NRC Research Press

ARTICLE

Wanted dead or alive: a state-space mark–recapture–recovery model incorporating multiple recovery types and state uncertainty

Nathan J. Hostetter, Beth Gardner, Allen F. Evans, Bradley M. Cramer, Quinn Payton, Ken Collis, and Daniel D. Roby

Abstract: We developed a state-space mark–recapture–recovery model that incorporates multiple recovery types and state uncertainty to estimate survival of an anadromous fish species. We apply the model to a dataset of outmigrating juvenile steelhead trout (*Oncorhynchus mykiss* (Walbaum, 1792)) tagged with passive integrated transponders, recaptured during outmigration, and recovered on bird colonies in the Columbia River basin (2008–2014). Recoveries on bird colonies are often ignored in survival studies because the river reach of mortality is often unknown, which we model as a form of state uncertainty. Median outmigration survival from release to the lower river (river kilometre 729 to 75) ranged from 0.27 to 0.35, depending on year. Recovery probabilities were frequently ≥0.20 in the first river reach following tagging, indicating that one out of five fish that died in that reach was recovered on a bird colony. Integrating dead recovery data provided increased parameter precision, estimation of where birds consumed fish, and survival estimates across larger spatial scales. More generally, these modeling approaches provide a flexible framework to integrate multiple sources of tag recovery data into mark–recapture studies.

Résumé : Nous avons mis au point un modèle d'espace d'états de marquage–recapture–récupération qui incorpore différents types de récupération et une incertitude relative à l'état pour estimer les taux de survie d'une espèce de poisson anadrome. Nous appliquons ce modèle à un ensemble de données sur des truites arc-en-ciel anadromes (*Oncorhynchus mykiss* (Walbaum, 1792)) juvéniles en dévalaison dotées de radio-étiquettes passives intégrées, recapturées durant la dévalaison, et dont les étiquettes ont été récupérées dans des colonies d'oiseaux dans le bassin du fleuve Columbia (2008–2014). Les récupérations dans des colonies d'oiseaux ne sont souvent pas incluses dans les études sur la survie parce que le tronçon de rivière dans lequel la mortalité a eu lieu est souvent inconnu, un aspect que nous modélisons sous forme d'incertitude relative à l'état. Les taux de survie médians durant la dévalaison du lieu du lâcher jusqu'au cours inférieur du fleuve (des kilomètres 729 à 75 au fil du fleuve) vont de 0,27 à 0,35 selon l'année. Les probabilités de récupération sont souvent ≥0,20 dans le premier tronçon suivant le lieu du marquage, ce qui indique qu'un poisson sur cinq morts dans ce tronçon a été récupéré dans une colonie d'oiseaux. L'intégration de données sur la récupération de poissons morts offre une précision accrue des paramètres, une estimation des lieux où les oiseaux consomment les poissons et des estimations de la survie à de plus grandes échelles spatiales. Plus généralement, ces approches de modélisation fournissent un cadre souple permettant d'intégrer différentes sources de données sur la récupération d'étiquettes dans des études de marquage–recapture. [Traduit par la Rédaction]

Introduction

Survival is one of the fundamental processes governing population dynamics (Morris and Doak 2002). Accurate and precise estimates of survival are vital for evaluating hypotheses about factors influencing population growth rates, forecasting future trajectories, and evaluating conservation and management actions (Williams et al. 2002; Morris and Doak 2002). Mark–recapture methods are widely used to estimate survival in the presence of imperfect detection and encompass some of the most popular statistical models in all of ecology (Pollock 1991; Royle and Dorazio 2008). Relatively high recapture probabilities are key for estimating parameters of interest with satisfactory precision, but the effort required to collect adequate numbers of recaptures is often a critical limitation (Williams et al. 2002).

There is a growing body of literature on the integration of mark-recapture data with auxiliary sources of data that may vary in quantity and quality (e.g., Barker 1997; Besbeas et al. 2002; Pradel 2005). One of the most widely used integrated models is the joint analysis of mark–recapture–recovery data (Burnham 1993). Here, mark–recapture studies that rely on detections of uniquely marked live individuals are combined with dead recovery data that can be provided from separate studies or information available from the public (e.g., fishing and hunting surveys, citizen science, predation studies; Burnham 1993; Barker 1997; Catchpole et al. 1998; Kendall et al. 2006). Joint analysis of mark–recapture–recovery

Received 13 June 2016. Accepted 8 September 2017.

