composite detection parameters λ_{VC} and λ_{GR}, we do not present detailed results here. To model the probabilities of interest, we defined the following covariates for individual fish k ($k = 1, \ldots, n_{ij}$) implanted with tag size j ($j = 1$ for 12-mm tags; $j = 2$ for 9-mm tags) in migration year i ($i = 1$, 2, and 3 for 2012, 2013, and 2014, respectively) as follows:

$year_{Y,ijk}$ = a set of two indicators for years 2013 and 2014 ($Y = 2$ or 3; $year_{Y,ijk} = 1$ when $i = Y$ and 0 otherwise)

tag_{ijk} = an indicator for the 12-mm tag size ($tag_{ijk} = 1$ when $j = 1$; $tag_{ijk} = 0$ when $j = 2$)

$length_{ijk}$ = the length of fish ijk at the time of tagging (mm)

Thus, in the fullest possible model for a given probability θ (i.e., survival ϕ, detection p, or composite λ), with all possible interactions of main effects, the logit of the probability for individual fish k tagged with tag size j in year i was

$$\text{logit}(\theta_{ijk}) = \beta_0 + \boldsymbol{\beta_1}\mathbf{year}_{Y,ijk} + \beta_2 tag_{ijk} + \boldsymbol{\beta_3}\mathbf{year}_{Y,ijk} \bullet tag_{ijk} + \beta_4 length_{ijk} + \boldsymbol{\beta_5}\mathbf{year}_{Y,ijk} \bullet length_{ijk} + \beta_6 tag_{ijk} \bullet length_{ijk} + \boldsymbol{\beta_7}\mathbf{year}_{Y,ijk} \bullet tag_{ijk} \bullet length_{ijk},$$

where β_0 is the intercept, $\boldsymbol{\beta_1}$ is a vector of the two main effects for years 2013 ($Y = 2$) and 2014 ($Y = 3$), β_2 is the main effect of tag size, β_4 is the main effect of fish length, and the remaining slopes are the effects of the two- and three-way interactions.

Main effects for year were included in every candidate model, and models with interaction terms also included all corresponding lower order terms. The complete set of 14 parameterizations that we considered is listed in Table S2. We used year (Y), tag (T), and length (L) as terms in each model. For example, the fullest possible model (M14) was denoted Y + T + YT + L + YL + TL + YTL or by the shorthand Y × T × L. This fullest model had 12 effect parameters to be estimated, including the intercept.

The parameterization Y × T for M03 included the main effect of year, a unique tag effect in each year, and no effect of fish length. Except for the use of the logit link, the model that used M03 for all three probabilities was equivalent to the standard CJS model, in which all three probabilities were estimated independently for each cohort.

As time passes after tagging, fish length becomes a less reliable index of fish size and there is a potential association of fish size with various probabilities. Nevertheless, length at tagging was the covariate available to us. Processes associated with detection and survival probabilities from release to the Valley Creek monitors take place soon enough after tagging that length at tagging is a reliable index of the size of fish when experiencing those processes.

Length at tagging was also relevant to survival in the reach from release to Lower Granite Dam, as survival to the dam "begins" immediately after tagging and release. However, most study fish arrived at Lower Granite Dam (and then continued to migrate downstream of the dam) in the spring of the year after release. There was evidence that length at tagging was not a meaningful representation of fish length at the time of passing Lower Granite Dam (see Supplemental Discussion in the Supplemental Material in the online version of this article). Thus, although processes that occurred at or beyond the dam may well have been influenced by the size of study fish when they experienced those processes, we did not consider fish length at tagging as a reliable index for analysis of detection data from Lower Granite Dam and points downstream.

Based on these considerations, the fullest possible parameterization that we used for detection, survival, and composite probabilities at Valley Creek (p_{VC}, ϕ_{VC}, and λ_{VC}) and for survival at Lower Granite Dam (ϕ_{GR}) was M14 (Table S2). This model included year, tag size, and fish length as main effects along with all two- and three-way interactions. For the probability of detection at Lower Granite Dam and composite sites downstream (p_{GR} and λ_{GR}), we did not consider any model that included fish length at tagging. This restricted the set of possible models to M01, M02, and the fullest possible model, M03.

In the CJS framework, suites of probabilities for survival, detection, and composite downstream detection are modeled jointly, and the resulting estimates of effects are not statistically independent. For example, effects on detection probability at Valley Creek (p_{VC}) can be estimated only in the context of simultaneous parameterization for the other probabilities. This nonindependence meant that the parameterization for survival and composite detection below Valley Creek (ϕ_{VC} and λ_{VC}) could affect the results for Valley Creek detection probability (p_{VC}).

Jointly modeling these three parameters, there were $14 \times 14 \times 14 = 2744$ possible parameterizations for the Valley Creek data and $14 \times 3 \times 3 = 126$ possible parameterizations for the Lower Granite Dam data. We used information-theoretic approaches to multi-model inference to explore the full suite of possibilities (Burnham and Anderson 2002). We used the RMark package (Laake 2013) in the R statistical environment (R Core Team 2021) to fit all 2744 possible models for the Valley Creek data and all 126 possible models for the Lower Granite Dam data. We then obtained Akaike's information criterion corrected for small sample size (AIC_c) for each model; we calculated the Akaike difference (ΔAIC_c) and then calculated the Akaike weight based on ΔAIC_c (Burnham and Anderson 2002). We calculated model-averaged predicted values and relative variable importance for the various effects (Table S2) on each of the probabilities for both Valley Creek (ϕ_{VC}, p_{VC}, and λ_{VC}) and Lower Granite Dam (ϕ_{GR}, p_{GR}, and λ_{GR}). Relative variable importance for each term was calculated as the sum of Akaike weights of all models that included the term (Giam and Olden 2016).

Migration timing

For each cohort, we tabulated observed daily detections at Valley Creek or Lower Granite Dam and computed cumulative distributions of detection time. We standardized the cumulative distributions by dividing them by the total number of detections. Comparison of these standardized distributions did not require tags of different sizes to be equally detectable at either monitoring site. Tag size differences in migration timing patterns out of Valley Creek were evaluated using the nonparametric Kaplan–Meier (K–M) test (Hosmer et al. 2008; Sandford et al. 2012). This test is part of a class of "time-to-event" methods, which in this case was "time to detection" at each monitoring site. We used a log-rank chi-square test (Tableman and Kim 2004) to assess differences between K–M detection curves (i.e., timing patterns) for the pair of tag-size cohorts in each year. When the K–M test indicated a significant difference between timing distributions, we visually inspected the plots to determine the direction of the difference. For these analyses, we used the survival package in R (Therneau 2015; R Core Team 2021).

