

RESEARCH ARTICLE

Estimation of Survival Probability Through Downstream Dam Passage Using Simulation Models From Experimental Data

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ABSTRACT

The migration of juvenile anadromous salmonids in the Interior Columbia River Basin requires passing various hydroelectric dams, which pose risks of injury or death. Mark-recapture studies are used to estimate direct and indirect survival of juvenile salmonids during dam passage. In these studies, data interpretation can be challenging when ideal study parameters are constrained by small sample sizes and inadequate replication as a result of unpredictable events. Even ideal field studies are complicated by fish that cannot be recaptured and whose survival is uncertain. To address cases when field trials yield imperfect or unclear data, or established methods cannot be applied, we developed novel simulation models that incorporated field trials in order to decrease variation around recapture survival estimates for a passage study through McNary Dam on the Columbia River (Washington/Oregon, USA). There were two types of models: one was a randomization model akin to bootstrapping the recapture data to decrease the coefficient of variation; the other type was a Bayesian model that simulates different scenarios to estimate release survival, by incorporating fish with unknown fates. Simulations showed the expected similarity in survival estimates and considerably reduced the variation in those estimates. The Bayesian model showed further reduction in variation around survival compared with the randomization model. It also indicated that concerns around small sample size could be conceptually mitigated by the modeling approach. The model also incorporated individuals that were not recaptured and demonstrated that the modeled worst-case scenario, where all unrecovered individuals are assumed to be dead, shows higher survival than the mean release survival from the field trials and is comparable to, but slightly lower than, the field recapture survival. All of these findings suggest that the simulation model provides an effective tool widely applicable to field studies of survival when the observed data are imperfect.

1 | Introduction

Migration of anadromous salmonids requires successful transit between natal streams and the ocean. In the Interior Columbia River Basin of northwestern North America, this migration involves several hundreds of river kilometers and requires passage through an extensive network of hydroelectric dams that present the risk of physical trauma or death

to fish as they migrate through various spillways, turbines, ladders, locks and bypass systems. Responsible operation of the dams means ensuring that passage of fish through them is as successful as possible. To demonstrate the level of success, dam passage survival studies have been undertaken for the past few decades (e.g., Mathur et al. 1996; Skalski et al. 2002; Normandeau Associates and Skalski 2006). Optimally designed survival studies must account for a range of variables,

including but not limited to variable environmental conditions, life stages of the migrating fish, or the effects of tagging on fish (e.g., Skalski et al. 2009; Elder et al. 2016). In such studies, survival is estimated via mark-recapture techniques that usually allow for the retrieval or detection of fish whether they survive or not. However, estimation of survival is particularly difficult when there is uncertainty in the fate of fish not physically recaptured, e.g., in telemetry studies when fish die but still get detected (Harnish et al. 2020). A further complication is deviation from the optimal study design caused by the logistical constraints of conducting the release-recapture trials that can result in small or imbalanced data sets. It may therefore be valuable to explore methods that enable the examination of survival rates, even when working with imperfect or limited data that do not allow for the application of established methods.

The aforementioned impediments to reliable estimates of dam passage survival can affect compliance with federal requirements in order to maintain operations when species protected by the US Endangered Species Act (ESA, National Marine Fisheries Service (2025)) are present. One example is ESA-listed anadromous spring-run Chinook salmon (*Oncorhynchus tshawytscha*), thousands of which migrate annually through Columbia River dams, both upstream and downstream. Juvenile salmonids moving downstream through dams have multiple routes available, such as juvenile bypass systems, spillways, bottom outlets, and turbines, each of which can affect dam passage survival differently (Bestgen et al. 2018; Chanson and Gonzalez 2024). ESA-listed juvenile spring-run Chinook salmon survival rates are expected to fall within specific statistical parameters. While these statistical requirements can be readily incorporated into large-scale survival studies given sufficient planning time and funding, they are more difficult to meet under study conditions constrained by limited time or resources, e.g., when responding to emergency operational changes. What is needed is a method by which information on survival can be gained from imperfect sampling data in order to be able to evaluate—at least conceptually—the impacts on fish survival under challenging conditions.

Survival studies at dams usually target estimating survival of (1) fish passing the dam in general, independent of the passage route (e.g., Skalski et al. 2010; Harnish et al. 2020), or (2) estimating or comparing survival of individuals passing the dam through specific routes such as turbines or different spillway configurations (e.g., Mathur et al. 1996; Skalski et al. 2002; Bestgen et al. 2018; Tuononen et al. 2022). Juvenile survival during downstream movement through dams in general is defined as survival occurring between the upstream face of the dam and the immediate tailrace, 1–2 km downstream of the dam (Columbia Basin Federal Caucus 2024). To estimate survival of individuals passing the dam through a specific route, a paired control release schedule is necessary to be able to identify mortality caused by dam passage. Such studies can be confounded by imbalanced pairing of control and test individuals and by the need to make inferences about individuals that could not be recaptured and therefore have an unknown fate, which may require alternative approaches or analytical techniques for evaluating survival.

Dam passage survival, particularly downstream passage, can be affected by the structural properties of the spillway

through which fish migrate (Bestgen et al. 2018; Chanson and Gonzalez 2024). If there are multiple passage routes consisting of different spillway types, then downstream survival may even vary within a single dam. Spillway smoothness and the existence of obstructions onto which water spills can greatly affect the physical force experienced by the fish (Bestgen et al. 2018). It is therefore reasonable to hypothesize that attempts to quantify survival with release-recapture studies will yield survival estimates that vary with spillway type. This further highlights the need for effective analytical tools that accurately estimate survival.

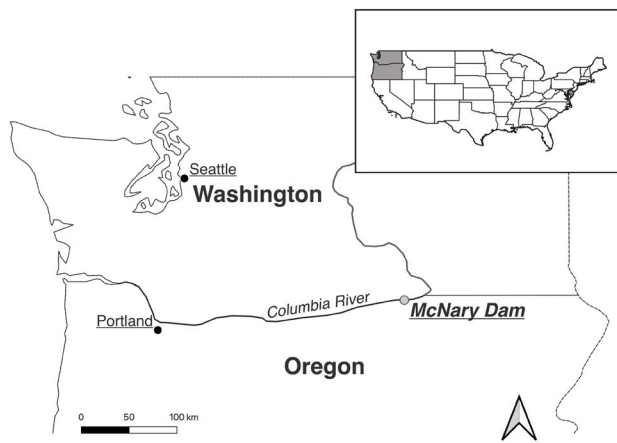
Most existing statistical survival models, e.g., the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965), the ViPRE model (Skalski et al. 2010), or the ViRDCT model (Harnish et al. 2020) seek to ensure that estimates from field data reflect true survival as accurately as possible, but the required number of fish that need to be released to reach a specific level of precision depends on the actual survival and recapture/detection rates measured in the field (Mathur et al. 1996; Skalski et al. 1998, 2016; Harnish et al. 2020). This is both time consuming and expensive (Skalski et al. 2016), and thus not always tractable. Given that survival and recapture/detection rates can vary with varying conditions, species, or life stages, predicting and releasing the required number of fish to achieve a given level of precision can be challenging, especially if study conditions cause unexpected changes to the experimental design that add uncertainty to field data.