N.J. Hostetter.* Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA.
B. Gardner. School of Environmental Sciences and Forestry, University of Washington, Seattle, WA 98195, USA.
A.F. Evans, B.M. Cramer, Q. Payton, and K. Collis. Real Time Research, Inc., 1000 SW Emkay Drive, Bend, OR 97702, USA.
D.D. Roby. U.S. Geological Survey — Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA.
Corresponding author: Nathan J. Hostetter (email: njhostet@ncsu.edu).
*Present address: U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA.

Table 1. Numbers of juvenile steelhead tagged, recaptured (live), and recovered dead on bird colonies (dead).

			McNary		John Day		Bonneville		Trawl	Estuary
Year	No. released	No. of weeks	Dead	Live	Dead[a]	Live	Dead[a]	Live	Live	Dead
2008	7 193	8	354	636	153	821	42	383	78	487
2009	7 036	8	475	661	158	428	42	428	112	431
2010	7 346	9	405	364	158	307	35	976	104	397
2011	7 687	8	354	358	142	1126	30	147	71	274
2012	6 544	7	306	392	75	543	24	337	94	180
2013	5 651	6	330	322	144	221	27	390	117	165
2014	7 611	8	117	350	288	341	40	524	136	347
Total	49 068	54	2341	3083	1118	3787	240	3185	712	2281

Note: Live and dead encounter columns are ordered by distance from the release site (see Fig. 1).
[a]Mortality location was unknown.

data can improve parameter precision, address broader hypotheses about survival, migration ecology, and the distribution of harvest, and possibly reduce sampling costs, as similar levels of precision may be achieved with smaller sample sizes (Burnham 1993; Catchpole et al. 1998; Taylor et al. 2005; Martins et al. 2011). This is especially true for studies of species that are difficult to recapture or have large numbers of recoveries (Kendall et al. 2006; Hewitt et al. 2010). Here, we combine a mark–recapture study that used fixed recapture locations with dead recovery data collected at multiple locations across a broader spatial scale to investigate survival of anadromous steelhead trout (*Oncorhynchus mykiss* (Walbaum, 1792)). The state-space mark–recapture–recovery model described herein provides a robust framework to incorporate covariates on the survival, detection, and recovery processes, estimate secondary ecological parameters of interest (e.g., multi-occasion or cumulative survival), and relax the traditional mark–recapture–recovery requirement of known mortality occasion for recovered individuals (Burnham 1993; Catchpole et al. 2001).

Declines in many salmonid populations have led to widespread protections under the United States Endangered Species Act (ESA; Good et al. 2005). In the Columbia River basin of western North America, 13 evolutionarily significant units (ESUs) of anadromous Pacific salmonids (*Oncorhynchus* spp.) are currently listed as threatened or endangered under the ESA. As part of recovery efforts, tens of thousands of juvenile salmonids from multiple ESUs are tagged annually with passive integrated transponders (PIT tags) and subsequently recaptured to estimate juvenile migration survival (Muir et al. 2001; McClure et al. 2003). These mark–recapture monitoring programs are costly and logistically challenging due to exceptionally low recapture probabilities (generally <0.20) and the consequent large sample sizes of marked smolts required to achieve adequate precision (>20 000 to >100 000 individuals tagged annually; Muir et al. 2001; McMichael et al. 2010; Skalski et al. 2012). Since 1996, independent studies have also recovered thousands of smolt PIT tags on piscivorous waterbird colonies located throughout the Columbia River basin in an effort to estimate avian predation rates (Collis et al. 2001; Ryan et al. 2003; Schreck et al. 2006; Evans et al. 2012; Hostetter et al. 2015). Recoveries of tags on bird colonies provide important information that an individual smolt died during outmigration, but the river reach where mortality occurred is often unknown (Evans et al. 2016). Uncertainty in the mortality occasion violates a basic requirement of mark–recapture–recovery methods, where the mortality occasion for all recovered individuals must be known with certainty (Burnham 1993; although see Catchpole et al. 2001). To date, published PIT tag survival studies in the Columbia River basin have ignored dead recovery data, in part due to the challenges of modeling different levels of state uncertainty in recovery data (i.e., the occasion of mortality for recovered individuals is only partially known).