Growth

A portion of the study fish that were detected at Lower Granite Dam were diverted to tanks using a sort-by-code system (Downing et al. 2001). We recorded the FL (mm) and weight (g) of recaptured study fish before releasing them to continue their downstream migration. For fish with length and/or weight records from both the time of release and the time of detection at Lower Granite Dam, we calculated mean daily growth. For each of these fish, we calculated three metrics:

- Change in length (mm) divided by the number of days from release as parr to detection at Lower Granite Dam as smolts
- Change in weight (g) divided by the number of days from release as parr to detection at Lower Granite Dam as smolts
- Change in Fulton's *K*, as defined above

We used two-sample *t*-tests to evaluate differences in these metrics between tag-size cohorts (Zar 2010). Because the number of fish measured was small, data pooled across the three migration years were used for the *t*-tests.

RESULTS

During July–August of 2011–2013, we captured a total of 12,274 wild Chinook Salmon parr over a distance of about 12 km within Valley Creek (Table 1). Of the fish collected, 4211 were implanted with standard 12-mm PIT tags, while 4232 were implanted with 9-mm tags (Table 1). Mortality associated with collection, handling, and tagging was low throughout the study. Overall collection mortality was 1.2%, and short-term tagging mortality was 0.1% (19 total fish; no comparison was made between tag types), with six tags observed at the bottom of holding enclosures prior to release (tag shedding rate = 0.07%).

Fish length distribution at release appeared to be nearly identical between the tag-size cohorts in each year (Table 1); from Mann–Whitney *U*-tests for 2011, 2012, and 2013, the respective *p*-values were 0.518, 0.996, and 0.905. Distributions of fish weight were not significantly different among successive tagging years, with *p*-values of 0.939, 0.933, and 0.305. Differential tag burden across all years was 3.0% and 2.4%, respectively, for fish with 12- and 9-mm tags. Distributions of Fulton's *K* were not significantly different between tag-size groups in 2011 ($p = 0.603$), but they were significantly different in 2012 ($p = 0.025$) and were nearly significantly different in 2013 ($p = 0.056$). In both 2012 and 2013, mean Fulton's *K* was greater for the 12-mm tag cohort than for the 9-mm tag cohort.

Survival and tag performance at Valley Creek

At Valley Creek, estimated detection probabilities varied annually, with both tag types less likely to be detected in 2013 (Table 2). There were also large differences in detection rate between tag types. For the migration years 2012, 2013, and 2014, estimated detection probabilities were 81, 74, and 49%, respectively, for fish with 12-mm tags and 39, 48, and 16%, respectively, for fish with 9-mm tags. Detection rates for 9-mm tags were considerably lower than those for 12-mm tags.

Estimated survival between release and Valley Creek also varied among migration years (Table 2). Survival probabilities were nearly equal between the respective 12- and 9-mm tag-size cohorts for the first two migration years: 50.8% versus 50.2% in 2012 and 43.4% versus 44.0% in 2013. In 2014, the difference between estimates was larger, as survival probability was 63.2% for the 12-mm tag cohort and 87.1% for the 9-mm tag cohort; however, the latter estimate was very imprecise. In all 3 years, survival estimates were less precise for the 9-mm cohorts because of their lower detection rates.

TABLE 1 Summary of tagging and release of wild Chinook Salmon parr measured for fork length (mm), weight (g; minus the weight of the tag), and Fulton's condition factor (K). Fish were tagged with 9- and 12-mm passive integrated transponder tags in Valley Creek, Idaho, during summer 2011–2013. N, number of fish tagged, measured, and released; SD, standard deviation.

							Percentile of distribution at release					
	12 mm			9 mm			12 mm			9 mm		
Tag year	*N*	Mean	SD	*N*	Mean	SD	5th	50th	95th	5th	50th	95th
Length (mm)												
2011	1856	62.8	5.6	1876	62.8	5.7	55	62	74	55	62	73
2012	1100	62.2	5.8	1099	62.2	5.8	55	61	73	55	61	74
2013	1249	63.2	6.5	1244	63.4	6.8	55	62	75	55	62	77
Total or mean	4205	62.8	5.6	4219	62.8	5.7	55	62	74	55	62	74
Weight (g)												
2011	603	3.22	1.04	626	3.18	1.04	2.00	3.00	5.19	2.12	2.92	4.90
2012	867	3.43	1.19	865	3.39	1.12	2.20	3.10	5.50	2.14	3.12	5.82
2013	602	3.38	1.31	601	3.26	1.19	2.00	3.00	5.90	1.92	2.92	5.52
Total or mean	2072	3.35	1.04	2092	3.29	1.04	2.10	3.10	5.50	2.02	3.02	5.52
Fulton's *K*												
2011	603	1.299	0.148	626	1.304	0.164	1.096	1.284	1.558	1.087	1.267	1.577
2012	863	1.379	0.157	859	1.364	0.165	1.158	1.355	1.673	1.138	1.341	1.677
2013	602	1.254	0.154	600	1.239	0.147	1.020	1.250	1.525	1.034	1.224	1.497
Total or mean	2068	1.319	0.148	2085	1.310	0.164	1.081	1.299	1.620	1.087	1.285	1.619

As is typical for release–recapture data of this type, fitting all 2744 possible models of the Valley Creek data set resulted in many different parameterizations that gave very similar predicted values for the probabilities across the range of fish lengths, and no model dominated in terms of AIC_c (Table S3). The model with the minimum AIC_c value had only 4.7% of the total Akaike weight. That model—in fact, all 20 models with the greatest Akaike weights—included a year-specific tag effect on detection probability at Valley Creek and fish length effects on both detection probability and the probability of survival from release to Valley Creek. Other terms that appeared among the top-20 models were a tag effect on survival and additional interaction effects on detection probability.

In terms of relative variable importance, the main effect of tag size on detection and the main effect of fish length on survival received 100% of the Akaike weight, as did the main effect of fish length on the composite detection probability (Table 3). Other effects with nearly 100% of the weight were the main effect of fish length and the year × tag size interaction effect on detection probability and the year × fish length interaction effect on the composite probability. There was less support for other effects, notably for tag size on survival probability, which had 52% of the Akaike weight.