Because field passage studies are susceptible to the aforementioned difficulties, the models mentioned above can be intractable and would benefit from (1) a way to compensate for non-ideal data in cases where experimental constraints prevent well-established methods (e.g., Mathur et al. 1996) from being applied, and (2) a novel means of using the available data in realistic simulations that can estimate survival rates with low variation around the mean. Here we develop two computer simulation models that incorporate field trials to better interpret imbalanced and variable mark-recapture data, and to provide survival estimates through a hydropower facility on the Columbia River. The models offer an opportunity to analyze survivorship data when the field trials are too variable to make inferences through typical statistical analyses. These modeling approaches are therefore applicable to other dam passage studies in the Columbia and other river systems, and to myriad other survivorship studies where observations are uncertain. These models ultimately show that the data sets can still be expected to contain sufficient information for reasonable conclusions.

2 | Materials and Methods

2.1 | Study Site—Hydropower Facility

McNary Dam is a 2.2 km long dam spanning the width of the Columbia River between Washington and Oregon at 45.935° N, 119.298° W (Figure 1). It is the 4th major dam upstream of the mouth of the Columbia River, located at river km 470. The dam operates its spillway using gate hoists and traveling cranes. The US Army Corps of Engineers commissioned this study to determine whether the use of a split-leaf spillway or a Temporary



(a)



(b)

FIGURE 1 | Location of McNary Dam in Washington, USA (a) and image of McNary Dam (b). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/ra.20117)]

Spillway Weir (TSW) was most effective in reducing fish injury during downstream passage. The study was commissioned for a very short duration due to operational restrictions that did not allow for normal spill operations. The field study compared four treatment release pipes, designed to release fish into the split-leaf spillway (slot 21) and the TSW (slot 20) at two specific elevations for each location. The dam deck is roughly 7 m from the water surface. The split-leaf treatment release pipes extended approximately 12.3 and 13.4 m down from the deck to release fish 0.5 m (split-leaf deep-depth) and 1.5 m (split-leaf mid-depth) above the top of the bottom split gate. The TSW treatment release pipes extended 8.8 m (TSW mid-depth) and 10.5 m (TSW deep-depth) from the dam deck to release fish at two levels differing by about 1.7 m near the TSW spill crest. Consequently, fish released at mid-depths likely experienced a greater vertical drop through the spillway waterfalls. Each release pipe consisted of a steel pipe fitted to a plastic flex-hose extending to a quick-connect fitting for attachment as needed to a release basin. A separate control release basin and hose system was installed off a concrete pier extending into the powerhouse tailrace.

2.2 | Study Specimens

Upper Columbia summer run Chinook salmon yearlings (not ESA-listed) were obtained from the Entiat National Fish Hatchery, Entiat, WA. The size of fish at the time of transfer was about 20 fish/lb., with an average fork length of 138 mm (± 12 mm), typical of smolts that pass downstream through the Columbia River dams. Fish were transported and handled by Hinchinbrook Inc. under Washington Fish Transport Permit #9527-02-16-24, Washington Scientific Collection Permit #24-086 and Oregon Scientific Take Permit #28049. At the dam, fish were moved into large aerated holding tanks with constant river water exchange. Fish remained in these tanks until used in field trials. After recapture, they were moved into separate monitoring tanks for 48 h before being released into the Columbia River (downstream of the dam) once the 48 h observation period was over.

2.3 | Field Passage Trials

Fish release and recapture trials were conducted during the limited period when dam operations allowed, thus occurred between 29 March 2024 and 4 April 2024. Each day's release fish were randomly selected from fish in the holding tanks and transferred to a tagging trailer located near the spillway release sites. Only healthy fish exhibiting normal behavior during the tagging process and before being released were used for the study. Fish were anesthetized using Tricaine Methanesulfate (MS-222) buffered with sodium bicarbonate. Each fish was pierced with two anchor devices that were surgically inserted through the dorsal musculature both anterior and posterior of the dorsal fin and above the trunk vertebrae. These anchor devices provided an attachment loop for balloon tags on either side of the fish and were also used to attach a uniquely encoded radio transmitter, 148–152 MHz, 30 ppm (ATS F1915) to each individual. To enable individual identification through the full chain of custody from tagging through release, recapture, and post-passage observation, each fish was also tagged with a uniquely encoded PIT tag, 9 mm 134.2 kHz FDX-B (VodaIQ HQ9), surgically implanted in the body cavity using standard protocols (Murphy and Willis 1996). Fish were tagged each day by the same personnel to reduce variability in tagging quality.

After tagging, fish were transferred in portable holding tanks for recovery (60 min) and transported to one of the release sites. Immediately prior to release, two balloon tags (Salalila et al. 2023) were attached to the fitted anchor devices on the fish after activating the inflation-inducing chemical reaction. The inflation-inducing reaction caused released fish to surface 2–5 min after the start of the reaction. Inflation timing was based on the average experimental time required from activation through release, spillway travel, and recapture. Also prior to release, PIT tags were scanned for identification and to record the release time.

Fish were released through a portable basin and flexible pipes continuously filled with pumped river water and connected

TABLE 1 | Numbers of released fish per day and release location.

Release location	No. released/Day							Release total
	3/29	3/30	3/31	4/1	4/2	4/3	4/4	
Split-leaf deep	0	0	39	82	0	0	6	127
Split-leaf mid	0	18	0	11	60	0	20	109
TSW deep	0	0	20	21	0	62 (1)	4	107 (1)
TSW mid	2	16	20	0	0	57 (1)	18	113 (1)
Control	11 (1)	0	0	7	25	0	57 (1)	100 (2)
Release total	13 (1)	34	79	121	85	119 (2)	105 (1)	556 (4)

Note: Numbers in parenthesis show individuals removed from the analysis because of tagging injuries, equipment malfunction, and one fish jumped from the holding tank (see Section 3.2).

through the appropriate release pipe for quick delivery of the fish to the correct location/elevation. Timing of fish release was coordinated closely with the recovery boats, typically with several fish released in close succession followed by a sufficient lapse in order to optimize recapture by boat personnel and reduce subsequent loss of fish downstream of the boats. Fish were released in batches of 20 individuals when possible. Smaller batches occurred when environmental or dam operation conditions changed, recapture times increased, or daylight faded before the entire batch could be released. Because recapture efficiency had the potential to vary with weather and wind, time of day, and variability in turbulence and flow conditions downstream, we occasionally released tagged test fish and test balloons in order to calibrate passage and recovery timing and expected location of surfacing. Test fish were not included in the analysis. Release locations for a given batch were alternated during the day between different treatment or control release pipes in an attempt to maximize release numbers at treatment sites and recapture success with the personnel available, while distributing effort across treatments temporally. The need to release a sufficient number of individuals at each treatment location under the above logistical constraints prevented us from including a paired control release on some release days.