We use a state-space mark–recapture–recovery model that incorporates recaptures from formal sampling occasions and recoveries that can occur at any time but may only provide partial information on where an individual died. These methods build upon delayed-recovery mark–recapture–recovery models described by Catchpole et al. (2001) and King (2012). We applied this approach to a 7-year mark–recapture–recovery study of upper Columbia River steelhead, an ESA-listed (threatened) population. Our goal was to utilize live recapture and dead recovery data to (*i*) investigate river reach and cumulative migration survival through the Columbia River hydrosystem, (*ii*) estimate survival in the unimpounded lower river (hereafter, Lower River), a poorly understood river reach that is not estimable using mark-recapture data alone, and (*iii*) examine where fish were consumed by birds, which can only be addressed by jointly analyzing live recapture and dead recovery data. We then conducted a simulation study to quantify gains in relative efficiency from integrating dead recovery data. That is, we investigated whether mark–recapture–recovery methods could use smaller sample sizes relative to mark–recapture methods, without a loss in precision of survival estimates. We describe the methods relative to the steelhead case study, but the general framework is applicable to any study interested in integrating live and dead recovery data.

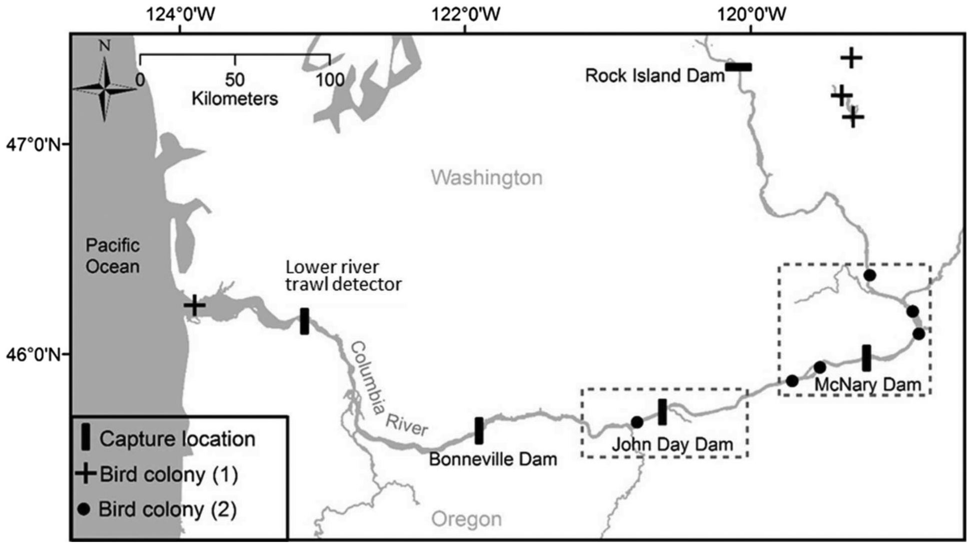
Methods

State-space models decompose an observed time-series of data into an ecological process model (e.g., survival) and observational process model (Kéry and Schaub 2012). State-space models are increasingly used to analyze complex ecological data where there is uncertainty in the observation process, including count data (Hostetler and Chandler 2015), detection nondetection data (Royle and Kéry 2007), and capture–recapture data (King 2012). Modeling mark–recapture–recovery data in a state-space framework provides several benefits, including estimation of the ecological process of interest (survival), integration of multiple sources of observation data (recaptures and recoveries), and permitting additional complexity such as covariates. Here, we describe a state-space mark–recapture–recovery model that tracks the "state" of an individual (i.e., alive or dead) through consecutive steps while accounting for imperfect detection. This individual-based model allows for covariates on survival, detection, and recovery probabilities and extends traditional mark–recapture–recovery models (Burnham 1993) to allow for uncertainty in the mortality occasion of recovered individuals. Additionally, we demonstrate how multiple secondary ecological parameters of interest and their full uncertainty are easily derived within this framework (e.g., occasion specific and cumulative survival).