For survival probability from release to Valley Creek, model-averaged predicted values ranged from around 40% for the smallest fish (~50 mm FL) to 80% or greater for the largest (Figure 2). Among the smallest fish, estimated probabilities of survival to Valley Creek were slightly higher for the 9-mm tag cohort than for the 12-mm tag cohort in all 3 years. However, the 95% CIs were relatively wide and overlapping, support for a tag size effect was moderate (52% of the weight), and support for an interaction effect of tag size and fish length was low (21% of the weight). In contrast, among the largest fish, survival probability was slightly higher for those with 12-mm tags. As expected, given the relative variable importance values, model-averaged predicted values for detection probability at Valley Creek showed large differences between tag types (Figure 2) and a strong association with fish length. Larger fish were notably less likely than smaller fish to be detected at Valley Creek, regardless of the tag size they carried.

Survival and tag performance at Lower Granite Dam

At Lower Granite Dam, as at Valley Creek, the probability of detection was lower for fish implanted with 9-mm tags than for those implanted with 12-mm tags in all three migration years (Table 2). Although these differences were consistent in direction, 95% CIs for the

TABLE 2 Estimated detection and survival probabilities (with associated standard errors [SEs]) from the Cormack–Jolly–Seber model of Valley Creek Chinook Salmon releases for migration years 2012–2014. Data were detections of tagged fish at Valley Creek instream arrays (VC), at Lower Granite Dam (GR), and at detection sites downstream of Lower Granite Dam. Asymptotic 95% confidence intervals (CIs) are given for the difference between estimates for the two tag-size cohorts in each year. p_{GR}, probability of detection at Lower Granite Dam; p_{VC}, probability of detection at the Valley Creek monitors; ϕ_{GR}, probability of survival from release to Lower Granite Dam; ϕ_{VC}, probability of survival from release to the Valley Creek monitors.

		Detection probability *p*			Survival probability ϕ		
Migration year	**Tag-size cohort**	**Estimate**	**SE**	**95% CI of difference**	**Estimate**	**SE**	**95% CI of difference**
Valley Creek (p_{VC} and ϕ_{VC})							
2012	12 mm	0.805	0.028	(0.335, 0.499)	0.508	0.019	(−0.074, 0.086)
	9 mm	0.388	0.031		0.502	0.037	
2013	12 mm	0.738	0.056	(0.082, 0.434)	0.434	0.034	(−0.147, 0.135)
	9 mm	0.480	0.071		0.440	0.063	
2014	12 mm	0.489	0.075	(0.156, 0.508)	0.632	0.095	(−0.811, 0.333)
	9 mm	0.157	0.051		0.871	0.276	
Lower Granite Dam (p_{GR} and ϕ_{GR})							
2012	12 mm	0.371	0.036	(−0.045, 0.143)	0.135	0.011	(−0.064, 0.002)
	9 mm	0.321	0.032		0.166	0.013	
2013	12 mm	0.385	0.068	(−0.066, 0.302)	0.069	0.010	(−0.018, 0.040)
	9 mm	0.267	0.066		0.058	0.011	
2014	12 mm	0.528	0.083	(−0.181, 0.259)	0.042	0.007	(−0.025, 0.016)
	9 mm	0.489	0.075		0.046	0.007	

TABLE 3 Relative variable importance from all possible models of (1) the probability of Chinook Salmon survival from release to the Valley Creek monitors (ϕ_{VC}), the probability of detection at those monitors (p_{VC}), and the composite probability of additional detection downstream (λ_{VC}); and (2) the probability of survival from release to Lower Granite Dam (ϕ_{GR}), the probability of detection at the dam (p_{GR}), and the composite probability of additional detection downstream (λ_{GR}). Model terms are the main effects of year (Y), tag size (T), fish length (L), and interactions among those effects. All models in the set included the main effects of Y on all three parameters.

	Weight for effect on parameter in Valley Creek data set			Weight for effect on parameter in Lower Granite Dam data set		
Model term	ϕ_{VC}	p_{VC}	λ_{VC}	ϕ_{GR}	p_{GR}	λ_{GR}
T	0.520	1.000	0.715	0.758	0.591	0.373
YT	0.166	0.931	0.356	0.329	0.117	0.066
L	1.000	0.973	1.000	1.000	–	–
YL	0.253	0.193	0.999	0.997	–	–
TL	0.209	0.359	0.361	0.399	–	–
YTL	0.005	0.012	0.024	0.024	–	–

estimated differences were all wide and all CIs included 0.0, so we could not conclude that the differences were significant.

The river segment, spanning from release to Lower Granite Dam, combines the lower end of Valley Creek and parts of the Salmon and Snake rivers. For this segment, the survival estimate encompasses parr-to-smolt survival over the winter. Estimated survival probabilities in this segment ranged from 17% for the 9-mm tag cohort in migration year 2012 to only 4% for the 12-mm tag cohort in migration year 2014 (Table 2). There was no evidence of a consistent tag-related difference in survival across years.

However, the year with greatest survival overall (2012) also had the largest difference. For that year, estimated survival was 16.6% for the 9-mm cohort versus 13.5% for the 12-mm cohort—a relative difference of 23%.

Fitting all 126 possible models of the Lower Granite Dam data set resulted in a variety of parameterizations that gave very similar predicted values for the probabilities across the range of fish length, and no model dominated in terms of AIC_c (Table S4). The best supported models largely excluded year-specific tag effects on p_{GR} and λ_{GR}. All 20 models with the greatest weight included a year-specific effect of fish length on survival probability from release to Lower Granite Dam. Most of the top models included a tag size effect on survival, and several top models included survival effects from the tag size × fish length interaction (likely because tag effects depended on fish size).

In terms of relative variable importance for the various effects on probabilities, the main effect of fish length on survival received 100% of the Akaike weight and the fish length × year interaction had 99.7% of the Akaike weight (Table 3), indicating that the fish length effect varied by year. There was strong support for tag size as a main effect on survival, with 76% of the weight. At Lower Granite Dam, there was moderate support for a tag effect on detection probability (59% of the Akaike weight) and for an effect on survival from the tag size × fish length interaction (40% of the weight).