Up to two boats were used to track and recapture fish downstream in the spillway tailrace. Each boat was equipped with a radio receiver (ATS R4000) and a unidirectional Yagi antenna to locate the fish after dam passage. Fish were recovered with long-handled dip nets, visually inspected for immediate injury/mortality, and transferred to an aerated live-well on the boat where they were held until the boat returned to shore. PIT tag ID and recapture time were recorded, and radio and balloon tags were removed from the fish. All recaptured fish were transferred to the onshore holding tanks within an hour after recapture for further condition and survival evaluation, then transferred into larger holding tanks for a 48-h monitoring period.

2.4 | Sample Size

The numbers of all study fish that were released each day from each location are listed in Table 1. A total of 560 fish were released and 498 subsequently recaptured between 29 March 2024

and 4 April 2024. This total does not include fish that were released for the purpose of testing and calibrating equipment and methodologies. However, it includes four individuals that were recaptured but later removed from the analysis (see Section 3.2). The total sample size and release schedule were restricted by fish and personnel availability as well as temporal constraints, dam operations, and environmental conditions. All fish alive at the time of recapture were held onsite for at least 48 h of further observation before releasing them into the Columbia River, with the study concluding on 6 April 2024.

2.5 | Data Analysis

To assess, both prior to and during the study, how much field data would be required to apply established methods, we used the approach of Mathur et al. (1996). However, the data-collection constraints described above hindered our ability to obtain the sample sizes necessary for those methods, resulting in an imperfect field data set. Namely, it lacked a consistent paired control release schedule and the sample size was too small to apply established analytical methods for survival estimates because of a high number of individuals with unknown fate (see Results). Nevertheless, we used a basic χ^2 analysis to determine whether we observed any survivorship differences among release locations (i.e., spillway types) in general. We also conducted χ^2 tests for homogeneity in the data to follow the general approach of Normandeau Associates et al. (2002) in determining whether data could be pooled between batches among release locations. Because of the small size of a number of the release batches, we expected this homogeneity to be relatively weak. However, the models that we use in the simulation study (see below) did not depend on homogeneity because they are constructed around sample draws from the entire data set. In fact, not assuming homogeneity a priori is a more conservative approach with the models because they are less likely to be influenced by days with very low or very high percent survival of a low number of released fish. These models furthermore used a consistent modeled release size of 20 individuals per batch to resolve the problem of imbalanced release batches in the field.

After confirming data homogeneity among release locations, the percentages of survival, mortality (immediate and delayed within 48 h), individuals of which only radio tags were

recovered, and fish lost to the study, were calculated for each release batch per release group, i.e., for each spillway configuration and depth independently. The final outcomes were combined for each release location and described as follows: (1) Release survival, i.e., surviving fish recovered as a proportion/percentage of the total number initially released. (2) Recapture survival, i.e., surviving fish as a percentage of the total number recovered. (3) Fish of unknown fate, i.e., those released individuals for which only a radio and/or balloon tag was recovered, and those not recovered at all and therefore lost to the study. All of these designations were important to the development of the analytical simulation models (below). We then calculated the mean and 95% confidence intervals of recapture survival, plus its coefficient of variation (CV) across all batches at each release location.

The models consisted of a simulation method that could both reduce variation around the survival estimates and predict the extent to which the fish of unknown fate change those estimates over a plausible range of simulated recapture rates. The simulation method utilized the field data with two classes of models:

2.5.1 | Randomization Model

We combined all data of the individuals of known fate into one large data set per release location with 95–102 individuals/data set and location. Individuals of known fate are those individuals that were either recaptured alive, recaptured dead, or died within 48 h after recapture. From the combined field data sets for each release location, we randomly selected 20 individuals with replacement to create 100 new data batches of 20 individuals of known fate. We then calculated the recapture survival for each batch individually and the mean recapture survival across all batches per release location, including the CV. Because these draws were from a pool that reflected the distribution of recapture survival, we expected the resultant survival percentage to match the recapture survival found in our field data. We further expected the CV of survival to be reduced relative to the field data as described by Fieberg et al. (2020). This model is labeled *ModelRandom*.

2.5.2 | Bayesian Model

We built a Bayesian model (see Griep (2025)) using *stan* in the R programming environment (Stan Development Team 2024) to create 100 simulated data batches of 20 individuals per release location. The 20 individuals per simulated data batch were drawn from a posterior Bernoulli distribution that was generated by (1) a likelihood function that describes how likely it is to encounter the proportion of fish that were recaptured alive or dead given a specific survival rate in form of a prior distribution, (2) a prior Beta distribution whose shape is defined by one survival ($\alpha = \alpha_{\text{survival}}$) and one mortality ($\beta = \alpha_{\text{mortality}}$) parameter, where their values influence the likelihood of a particular outcome (alive/dead; see below) and (3) evidence in form of collected field data per release location according to Bayes' Rule:

$$\text{posterior} = \text{likelihood} * \text{prior} / \text{evidence} \quad (1)$$

The model is implemented as described above with the following model parameters: the evidence are the combined field data sets of fish that were recaptured per release location. The prior Beta distribution belongs to a family of continuous multivariate probability distributions parameterized by two positive reals (α_{survival} , $\alpha_{\text{mortality}}$). The two α values determine the relative likelihood of each category in the prior Beta distribution. The two categories are (1) recaptured individuals that survived and (2) recaptured individuals that died. We initialized the two α values (α_{survival} , $\alpha_{\text{mortality}}$) as different encountered or expected numbers of individuals that belong to each category. If $\alpha_{\text{survival}} \gg \alpha_{\text{mortality}}$, the distribution is skewed right toward high survival, if $\alpha_{\text{mortality}} \gg \alpha_{\text{survival}}$, the distribution is skewed left toward low survival, and if $\alpha_{\text{survival}} \approx \alpha_{\text{mortality}}$, the distribution is more symmetric. In effect, the α values allowed us to use the model to predict survival probabilities if some proportion (0%–100%) of the individuals of unknown fate indeed survived (see below). We parameterized the Bayesian model (labeled *ModelBayesian*) in two approaches, one to further reduce the variance of the survival estimates relative to the field data and estimates from *ModelRandom*, and one to address varying recapture rates and individuals of unknown fate:

1. In the first approach, we created a model for comparison with *ModelRandom*, in which the α values matched the number of individuals recaptured alive and dead as observed in the field data per release group ($\alpha_{\text{survival}} = N_{\text{alive}}$, $\alpha_{\text{mortality}} = N_{\text{dead}}$). In other words, the α value for fish that survived (α_{survival}) was equal to the number of fish that were recaptured alive in each release group (combined data set). The α value for the fish that died ($\alpha_{\text{mortality}}$) was equal to the number of fish that were recaptured dead or died within 48 h after recapture at each release location. Given that the numbers of individuals that survived was significantly larger than the number of mortalities, i.e., $\alpha_{\text{survival}} \gg \alpha_{\text{mortality}}$, the prior was consequently highly skewed toward survival. These modeled data sets, as with the modeled data sets from *ModelRandom*, therefore consisted of fewer categories than the field data because they did not include individuals of unknown fate and the source data set [see “evidence” above, Equation (1)] only included data from recaptured individuals with known survival/mortality distributions. We then ran the simulations as described above and calculated the mean percentage of survival across all simulated batches, including CVs from the simulated data. We compared CVs because we expected the confidence intervals of modeled data to be very small relative to the field data. The *ModelBayesian* differs from *ModelRandom* in that *ModelRandom* consists of simple random draws from the field data set of recaptured individuals without applying Beta distributions and respective likelihood values. Given that our alpha values that define the prior were equal to the number of individuals recaptured alive or dead in the field data, we expected the resultant posterior to be very close to the observed recapture survival estimate from the field trials and the modeled recapture survival from *ModelRandom*. We used this model to demonstrate reduced variation and to test model performance by comparing mean percentages of survival and CVs between this model, the field data, and *ModelRandom*.

The implication of a reduced CV relative to *ModelRandom* and the field data is that precision has been increased.

2. The second approach tested the effects of different prior beta distributions on survival estimates by varying the values of α_{survival} . As in the previous approach, α_{survival} represented the number of individuals recaptured alive per release location. However, instead of using the values observed in the field data, the modeled number of fish that survived (α_{survival}) ranged from 50 to 150 individuals with the value of fish that died ($\alpha_{\text{mortality}}$) held constant at two different values (see below). This leads the prior distribution to be consistently skewed toward survival but with increasing value, the distribution becomes increasingly concentrated around survival, i.e., its variance decreases. For each pair of values ($\alpha_{\text{survival}}, \alpha_{\text{mortality}}$) 100 simulated data sets of 20 individuals each were created and the mean survival across all data sets per pair and release location was calculated. We used this approach to (1) better understand the effect on the modeled survival of the overall population resulting from varying the survival rates of the fish of unknown fate in the simulated data and (2) to test the effect of varying survival distributions on the *ModelBayesian* results. The limits 50 and 150 were chosen because they covered approximately the range of the number of recaptured individuals per release group in the field experiment $\pm 50\%$. The source data set (see “evidence” above, Equation (1)) still consisted of recaptured individuals with known survival/mortality distribution only, assuming that survival/mortality distributions within recapture data sets are similar to field data recapture survival rates, including individuals with unknown fate. We ran two simulations under this approach in order to evaluate the best and worst case scenarios assigned to individuals with unknown fate (see below) and compare them to recapture and release survival from the field data.

In the first set of simulations of the second approach we initialized the α values with $\alpha_{\text{survival}} = [50 \dots 150]$, shifting the prior distribution increasingly toward survival, while $\alpha_{\text{mortality}}$ was constant and equal to the number of individuals that were recaptured dead or that died within 48 h of being captured alive ($\alpha_{\text{mortality}} = N_{\text{dead}}$), taken from the field data. For each simulated data set and each integer α_{survival} value from 50 to 150, we then compared the mean release survival values from the field data at each release location. By considering the modeled mean survival and mortality at the α_{survival} value that was equal to the number of individuals that were recaptured alive at each release location in the field trials plus the number of individuals of unknown fate ($\alpha_{\text{survival}} = N_{\text{alive}} + N_{\text{unknown}}$), and the $\alpha_{\text{mortality}}$ value that was equal to the number of individuals that were recaptured but died in the field trials ($\alpha_{\text{mortality}} = N_{\text{dead}}$), we were able to model the best case mean release survival and compare it to the observed and modeled recapture and release survival. It is the best case because it assumes all individuals with unknown fate survived.

In the second set of simulations α_{survival} again ranged between 50 and 150 but $\alpha_{\text{mortality}}$ was constant at the number of individuals that died plus the number of individuals of unknown fate ($\alpha_{\text{survival}} = [50 \dots 150]$, $\alpha_{\text{mortality}} = N_{\text{dead}} + N_{\text{unknown}}$). As before, we compared the modeled mean survival rates for each α_{survival}

value to the mean recapture and release survival rates from the field data. That way, we were able to also model the worst case release survival by considering the α_{survival} value that was equal to the observed number of individuals recaptured alive at each release location ($\alpha_{\text{survival}} = N_{\text{alive}}$), and the $\alpha_{\text{mortality}}$ value that was equal to the number of fish that were recaptured dead plus the individuals of unknown fate ($\alpha_{\text{mortality}} = N_{\text{dead}} + N_{\text{unknown}}$). In other words, in this scenario, we expected all individuals with unknown fate to be dead.

We then plotted the results of both model simulations in one plot per release location to understand how different priors defined by modeled numbers of individuals that are recaptured and survive or die would affect model results. The two simulation runs with $\alpha_{\text{mortality}} = N_{\text{dead}}$ and then with $\alpha_{\text{mortality}} = N_{\text{dead}} + N_{\text{unknown}}$ gave two sets of points for each release site showing the resulting mean survival rates as a function of simulated recapture rates (i.e., the range of α_{survival} values = [50...150]). On the plots, we highlighted the value of the modeled recapture survival for which α_{survival} was equal to the number of individuals that were recaptured and survived in the field trials ($\alpha_{\text{survival}} = N_{\text{alive}}$), and $\alpha_{\text{mortality}}$ was equal to the number of fish that were recaptured but died ($\alpha_{\text{mortality}} = N_{\text{dead}}$) at that release location. This value is the same as in the first approach used to compare each location's CV with the field data and with *ModelRandom*. We next added the mean recapture survival and release survival values estimated from the field trials including 95% confidence intervals to the plots. This would show how the modeled best and worst case release survival values compare to the field recapture and release survival and their confidence intervals. The value generated by the model for $\alpha_{\text{survival}} = 50$ and all unknown individuals dying gives the lowest modeled mean survival rate, and the value generated for $\alpha_{\text{survival}} = 150$ combined with the observed number of recaptured mortalities gives the highest modeled mean survival rate.