Tagging, recapture, and recovery

Mark, recapture, and recovery data from more than 49 000 PIT-tagged (hereafter "tagged") juvenile upper Columbia River steelhead were collected across a 7-year study (2008–2014; Table 1). Each year, juvenile steelhead were captured and tagged at Rock Island Dam (RIS; river kilometre (rkm) 729), Columbia River, Washington, USA, across the peak smolt outmigration season, beginning in mid-April and ending in late-June (Fig. 1; see Evans

Fig. 1. Locations of capture, tagging, and release (Rock Island Dam) and downstream recapture locations for PIT-tagged upper Columbia River steelhead migrating to the Pacific Ocean. Locations of dead recoveries included (1) bird colonies where the river reach of mortality was known (+) or (2) bird colonies where recoveries indicated mortality in one of two river reaches (●; dashed boxes indicate the two river reaches where predation may have occurred). See Fig. 2 for a schematic of the estimable parameters.



et al. (2014) for detailed tagging protocols). Tagged steelhead were grouped into weekly cohorts, and only weeks when >100 individuals were tagged and released were used for analysis, resulting in 6–9 weekly cohorts per year (Table 1). Released steelhead were recaptured alive (passive detections) when passing downstream PIT-tag detection facilities at McNary Dam (MCN; rkm 470), John Day Dam (JDA; rkm 347), Bonneville Dam (BON; rkm 235), and by a net-mounted detector deployed by pair-trawlers in the lower Columbia River (Trawl, rkm 75; Fig. 1; Prentice et al. 1990; Ledgerwood et al. 2004). Most fish were not physically handled when detected at these locations, but we use the term "recapture" to denote live encounters or resightings.

Dead recovery data were collected by scanning for PIT tags on bird colonies located throughout the basin (see Evans et al. (2012) for detailed recovery protocols; Fig. 1). Tags recovered on bird colonies provided information that an individual steelhead died; however, for bird colonies located within foraging distance of recapture locations (e.g., dams), it was unknown if the individual steelhead died upstream or downstream of the recapture location (Fig. 1). Conversely, the river reach of mortality was known with certainty for recoveries on bird colonies located beyond the foraging range of the nearest recapture location (Fig. 1). Therefore, the amount of information provided by recovery data depended on the bird colony of recovery, where recoveries on some bird colonies identified the specific river reach of mortality, whereas recoveries on other colonies indicated that the individual died, but the exact river reach of mortality was unknown (Fig. 1). Tag recovery data for this study included 15 bird colonies consisting of five bird species: Caspian terns (*Hydroprogne caspia* (Pallas, 1770)), double-crested cormorants (*Phalacrocorax auritus* (Lesson, 1831)), Brandt's cormorant (*Phalacrocorax penicillatus* (Brandt, 1837)), California gulls (*Larus californicus* Lawrence, 1854), and ring-billed gulls (*Larus delawarensis* Ord, 1815). We used estimates reported by Anderson et al. (2004), Anderson et al. (2007), and Evans et al. (2016) to define foraging ranges and the selection of possible mortality reaches for recovered tags.

State-space mark–recapture–recovery model

Given the mark–recapture–recovery data available, we developed a state-space extension of the mark–recapture–recovery model that allowed for multiple recovery types with varying levels of uncertainty. A schematic of the estimable parameters is provided in Fig. 2.

Survival, recapture, and recovery data associated with individual i (i = 1, 2, …, n) were modeled through a series of Bernoulli random variables. We let z_{ik} be the state of fish i at location k (k = 1, 2, …, K; e.g., dams), where $z_{ik} = 1$ if the individual was alive and $z_{ik} = 0$ if the individual was dead. Steelhead were released in weekly cohorts w (w = 1, 2, …, W weeks) to account for possible variation in survival and detection processes throughout the outmigration season. We assumed that individual i survived from location k to k + 1 with survival probability $\phi_{w[i]k}$, conditional on individual i being alive at location k. That is

$$z_{ik+1} \sim \text{Bernoulli}(\phi_{w[i]k} z_{ik})$$

where $w[i]$ indicates the release week for individual i. This allowed steelhead survival to vary by week (w) and river reach, following similar methods used in other salmonid survival studies (Muir et al. 2001; Haeseker et al. 2012).