Model-averaged predicted values for survival probability from release to Lower Granite Dam ranged from around 5–15% for the smallest fish (~50 mm FL) to 25–40% for the largest fish (Figure 3). Support for a tag size × fish length interaction was illustrated by larger differences between tag sizes in predicted survival for the largest fish. As with the Valley Creek data set, among the very smallest fish, those with 9-mm tags had very slightly higher predicted survival to Lower Granite Dam than those with 12-mm tags. Model-averaged predicted values for detection probability at Lower Granite Dam were higher for fish with 12-mm tags than for those with 9-mm tags. Model-averaged values were very nearly equal to the estimates from the standard CJS model (Table 2).

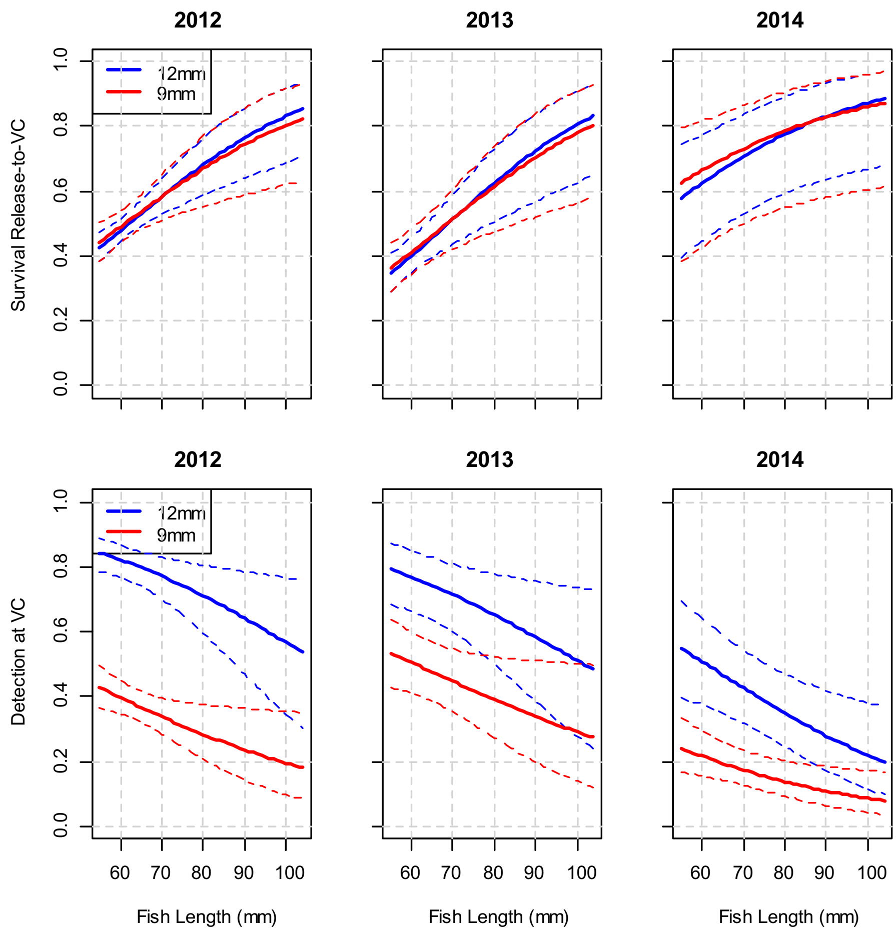

FIGURE 2 Model-averaged predicted values for the probability of survival from release to the monitoring system at Valley Creek (VC) and the probability of detection at the system for Chinook Salmon tagged with 12-mm passive integrated transponder (PIT) tags (solid blue lines) or 9-mm PIT tags (solid red lines). Dashed lines show the 95% confidence intervals for the respective predicted values.

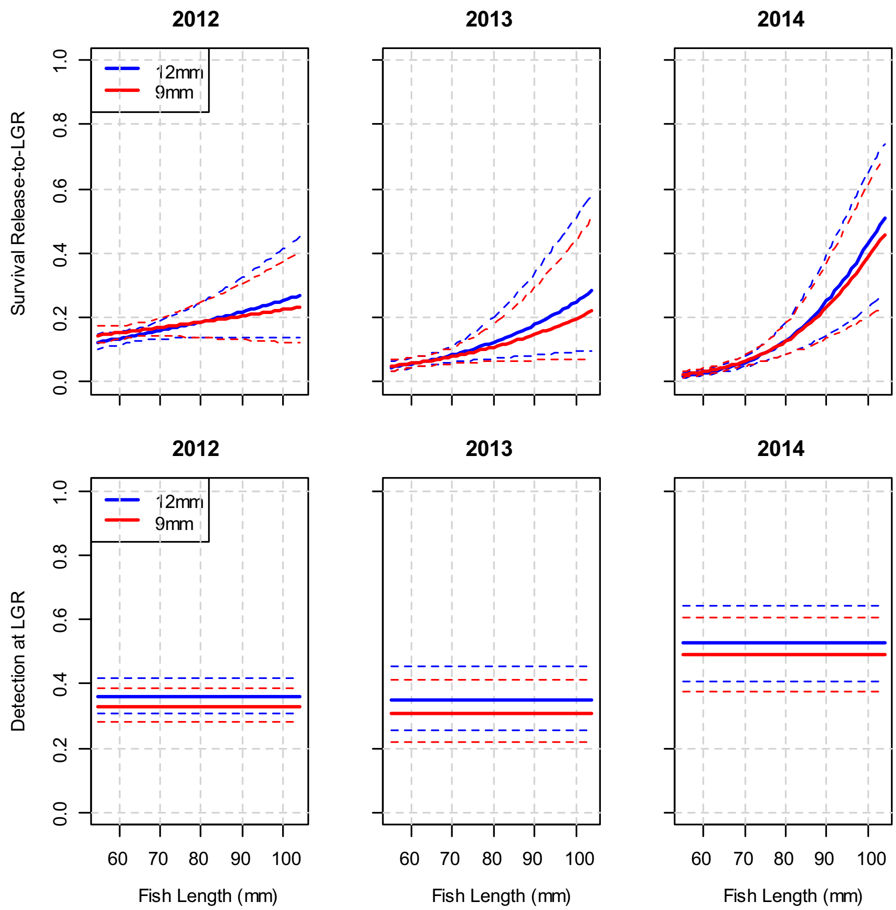

FIGURE 3 Model-averaged predicted values for the probability of survival from release to Lower Granite Dam (LGR) and the probability of detection at the dam for Chinook Salmon tagged with 12-mm passive integrated transponder (PIT) tags (solid blue lines) or 9-mm PIT tags (solid red lines). Dashed lines show the 95% confidence intervals for the respective predictions.