3 | Results

3.1 | Data Homogeneity and Sample Size

Owing to the number of individuals of unknown fate, our calculated number of individuals necessary to meet all of the assumptions of previously established methods was approximately 800 individuals, which is significantly more than we were able to release given the study constraints. Additionally, because we only released 560 fish, there were several batches that fell short of the target number of 20 individuals, and 3 days during which there were no paired control and “treatment” releases (Table 1). χ^2 test results indicated homogeneity among release groups (dates) for each release location, and significant differences between each site and its respective control (Table A1), but as expected significance of the results was weak due to small sample sizes on some days.

3.2 | Field Recapture Counts

There was variability in the number of recaptured individuals among the individual trials (see Tables 2 and A2). A variable number ($N = 0 - 12$) of tags that were attached to the fish

TABLE 2 | Numbers of fish per recapture group from each release location that were (1) recaptured alive and survived through 48h observation, (2) recaptured dead or died within 48h, (3) radio/balloon tags that were recaptured without fish attached, and (4) fish completely lost to study, i.e., tags not recovered.

Release location	Fish count per recapture group				
	1	2	3	4	Total
Split-leaf deep	101	1	12	13	127
Split-leaf mid	90	5	4	10	109
TSW deep	96	2 (1)	4	5	107 (1)
TSW mid	94	5 (1)	8	6	113 (1)
Control	100	0 (2)	0	0	100 (2)
Total	481	13 (4)	28	34	556 (4)

Note: Numbers in parenthesis show individuals removed from the analysis as described in Section 3.2. Circumstances for removal were tagging injuries, equipment malfunction, and one fish jumped from the holding tank.

during release were recovered as balloon and radio tag assemblies with the fish missing. These individuals were counted as fish of unknown fate given that there was no way to distinguish between individuals that died or simply shed the tag. A majority of these occurred on the day with the highest occurrence of observed avian activity and confirmed avian predation on tagged fish (April 3rd). However, the highest number ($N = 12$) also occurred at a single release pipe at split-leaf deep-depth.

Of the 560 fish evaluated across all release groups, 17 were confirmed as dead either immediately or within 48h of recapture, one fish died after more than 48h (see Table A3). Of the 17 total recorded mortalities, three can be attributed to confirmed avian predation attempts including observed bird strikes, beak marks, and clean decapitations (split-leaf mid, TSW mid). Even though these mortalities may not directly be related to dam passage, we left them as such in the data set to ensure that we did not overestimate survival. Two were attributed to tagging injuries (TSW deep/mid), and those were removed from the analysis. One jumped from the holding tank during the night and died (control), and another one got stuck in the release pipe for several minutes due to pump equipment malfunction (control). Both of these individuals were the only mortalities recorded at the control site and were removed from the analysis. The one mortality that occurred more than 48h after recapture (TSW mid) was consequently counted as alive.

3.3 | Observed and Modeled Recapture Survival

As expected, the mean recapture survival calculated from the field data and simulated data sets, modeled with *ModelRandom* and in the first approach of *ModelBayesian* for each release group, are comparable (Table 3). The CVs of the field data are higher compared to CVs calculated from model data at all release locations except for split-leaf deep depth, where the CV of *ModelRandom* is slightly higher compared to the field data but only by 5%. The CV of the *ModelBayesian* is lower compared to the field data and *ModelRandom* at all release locations

TABLE 3 | Mean calculated (field data) and modeled (random & bayesian) recapture survival (%) and respective CVs for each release location.

Release location	Field data		Model random		Model Bayesian	
	%	CV	%	CV	%	CV
Split-leaf deep	99.2	0.020	99.0	0.022	99.0	0.007
Split-leaf mid	94.9	0.068	94.7	0.052	94.8	0.017
TSW deep	98.1	0.046	98.0	0.032	98.0	0.011
TSW mid	94.6	0.066	95.1	0.051	95.0	0.017

Note: *ModelRandom* created simulated data by randomly selecting individual fates from the combined field data sets of each release site. *ModelBayesian* sampled from posterior distribution modeled by considering the combined recapture data sets per release location and prior Beta distribution defined by $\alpha_{\text{survival}} = N_{\text{alive}}$ and $\alpha_{\text{mortality}} = N_{\text{dead}}$. For details see Section 2.5.

indicating that the Bayesian model consistently reduced variance relative to the randomization model. The CVs decreased three- to six-fold between the field data and the models, though as single values, could not be analyzed for statistically quantifiable differences. This implies that recapture survival rates calculated from simulated data are comparable to the field data rates, but with less variability and well within the standard deviation of the field data. The field data and modeled recapture survival for all models and release groups is >94.5%. The shallower release depths show slightly lower (3–5 percentage points) observed and modeled percentages of recapture survival relative to their respective deeper depth locations.

3.4 | Modeled Recapture Scenarios

The Bayesian simulation runs resulted in two sets of modeled mean survival estimates per release site: one assuming $\alpha_{\text{mortality}} = N_{\text{dead}}$ combined with $\alpha_{\text{survival}} = [50, \dots, 150]$, and a second assuming $\alpha_{\text{mortality}} = N_{\text{dead}} + N_{\text{unknown}}$ combined with the same range of α_{survival} values. These two sets of modeled estimates (Figure 2, dotted lines), define the upper and lower bounds of modeled mean survival (y-axis) for each release location (panels). These bounds correspond to two scenarios: one in which all individuals of unknown fate survived (upper dotted lines in each panel) and one in which all individuals of unknown fate died (lower dotted lines in each panel), with the expected number of individuals recaptured alive ranging from 50 to 150 (x-axis).