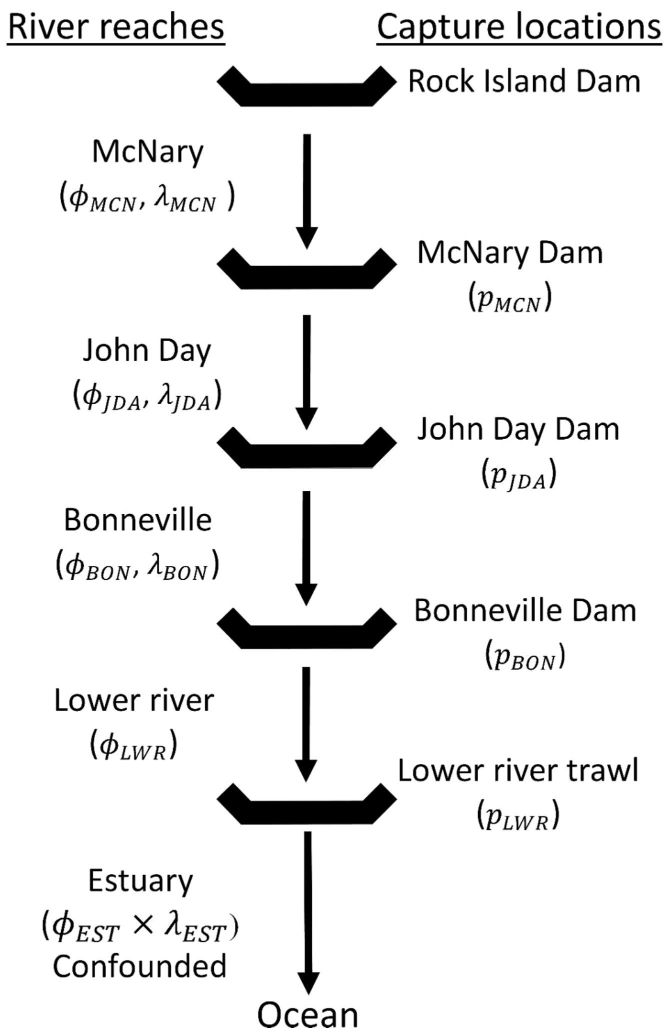
The true state process for each individual, however, is only partially observed, and downstream recaptures and recoveries are used to make inference about survival. For recaptures, we let y_{ik} be the random variable for the recapture of individual i at the kth recapture location, where $y_{ik} = 1$ if the individual was recaptured alive and $y_{ik} = 0$ otherwise. We assumed

$$y_{ik} \sim \text{Bernoulli}(p_{w[i]k} z_{ik})$$

where $p_{w[i]k}$ is the detection probability at location k for an individual released during week w, conditional on individual i being alive at location k. To reduce the number of estimated parameters and improve precision, we modeled detection probabilities on the logit scale as a realization of a random process described by a normal distribution with location-specific means μ_{p_k} and variances $\sigma^2_{p_k}$

$$\text{logit}(p_{wk}) \sim \text{Normal}(\mu_{p_k}, \sigma^2_{p_k})$$

Fig. 2. Schematic of steelhead tagged at Rock Island Dam (top) moving through a series of river reaches (left) and recapture locations (right). Individual fish are assumed to either survive and move into the next river reach (ϕ) or die. Individuals that die can be recovered on bird colonies with probability λ. Individuals alive at a recapture location are detected with probability p. Recovery probabilities in the Lower River were not included due to a lack of recovery locations in this reach (Fig. 1). Survival and recovery probabilities in the estuary are confounded. See Fig. 1 for map of study area.



Dead recoveries were integrated into the process as another Bernoulli random variable. We let x_{ik} be the random variable for the recovery of individual i in the interval $(k, k+1]$, where $x_{ik} = 1$ if the individual was recovered dead and $x_{ik} = 0$ otherwise. Because birds at some colonies forage over multiple river reaches, recoveries only provide partial information on the state process (e.g., a recovered individual died in the interval $(k, k+1]$ or $(k-1, k]$; Fig. 1). To address this, we defined the vector $m[k]$, denoting the last occasion an individual recovered in the interval $(k, k+1]$ is known to be alive. Incorporating partial knowledge of mortality occasion from dead recoveries is then achieved though restrictions on m, where the mortality occasion is known for some recoveries or may occur in one of two river reaches for other colonies. We write this recovery process as

$$x_{ik} \sim \text{Bernoulli}\left(\lambda_{w[i]k}(z_{im[k]} - z_{ik})\left(1 - \sum_{j=1}^{k-1} x_{ij}\right)\right)$$

where $\lambda_{w[i]k}$ is the probability an individual released in week w is recovered in the interval $(k, k+1]$ given they died in the interval $(m[k], k]$. The second term of the recovery formula $(z_{im[k]} - z_{ik})$ ensures that recovery probability is only nonzero in the interval of possible mortality, that is when the individual was alive at occasion $m[k]$ and is dead at occasion k. The final term, $(1 - \sum_{j=1}^{k-1} x_{ij})$, removes an individual from the study once it is recovered. For comparison, the traditional mark–recapture–recovery model assumes that the mortality occasion is known with perfect certainty and occurs in the interval of recovery (Burnham 1993). This assumption is simply a restricted version of the model presented herein, where $m \equiv (k-1)$. Similarly, the fully relaxed version of this model is presented in Catchpole et al. (2001), where $m \equiv 1$ and an individual may die during any occasion prior to recovery.