Migration timing

At the Valley Creek monitors, cumulative detection for 9- and 12-mm tag cohorts was variable among years (Figure 4, left side), and there were also variable patterns between cohorts within years. The 9-mm tag cohort passed Valley Creek significantly later than the 12-mm tag cohort during migration years 2012 and 2014, with median differences of 6 and 4 days, respectively (2012: $p<0.001$; 2014: $p=0.080$). However, passage timing at the Valley Creek monitoring system was significantly earlier for the 9-mm tag-size cohort in 2013 (median difference = 21 days; $p=0.020$).

At Lower Granite Dam, cumulative passage was not significantly different between tag-size cohorts in any of the three migration years, with median differences of 1, 1, and 2 days in 2012, 2013, and 2014, respectively ($p=0.610$, 0.210, and 0.810; Figure 4). At neither detection site were the results consistent with respect to relative migration timing of the two tag-size cohorts, suggesting that tag size did not have a predictable effect on migration timing.

Growth

For combined yearly cohorts of juvenile fish, mean FL ranged from 62.2 to 63.4 mm, mean weight ranged from 3.18 to 3.48 g, and mean Fulton's K ranged from 1.239 to 1.379 at the time of tagging (Table 1). Among fish sampled when they arrived months later at Lower Granite Dam, means for yearly cohorts ranged from 100.5 to 105.4 mm FL, from 10.96 to 12.97 g in weight, and from 1.020 to 1.101 for Fulton's K. None of the tests that we conducted on mean changes in metrics was significant (minimum $p=0.524$). In other words, we found no evidence that growth between release in late summer and arrival at Lower Granite Dam the following year differed between fish that were tagged with 9- versus 12-mm tags.

DISCUSSION

Our study design of alternating the tag size during tagging was successful in avoiding bias from unequal fish length and weight distributions between cohorts. The observed

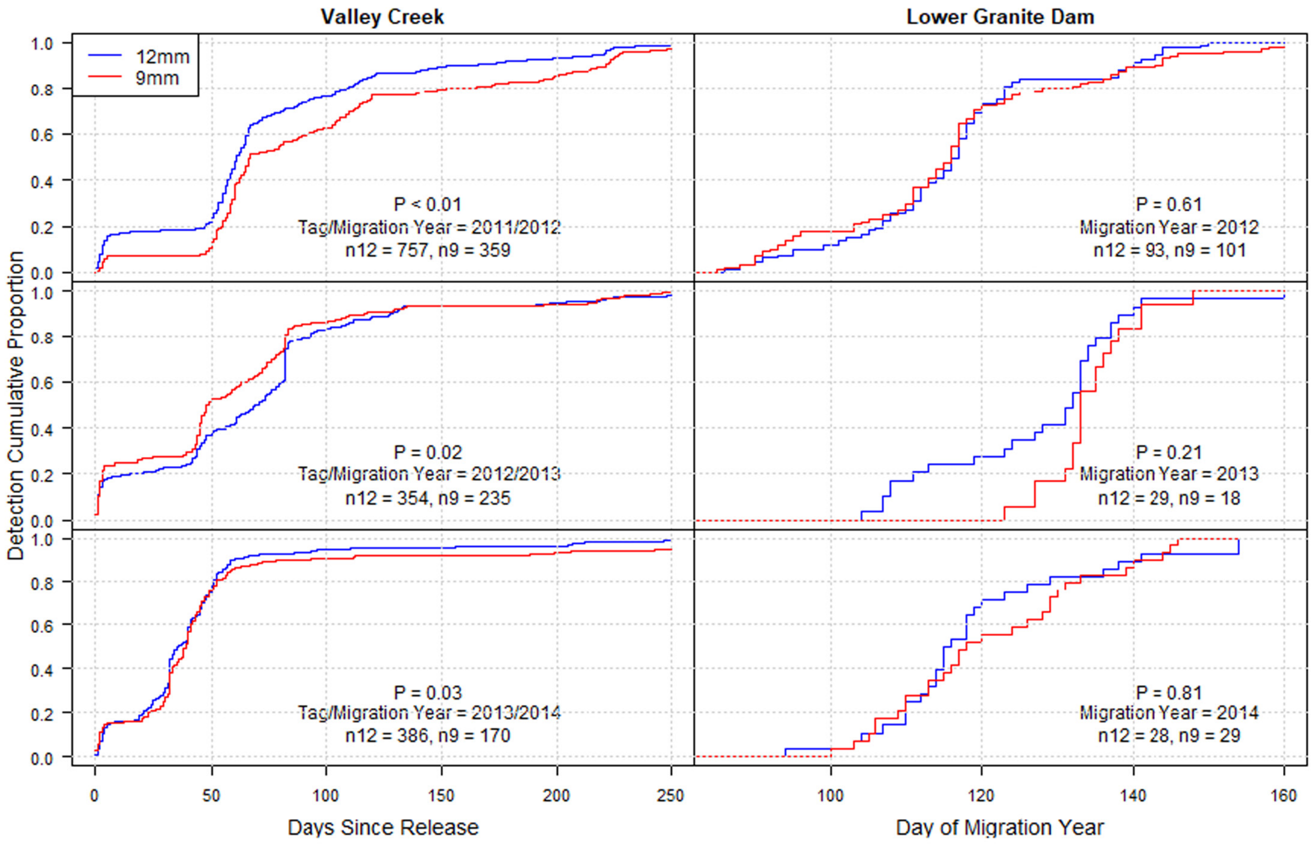

FIGURE 4 Cumulative passage distributions by tag-size cohort at Valley Creek and Lower Granite Dam. Blue lines indicate groups of Chinook Salmon with 12-mm passive integrated transponder (PIT) tags, while red lines indicate those with 9-mm PIT tags. For Valley Creek (left), the *x*-axis shows the number of days since release. For Lower Granite Dam (right), the *x*-axis shows the day of the migration year. The *p*-values are for tests of differences between cumulative distributions. n9, sample size of fish with 9-mm tags; n12, sample size of fish with 12-mm tags.

differences in Fulton's *K* were unexpected (Figure S1 available in the Supplemental Material in the online version of this article). However, because length and weight distributions were so similar, we reasoned that Fulton's *K* was unlikely to have driven differences in postrelease performance. Based on these results, we assumed that observed cohort-level differences in the probability of survival or detection, migration timing, or growth were attributable to differential effects of the tags themselves rather than to inherent differences between fish in the respective cohorts.