For each release location, we additionally plotted the estimated recapture survival from the field data ($\pm 95\%$ confidence interval), the estimated release survival from the field data ($\pm 95\%$ confidence interval), the modeled recapture survival from the previous Bayesian analysis with corresponding α values (Table 3, *ModelBayesian*), and the modeled best- and worst-case release survival values. The modeled best-case release survival assumes that the modeled number of individuals recaptured dead is equal the number of individuals recaptured dead in the field

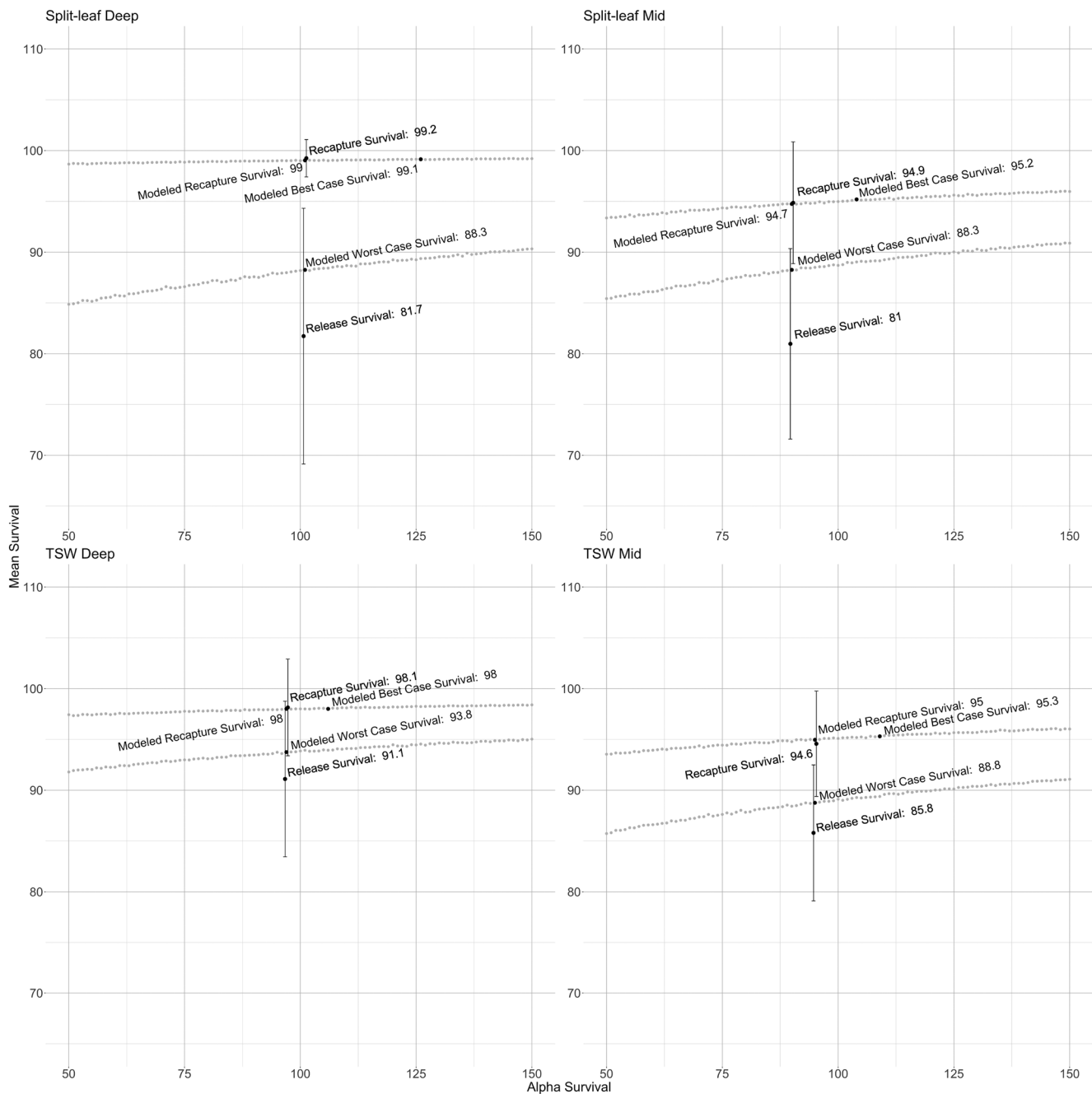


FIGURE 2 | Observed and modeled (using the Bayesian model) survival rates of released/recaptured individuals at release locations Split-leaf deep (top left) and Split-leaf mid (top right), TSW deep (bottom left), TSW mid (bottom right). The number of individuals recaptured alive was defined as a range between 50 and 150 individuals ($\alpha_{\text{survival}} = [50 \dots 150]$), while the number of recaptured mortalities equaled the number of observed mortalities per release group ($\alpha_{\text{mortality}} = N_{\text{dead}}$, upper line) or the number of mortalities plus the number of individuals with unknown fate ($\alpha_{\text{mortality}} = N_{\text{dead}} + N_{\text{unknown}}$, lower line). The black dots define the observed modeled recapture survival, the release survival estimated from the field data and modeled best/worst case survival rates, rounded to one decimal place. Observed survival rates show 95% confidence intervals while 95% credible intervals for modeled values were too small to be visualized. For details see Section 2.5.

while all individuals with unknown fate are modeled as alive ($\alpha_{\text{mortality}} = N_{\text{dead}}$, $\alpha_{\text{survival}} = N_{\text{alive}} + N_{\text{unknown}}$). In contrast, the worst-case scenario models all individuals with unknown fate as dead while only individuals recaptured alive in the field are modeled as alive ($\alpha_{\text{mortality}} = N_{\text{dead}} + N_{\text{unknown}}$, $\alpha_{\text{survival}} = N_{\text{alive}}$).

At every release location, the modeled best-case release survival occurred within the confidence interval of the recapture survival from the field data. Because the modeled recapture

survival was the same value as was generated in the previous analysis (Table 3, *ModelBayesian*), it remained close to the value of recapture survival from the field trials. The credible intervals of modeled values are not shown in the graph because they were trivially small as demonstrated by the CVs in the first analysis.

At three release sites, Split-leaf mid-depth and both TSW depths, both release survival and recapture survival confidence intervals overlapped reflecting the high variability in the field data

brought about by the sample size issues and individuals of unknown fate. The modeled worst-case release survival was greater than the release survival from the field data but within the release survival confidence interval. In one location, TSW deep, the modeled worst-case release survival was within the confidence intervals of both the recapture survival and the release survival from the field trial. At TSW deep, the modeled best-case release survival fell within the confidence interval of the measured release survival from the field data.

Modeled survival decreased as α_{survival} decreased, but the decline was relatively gradual, indicating that fewer individuals modeled as recaptured alive had only a small effect on survival estimates as long as the modeled number of individuals recaptured alive substantially exceeded the modeled number recaptured dead. In the lower-bound scenarios, however, reduced α_{survival} values had a qualitatively stronger influence on modeled survival when the modeled number of individuals recaptured dead ($\alpha_{\text{mortality}}$) was comparatively high, relative to the upper-bound scenarios. Even at very low modeled recapture levels of individuals that survived ($\alpha_{\text{survival}} = 50$), and under the assumption that all individuals of unknown fate had died, modeled mean survival remained approximately 85% or greater.