Our analysis showed that fish with 9-mm PIT tags were significantly less likely to be detected than fish with 12-mm tags when passing a typical instream monitoring system such as that in Valley Creek. This was most likely because of the greater turn-on voltage required by the 9-mm tag (456.6 mV) as compared to the 12-mm tag (335.9 mV; Table S1). In general, the greater the voltage required to excite the passive transponder, the lower the tag read range will be. Consequently, differences in detection rate will be greater during periods of high flow, when greater stream depth allows fish to pass at further distances from the antennas.

Modeled detection probabilities at Valley Creek showed that the average detection rate varied among years for both tag types, as did differences in detection rate between tag types. However, larger fish were notably less likely to be detected than smaller fish, regardless of the tag size that they carried. Differences in avoidance behavior, such as vertical versus horizontal swimming orientation, may have contributed to the varying detection rates at Valley Creek, with behaviors differing between fish that were larger versus smaller at the time of tagging. Differences in average detection rates among years were also likely due in part to varying environmental conditions in the stream, such as flow and temperature.

Instream monitoring systems vary in size, location, bathymetry, and technological components, meaning that each site will result in a different detection probability, and we advise caution in attempting to use 9-mm tags to collect data from such systems. Advances in technology have increased the performance of 9-mm (or smaller) PIT tags, and these advances will almost certainly continue; however, site-specific evaluation is recommended to ensure the feasibility of the 9-mm PIT tag for instream applications.

At Lower Granite Dam, application of the 9-mm tag presented a somewhat different outcome. Mean estimated detection probabilities at the dam were not significantly different between tag-size cohorts, with overlapping 95% CIs on the difference between CJS estimates. Nevertheless, the direction of the difference was consistent across years, as 9-mm tag cohorts were 3–12% less likely to be detected passing the dam. Studies have shown that a fish tagged with the standard 12-mm tag is extremely unlikely to pass undetected through the multiple monitors within a juvenile fish bypass system (Prentice et al. 1990; Muir et al. 2001; Axel et al. 2005). The greater turn-on voltage required by the 9-mm tag may have made it slightly less detectable, even within the short reading distances afforded by the bypass system pipes and flumes. Another possibility is that the small differences in detection rate resulted from fish with the smaller tag being less likely to enter the bypass system. The 9-mm tag does present a smaller physical burden than the 12-mm tag, and this difference in tag burden could result in small differences in vertical distribution or swimming behavior as fish approach the dam. A fish carrying a smaller tag might tend to enter the forebay higher in the water column, where it would more likely be attracted to spillway attraction flows and therefore would go undetected as a result of passing via the spillway rather than the powerhouse.

Cohort-level mean estimated survival probabilities, either from release to Valley Creek or from release to Lower Granite Dam, were not significantly different between tag-size cohorts, and the direction of observed differences was not consistent across years. However, in the year with the greatest survival (2011/2012), we observed a slightly higher survival probability from release to Lower Granite Dam for the 9-mm tag cohort (16.6%) than for the 12-mm tag cohort (13.5%).

Estimated survival in both the stream and river segments was strongly associated with fish length, with the largest fish having markedly higher survival than the smallest fish. There was also moderate support for models that included a tag type × fish length interaction. Model-averaged predicted values were slightly higher for the smallest fish when tagged with 9-mm tags, supporting the notion that the smaller tag presents a better choice for studies using small fish. However, the largest fish had higher predicted survival when they were tagged with 12-mm tags, and it is possible that 9-mm tags were more likely than 12-mm tags to be shed from larger fish. Very few shed tags (6 tags; 0.07%) were observed prior to release; therefore, tag shedding was not sufficient to evaluate this hypothesis. We assume that any actual difference in tag shedding rates would have a negligible impact on survival estimate differences.

Using PIT tag detection data from Lower Granite Dam, Achord et al. (2003b, 2007) studied a number of performance metrics in Salmon River fish that were tagged as parr in natal tributary streams. Those authors found that parr-to-smolt survival to the dam was highly variable among streams and across years, in part due to parr density. There were also differences in migration timing to Valley Creek between tag-size cohorts, and some were statistically significant. However, the direction of the difference was not consistent between years, and there were no statistically significant differences in migration timing to Lower Granite Dam. Previous studies have shown that passage timing distributions at the dam vary across years and among streams (Achord et al. 2007).

We observed no differences in growth between 9- and 12-mm tag-size cohorts from the time of tagging to the time of arrival at Lower Granite Dam the following spring. In similar observations, Achord et al. (2007) found that growth between tagging and detection at the dam was variable and related to the time since tagging and to length at the time of tagging. There may have been effects related to migration or passage preference at both the stream and dam detection sites (Faulkner et al. 2019), but these effects, if present, did not impact overall growth (Tiffan et al. 2021). Further research with much larger sample sizes would be needed to evaluate differences in parr-to-adult survival between tag sizes. Given the large numbers of fish that would be needed, such evaluations are not feasible in most situations. Present information needs would more practically focus on 9-mm tag performance in small fish (<55 mm) under various monitoring configurations.

Advances in PIT technology emerge regularly, providing improvements to what is alr-eady one of the best monitoring tools available. In addition to smaller tags, new antenna transceiver designs are engineered and tested annually, providing continual momentum for further advances. Improvements in passive transponder transmission and reception will continue to provide data sets of high quality, thus improving inferences drawn from fish monitoring and evaluation studies. Since the time of our study, the Valley Creek detection system has been reconfigured and updated to take advantage of improved technology (Pacific States Marine Fisheries Commission 2023).

Continued research and development of PIT technology are critical, as is the need to educate researchers and managers about these innovative tools that can provide valuable data to document fish migration behavior and survival. This study tested two important considerations regarding the development of smaller tags: (1) potential impacts on fish behavior and survival and (2) tag performance in riverine environments. Our study showed that while smaller tags may decrease the tag burden on study fish, especially smaller individuals, there may be situations in which the use of smaller tags is not advisable, depending on the planned method of detection and site location.

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CONFLICT OF INTEREST STATEMENT

The authors have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements) or nonfinancial interest (such as personal or professional relationships, affiliations, knowledge, or beliefs) in the subject matter or materials discussed in this article.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding authors (B. P. Sandford and S. G. Smith) upon reasonable request. The PIT tag data are available from PTAGIS (www.ptagis.org).

ETHICS STATEMENT

All activities associated with this project met the ethical criteria set forth by the National Marine Fisheries Service. Guidelines on the collection and handling of fish were followed in compliance with ESA Section 10(a) Permit Number 13381 (Pacific fish/invertebrates) and Idaho Department of Fish and Game Scientific Collection Permit F-31-88-11.

ORCID

Jesse J. Lamb https://orcid.org/0009-0007-1285-8257
Benjamin P. Sandford https://orcid.org/0000-0001-6144-8309

REFERENCES

Achord, S., Hockersmith, E. E., Sandford, B. P., McNatt, R. A., Feist, B. E., & Matthews, G. M. (2003a). Monitoring the migrations of wild Snake River spring/summer Chinook Salmon smolts, 2022 (Contract Report NMFS-NWFSC-CR-2023-11). National Oceanic and Atmospheric Administration. https://doi.org/10.25923/jcm7-j827

Achord, S., Levin, P. S., & Zabel, R. W. (2003b). Density-dependent mortality in Pacific salmon: The ghost of impacts past? *Ecology Letters*, *6*(4), 335–342. https://doi.org/10.1046/j.1461-0248.2003.00438.x

Achord, S., Mathews, G. M., Johnson, O. W., & Marsh, D. M. (1996). Use of passive integrated transponder (PIT) tags to monitor migration timing of Snake River Chinook Salmon smolts. *North American Journal of Fisheries Management*, *16*, 302–3013. https://doi.org/10.1577/1548-8675(1996)016<0302:UOPITP>2.3.CO;2

Achord, S., Sandford, B. P., Smith, S. G., Wassard, W. R., & Prentice, E. F. (2012). Instream monitoring of PIT-tagged wild spring/summer Chinook Salmon juveniles in Valley Creek, Idaho. In J. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. Mesa, & Q. Phelps (Eds.), *Advances in fish tagging and marking technology* (Symposium 76, pp. 163–176). American Fisheries Society. https://doi.org/10.47886/9781934874271.ch11

Achord, S., Zabel, R. W., & Sandford, B. P. (2007). Migration timing, growth, and estimated parr-to-smolt survival rates of wild Snake River spring/summer Chinook Salmon from the Salmon River basin, Idaho, to the lower Snake River. *Transactions of the American Fisheries Society*, *136*, 142–154. https://doi.org/10.1577/T05-308.1

Axel, G. A., Brooks, G. T., Brower, A., & Warf, D. (2017). *Comprehensive PIT tag evaluation procedure: Outline of tests that shall be conducted to determine if candidate tags can be acceptably detected by the PIT-tag systems installed throughout the Columbia River basin*. Bonneville Power Administration, Division of Fish and Wildlife; PIT Tag Steering Committee.

Axel, G. A., Brooks, G. T., & Sandford, B. P. (2021). *New marking and monitoring technologies for the passive integrated transponder, 2020*. Bonneville Power Administration, Environment, Fish, and Wildlife Program.

Axel, G. A., Prentice, E. F., & Sandford, B. P. (2005). PIT-tag detection system for large-diameter juvenile fish bypass pipes at Columbia River basin hydroelectric dams. *North American Journal of Fisheries Management*, *25*, 646–651. https://doi.org/10.1577/M04-071.1

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference* (2nd ed.). Springer.

Connolly, P. J., Jezorek, I. G., & Martens, K. D. (2008). Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. *North American Journal of Fisheries Management*, *28*, 402–417. https://doi.org/10.1577/M07-008.1

Cormack, R. M. (1964). Estimates of survival from the sightings of marked animals. *Biometrika*, *51*, 429–438. https://doi.org/10.1093/biomet/51.3-4.429

Dalbey, S. R., McMahon, T. E., & Fredenberg, W. (1996). Effect of electrofishing pulse shape and electrofishing-induced spinal injury on long-term growth and survival of wild Rainbow Trout. *North American Journal of Fisheries Management*, *16*(3), 560–569. https://doi.org/10.1577/1548-8675(1996)016<0560:EOEPSA>2.3.CO;2

Downing, S. L., Prentice, E. F., Frazier, R. W., Simonson, J. E., & Nunnallee, E. P. (2001). Technology developed for diverting passive integrated transponder (PIT) tagged fish at hydroelectric dams in the Columbia River basin. *Aquacultural Engineering*, *25*, 149–164. https://doi.org/10.1016/S0144-8609(01)00079-6

Endangered and Threatened Species; Threatened Status for Snake River Spring/Summer Chinook Salmon, Threatened Status for Snake River Fall Chinook Salmon, 57 F.R. 14653–14663. (1992). https://www.govinfo.gov/content/pkg/FR-1992-04-22/pdf/FR-1992-04-22.pdf

Evans, A. F., Payton, Q., Cramer, B. M., Collis, K., Hostetter, N. J., Roby, D. D., & Dotson, C. (2019). cumulative effects of avian predation on upper Columbia River steelhead. *Transactions of the American Fisheries Society*, *148*, 896–913. https://doi.org/10.1002/tafs.10197

Faulkner, J. R., Bellerud, B. L., Widener, D. L., & Zabel, R. W. (2019). Associations among fish length, dam passage history, and survival to adulthood in two at-risk species of Pacific salmon. *Transactions of the American Fisheries Society*, *148*, 1069–1087. https://doi.org/10.1002/tafs.10200

Giam, X., & Olden, J. D. (2016). Quantifying variable importance in a multimodel inference framework. *Methods in Ecology and Evolution*, *7*, 388–397. https://doi.org/10.1111/2041-210X.12492

Holcombe, E. F., Borsky, A. J., Biron, J. M., Bentley, P. J., Sandford, B. P., & Jaenecke, K. E. (2020). *Detection of PIT-tagged juvenile salmonids migrating in the Columbia River estuary, 2019*. Bonneville Power Administration.

Hollander, M., & Wolfe, D. A. (1973). *Non-parametric statistical methods*. John Wiley and Sons.

Hosmer, D. W., Jr., Lemeshow, S., & May, S. (2008). *Applied survival analysis: Regression modeling of time-to-event data* (2nd ed.). Wiley. https://doi.org/10.1002/9780470258019

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, *52*, 225–247. https://doi.org/10.1093/biomet/52.1-2.225

Laake, J. (2013). RMark: An R interface for analysis of capture-recapture data with MARK (Alaska Fisheries Science Center Processed Report 2013-01). National Oceanic and Atmospheric Administration. http://afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf

Lamb, J. J., Achord, S., Sandford, B. P., Axel, G. A., Nesbit, M. G., McIntyre, K. W., & Sanderson, B. L. (2013). *Monitoring the migrations of wild Snake River spring/summer Chinook Salmon juveniles, 2011-2012*. Bonneville Power Administration.