4 | Discussion

Hydroelectric dams represent substantial barriers to movement by fish upstream and downstream in major river systems. Managers must balance operational needs with evaluation of potential fishery impacts, often within narrow time constraints that preclude long-term studies conducted under optimal conditions, resulting in the collection of imperfect data. We encountered all of these limitations and others in field passage trials which, combined with the number of individuals that could not be recaptured (unknown fate), limited the use of established analytical tools and cast uncertainty onto estimates of survival. In order to improve the reliability of inferences made from the data, we appealed to models to determine whether this and other studies could yield reasonably defensible conclusions, despite underlying imperfections. We showed that, under specific assumptions and constraints, such data can be analyzed in multiple simulation models to identify trends with reduced coefficients of variation, and to better understand the data when there are individuals of unknown fate. In our case, these models indicated that, whether those individuals are assumed to be alive or dead, upper and lower bounds can be defined with low variability. The resultant survival estimate can be relatively high, and model results increased the confidence in the estimate made from the field data by reducing the variance around the estimate.

Many field studies may suffer from logistical constraints that affect sample size and data quality, and we present our modeling approach as an applicable solution. In our case, we were limited as to the number of individuals that could be released and the time period over which they could be released due to the short time frame of the study and the relatively inefficient methods available for recapture, especially with rapidly changing environmental conditions. This resulted in an imbalanced schedule of fish released through spillway mechanisms and control

pipes, thus reducing precision in our survival estimates when employing established analysis methods (Mathur et al. 1996). Although we were able to recover a relatively high number of fish that survived (high recapture survival; Table 2), we also had comparably small sample sizes and relatively high numbers of individuals with unknown fate. Thus, the detectable release survival in three of four release locations was below 90%. Although we cannot determine with certainty whether recapture survival accurately represents release survival, the sample size of approximately 100 individuals per release location contains a considerable amount of valuable information that can be further analyzed using simulations that approximately replicate the field observations. We showed through our first modeling approach that these simulations reduced variance around survival estimates.

Because the first model used random sampling from the fates of individuals recaptured in the field, we reduced the coefficient of variation associated with survival estimates generated from simulated recapture data (see Fieberg et al. 2020). The distribution of fates from individuals recaptured in the field informed the Bayesian model that made probabilistic predictions about the fates of individuals that were not recaptured. As expected, given the model structures, we were able to model recapture survival rates comparable to observed recapture survival, but with three- to six-fold lower variability (CVs in Table 3). Although we were only able to generate single values for CVs because they were derived from the mean and standard deviation of $N=100$ model simulations (and the mean and SD of all release groups in the field data), we maintain that the downward trend is likely quantitatively meaningful, given that magnitude of change.

By modeling all individuals of unknown fate as either alive or dead with the Bayesian model, we were able to simulate best-case and worst-case scenarios, which showed how the simulated number of recaptured individuals affected modeled survival estimates. Our finding that the modeled best-case survival estimate was always within the confidence interval of the observed recapture survival indicated that survival inferred from recapture data was more consistent with the modeled best-case scenario than with lower-bound survival estimates. However, this outcome may have occurred because of the nature of the field data and assumptions of the Bayesian model. In contrast, the TSW deep site showed a modeled best-case survival value within the confidence interval of the release survival value for that site. Thus, even though release survival considers individuals with unknown fate as mortality, it may sometimes include favorable survival rates (e.g., survival greater than 90%). For all sites, the modeled worst-case survival, though within the confidence interval of the observed release survival, was higher than the respective mean. Thus, the models suggest that the measured release survival may sometimes underestimate the true survival value, assuming that the field data contained the necessary information.

Although it is unsurprising that modeled recapture survival rates were comparable to the observed recapture survival because our models can only reflect the truth contained in the field data, it is reassuring that modeled means were within the confidence intervals of the field data. This both validates model results and indicates that the data simulation methods used here

are useful means of reducing variation of survival estimates and applicable to survival studies with observed recapture rates in general. This reduced variation may also allow for consideration of the differences in spillway characteristics that affect passage (Bestgen et al. 2018; Chanson and Gonzalez 2024). Because both the field data and model simulations indicated reduced survival among fish released at mid-depth spillway locations (Table 3), it is possible that survival is reduced by the physical trauma of a longer fall through the waterfall and impact on the downstream side of the dam. Reducing the variation around the survival estimates relative to the field data strengthens this inference. This would suggest that it is not necessarily the spillway type (temporary weir vs. split leaf), but the location that affects survival. Our models therefore can help provide general considerations for establishing guidelines for spillway construction and location.

More broadly, simulation models such as ours can improve precision (Fieberg et al. 2020) and parameter estimation (Cohen et al. 2001) in mark-recapture survival studies. However, modeled estimates are only as reliable as the data used to inform them, i.e., although they can increase precision they cannot improve the accuracy of the estimate, and must therefore be interpreted with caution. In our case, we were able to reduce the variance around survival estimates using the randomization model (*ModelRandom*) through straightforward bootstrapping of the recapture data. Furthermore, pooling the data across all release batches and days likely led to more conservative survival estimates, as sample size of release batches varied and some of the smaller release batches showed 100% release survival. Random draws from these smaller batches would have disproportionately increased survival estimates if analyzed separately. This approach strengthened the reliability of our recapture survival estimates, but because *ModelRandom* excluded individuals with unknown fates, it could not make any predictions about release survival. However, ignoring individuals with unknown fates can result in significantly over- or underestimating survival estimates, especially when sample size is low (Wisze et al. 2008), which would limit the broader applicability of the model.

Extending our modeling approach to develop *ModelBayesian* allowed us not only to further reduce the variance around recapture survival estimates (Table 3), but ultimately to make probabilistic assumptions about the fate of individuals that were not recaptured, as well as to evaluate various simulated numbers of recaptured individuals. Generating posterior survival distributions using a likelihood function and a prior informed by α values derived from the observed survival of recaptured individuals in the field allowed for both model validation and direct comparison with *ModelRandom*. By initially excluding individuals of unknown fate, we demonstrated that this Bayesian model produces comparable survival estimates and, in at least three of the four treatments, outperforms *ModelRandom* in terms of reducing the variance of modeled recapture survival.