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. https://doi.org/10.2307/2937171

Ledgerwood, R. D., Ryan, B. A., Dawley, E. M., Nunnallee, E. P., & Ferguson, J. W. (2004). A surface trawl to detect migrating juvenile salmonids tagged with passive integrated transponder tags. *North American Journal of Fisheries Management*, *24*(2), 440–451. https://doi.org/10.1577/M0-071.1

Marsh, D. M., Matthews, G. M., Achord, S., Ruehle, T. E., & Sandford, B. P. (1999). Diversion of salmonid smolts tagged with passive integrated transponders from an untagged population passing through a juvenile collection system. *North American Journal of Fisheries Management*, *19*, 1142–1146. https://doi.org/10.1577/1548-8675(1999)019<1142:DOSSTW>2.0.CO;2

Muir, W. D., Smith, S. G., Williams, J. G., & Hockersmith, E. E. (2001). Survival estimates for migrant yearling spring Chinook Salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. *North American Journal of Fisheries Management*, *21*, 269–282. https://doi.org/10.1577/1548-8675(2001)021<0269:SEFMYC>2.0.CO;2

Nash, R. D. M., Valencia, A. H., & Geffen, A. J. (2006). The origin of Fulton's condition factor—Setting the record straight. *Fisheries*, *31*, 236–238.

Nielsen, J. L. (1998). Electrofishing California's endangered fish populations. *Fisheries*, *23(12)*, 6–12. https://doi.org/10.1577/1548-8446(1998)023<0006:SSEECE>2.0.CO;2

National Marine Fisheries Service. (2020). Endangered Species Act Section 7(a)(2) biological opinion and Magnuson–Stevens Fishery Conservation and Management Act essential fish habitat response: Continued operation and maintenance of the Columbia River system. National Marine Fisheries Service. https://doi.org/10.25923/3tce-8p07

Pacific States Marine Fisheries Commission. (2023). *PTAGIS (Columbia Basin PIT Tag Information System)*. http://www.ptagis.org

Prentice, E. F., Flagg, T. A., McCutcheon, C. S., & Brastow, D. F. (1990). PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. In N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, & G. A. Winans (Eds.), *Fish-marking techniques* (Symposium 7, pp. 323–334). American Fisheries Society.

Prentice, E. F., Maynard, D., Frost, D., Kellett, M., Bruland, D., McConkey, P., Waknitz, W., Iwamoto, R., McIntyre, K., Paasch, N., & Downing, S. (1994). *A study to determine the biological feasibility of a new fish tagging system, 1990-1993*. Bonneville Power Administration.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. R-project.org/

Sandford, B. P., Zabel, R. W., Gilbreath, L. G., & Smith, S. G. (2012). Exploring latent mortality of juvenile salmonids related to migration through the Columbia River hydropower system. *Transactions of the American Fisheries Society*, *141*(2), 343–352. https://doi.org/10.1080/00028487.2012.664601

Seber, G. A. F. (1965). A note on the multiple recapture census. *Biometrika*, *52*, 249–259. https://doi.org/10.1093/biomet/52.1-2.249

Sharber, N. G., Carothers, S. W., Sharber, J. P., de Bos, J. D., Jr., & House, D. A. (1994). Reducing electrofishing-induced injury of Rainbow Trout. *North American Journal of Fisheries Management*, *14*, 340–346. https://doi.org/10.1577/1548-8675(1994)014<0340:REIIOR>2.3.CO;2

Skalski, J. R., Smith, S. G., Iwamoto, R. N., Williams, J. G., & Hoffmann, A. (1998). Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1484–1493. https://doi.org/10.1139/f97-323

Skov, C., Hansen, J. H., Baktoft, H., Brönmark, C., Brodersen, J., Chapman, B. B., https://archives.federalregister.gov/issue_slice/1992/4/22/14648-14663.pdf#page=6Hansson, L.-A., Hulthén, K., & Nilsson, P. A. (2020). A field evaluation of long-term effects of PIT tagging. *Journal of Fish Biology*, *96*(4), 1055–1059. https://doi.org/10.1111/jfb.14292

Smith, S. G., Muir, W. D., Williams, J. G., & Skalski, J. R. (2002). Factors associated with travel time and survival of migrant yearling Chinook Salmon and steelhead in the lower Snake River. *North American Journal of Fisheries Management*, *22*, 385–405. https://doi.org/10.1577/1548-8675(2002)022<0385:FAWTTA>2.0.CO;2

Tableman, M., & Kim, J. S. (2004). *Survival analysis using S*. Chapman and Hall/CRC.

Therneau, T. M. (2015). A package for survival analysis in S (Version 2.38). https://github.com/therneau/survival

Tiffan, K. F., Perry, R. W., Connor, W. P., Mullins, F. L., Rabe, C. D., & Nelson, D. D. (2015). Survival, growth, and tag retention in age-0 Chinook Salmon implanted with 8-, 9-, and 12-mm PIT tags. *North American Journal of Fisheries Management*, *35*(4), 845–852. https://doi.org/10.1080/02755947.2015.1052163

Tiffan, K. F., Rhodes, T. N., Bickford, B. K., Lebeda, D. D., Connor, W. P., & Mullins, F. L. (2021). Performance of subyearling fall Chinook Salmon tagged with 8-, 9-, and 12-mm passive integrated transponder tags in the Snake River. *North American Journal of Fisheries Management*, *41*(1), 176–186. https://doi.org/10.1002/nafm.10541

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*(sup1), S120–S138. https://doi.org/10.1080/00063659909477239

Zabel, R. W., & Achord, S. (2004). Relating size of juveniles to survival within and among populations of Chinook Salmon. *Ecology*, *85*(3), 795–806. https://doi.org/10.1890/02-0719

Zabel, R. W., Wagner, T., Congleton, J. L., Smith, S. G., & Williams, J. G. (2005). Survival and selection of migrating salmon from capture–recapture models with individual traits. *Ecological Applications*, *15*(4), 1427–1439. https://doi.org/10.1890/04-0940

Zar, J. H. (2010). *Biostatistical analysis* (5th ed.). Prentice-Hall.

SUPPORTING INFORMATION

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