Crucially, the ability of *ModelBayesian* to incorporate individuals of unknown fate allowed us to generate outcomes based on the assumption that their survival rates are comparable to those of recaptured individuals. Under this assumption, we demonstrate that even in the modeled worst-case scenario, although survival fell slightly below 90% at three of the four release locations, it is likely to be higher than the release survival observed

in the field data. This is because the second application of the Bayesian model allowed the prior distribution to be adjusted through the α values, effectively assigning survival or mortality to individuals of unknown fate and incorporating this information directly into the survival estimation process. That way, we can also show that the modeled best-case survival rates fall well within the confidence intervals of the observed recapture survival from the field trials, while the modeled worst-case release survival remains higher than the observed release survival but still within its respective confidence intervals. Thus, under the assumption that individuals with unknown fates have survival rates comparable to those recaptured, it is likely that observed release survival underestimates total survival across all release locations. Total survival is then likely closer to the observed recapture survival. Furthermore, even when α_{survival} values were reduced, specifically in terms of modeled individuals recaptured alive, survival estimates did not fall below 87%. This indicates that the limited sample size in our field study was not a strong factor leading to the observed release survival values, and that concerns about the impact of individuals with unknown fates may be somewhat allayed.

Our model was useful for addressing the limitations of small field trial data sets that did not allow for the application of established methods to estimate direct survival during dam passage. It offers a method for augmenting field data with simulations that produce survival predictions consistent with observed field patterns, while reducing variance around the estimates. In both the randomization model and the initial Bayesian approach, sampling directly from the field data or using the distribution of recapture data to inform the models enables us to improve the estimates as much as possible from the relatively small sample sizes typical of some field trials. The Bayesian simulations further provided extensions that enabled the exploration of both simulated recapture rates and fish of unknown fate. While this approach cannot replace larger, long-term studies that incorporate a wider range of time-dependent parameters, nor does it generate inference beyond what is supported by the underlying field data, it nonetheless provides a novel and powerful framework for maximizing information from small or short-term data sets. Because the model relies solely on survivorship data, it is broadly applicable to survival studies beyond dam passage contexts. In doing so, such models can reveal meaningful patterns and guide the design of more comprehensive future investigations.

5 | Conclusions

Fish survival during passage through hydroelectric dams can be difficult to estimate for many reasons. Variation in survival can arise due to the design of the dam spillway and designing field studies that can address this variation may be intractable. The two simulation models we built to address the issues of imperfect data and individuals of unknown fate in small-scale field trials of dam passage achieved two major objectives. First, both models reduced the variance around survival estimates by a factor of three to seven, with a Bayesian model showing the greatest improvement despite being based on the same data as a simple randomization model. Furthermore, the Bayesian model indicated that even under the conservative assumption that all individuals with unknown fate were recaptured dead,

the worst-case scenario still yielded higher survival estimates than the release survival observed in the field trial. Thus, modeling approaches such as these can augment sparse field data that generate only tenuous conclusions. While small data sets inherently provide limited information that should be validated with additional data in subsequent studies, these models offer a valuable approach for identifying trends and strengthening short-term results in studies constrained by time, sample size, or funding, ultimately helping to inform more detailed long-term research.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author, Stine Griep, upon reasonable request.

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Appendix A

TABLE A1 | P -values from χ^2 tests of homogeneity to compare field data release batches from the same release location but released on different dates (location vs. date), treatment release data with control release data (location vs. control), and between treatment release depths (location deep vs. location mid).

Compared groups	P
Split-leaf deep vs. date	0.43
Split-leaf mid vs. date	0.18
TSW deep vs. date	0.23
TSW mid vs. date	0.44
Split-leaf deep vs. control	0.00*
Split-leaf mid vs. control	0.00*
TSW deep vs. control	0.01*
TSW mid vs. control	0.00*
Split-leaf deep vs. Split-leaf mid	0.10
TSW deep vs. TSW mid	0.41

Note: Data that differed significantly are marked with an asterisk.

TABLE A2 | Numbers of fish per release group and date that were (1) recaptured alive and survived through 48 h observation, (2) recaptured dead or died within 48 h, (3) radio/balloon tags that were recaptured without fish attached, and (4) fish completely lost to study, i.e., tags not recovered.

Release date	Release group fish counts per condition				Release group counts total
	1	2	3	4	
Split-leaf deep					
3/31	33	0	1	5	39
4/1	62	1	11	8	82
4/4	6	0	0	0	6
Total	101	1	12	13	127
Split-leaf mid					
3/30	16	1	0	1	18
4/1	9	2	0	0	11
4/2	47	1	3	9	60
4/4	18	1	1	0	20
Total	90	5	4	10	109
TSW deep					
3/31	16	2	0	2	20
4/1	19	0	0	2	21
4/3	57	0 (1)	4	1	62 (1)
4/4	4	0	0	0	4
Total	96	2 (1)	4	5	107 (1)
TSW mid					
3/29	2	0	0	0	2
3/30	15	1	0	0	16
3/31	18	0	0	2	20
4/3	43	4 (1)	7	3	57 (1)
4/4	16	0	1	1	18
Total	94	5 (1)	8	6	113 (1)
Control					
3/29	11	0 (1)	0	0	11 (1)
4/1	7	0	0	0	7
4/2	25	0	0	0	25
4/4	57	0 (1)	0	0	57 (1)
Total	100	0 (2)	0	0	100 (2)

Note: Numbers in parenthesis show individuals removed from the analysis as described in Section 3.2. Circumstances for removal were tagging injuries, equipment malfunction, and one fish jumped from the holding tank.

TABLE A3 | Number of fish that died within each observation period (1 or 48 h) after recapture for each sampling location and respective condition prior to their demise.

Release location	Observation period (h)	Mortality count	Observed fish condition
Split-leaf deep	1	1	No external injuries
Split-leaf mid	1	1	Scale loss
Split-leaf mid	48	1	No external injuries
Split-leaf mid	48	2	Belly up
Split-leaf mid	48	1	Predation
TSW deep	1	1	Scale loss/laceration
TSW deep	48	1	Belly up
TSW deep	48	1	Tagging injury ^a
TSW mid	1	1	Predation
TSW mid	48	1	Belly up, missing/bulging eye
TSW mid	48	1	Belly up, predation
TSW mid	48	2	Belly up
TSW mid	48	1	Tagging injury ^a
TSW mid	> 48 ^b	1	Belly up
Control	48	1	Jumped from holding tank ^a
Control	48	1	Belly up, equipment malfunction ^a

Note: A majority of these conditions were observed within the first hour, even when mortality was delayed.

^aMortalities that were removed from the analysis because they could not be directly connected to dam passage.

^bThis individual was counted as “alive” because it died after more than 48 h.