As with recapture probability, we modeled recovery probabilities as a random process on the logit scale with river reach-specific means μ_{λ_k} and variances $\sigma^2_{\lambda_k}$

$$\text{logit}(\lambda_{wk}) \sim \text{Normal}\left(\mu_{\lambda_k}, \sigma^2_{\lambda_k}\right)$$

This allowed recovery probability to vary by week (w) and river reach, but information was shared across weeks to improve precision. Although our study focuses on weekly variation in survival, recapture, and recovery probabilities, we note that survival, recapture, and recovery probabilities can also be modeled as functions of individual, temporal, or location-specific covariates using an appropriate link function (e.g., logit; see review in King (2012)).

Mark–recapture–recovery and Cormack–Jolly–Seber mark–recapture (CJS) models (Cormack 1964; Jolly 1965; Seber 1965) were fitted using a Bayesian state-space framework (King 2012). A useful aspect of Bayesian methods is the ease with which parameters of ecological and management interest can be derived as part of the Markov chain Monte Carlo (MCMC) process. The primary objective of this study was to estimate reach-specific annual survival, estimated as the proportion of individuals alive at location k that survived to $k+1$ across the entire season. Similarly, annual cumulative survival from release to downstream detection locations was simply the proportion of individuals released at Rock Island Dam that were alive at downstream recapture locations. The mean 7-year survival for each river reach was derived as the median value across all years. A principal objective of estimating river reach, cumulative, and 7-year mean survival was to evaluate hypotheses on the spatial scale of mortality factors. Under the hypothesis that large-scale, basin-wide factors are the primary drivers of survival (e.g., high flow years; Berggren and Filardo 1993), one would expect river reach survival to be above or below average across all reaches within a given year. Alternatively, a lack of correlation in river reach survival within years supports alternative hypotheses, where survival is primarily affected by local factors that may vary by river reach (e.g., dam operations or predation; Muir et al. 2001; Evans et al. 2016). The 7-year mean survival (2008–2014) is also of particular management interest as it provides a metric for mean survival since the 2008 Biological Opinion (BiOp), which linked juvenile salmonid survival to the operation of the Federal Columbia River Power System (NOAA 2008). Finally, we calculated the proportion of dead recoveries assigned to each river reach to investigate where birds likely consumed steelhead (i.e., upstream or downstream of the nearest dam) and the proportion of individuals recovered given they died in a specific river reach (r_k). All values were calculated during each MCMC iteration, providing posterior distributions for each derived parameter that were summarized as medians and 95% credible intervals.

It is important to note that recovery probabilities denote the probability that an individual was recovered given it died (Brownie et al. 1985). Recovery probabilities are not predation rates, as predation rates generally estimate the probability or rate at which individuals alive at the beginning of the interval are consumed during or after that interval. Predation rates require a different parameterization and adjustments for retrieval probabilities, reporting probabilities, and the possibility of scavenging rather than depredation (Brownie et al. 1985; Evans et al. 2012). These topics are further described in the Discussion.

Finally, following CJS model notation, we use apparent survival ϕ rather than true survival S (Cormack 1964; Jolly 1965; Seber 1965). In this study, steelhead mortality and residualizing (i.e., halting migration) are confounded. Steelhead residualization rates are low (Hausch and Melnychuk 2012), and we found no evidence of residualization across our 7-year study. Apparent and true survival are likely very similar, if not equal, but to be cautious, we denote estimates as apparent survival ϕ.

Simulation study

To illustrate anticipated gains in efficiency from incorporating dead recovery data, we conducted a simulation study using values similar to those observed in this study and other survival studies of Columbia River basin salmonids (Muir et al. 2001; McMichael et al. 2010; Hostetter et al. 2011; Appendix Table A1). We simulated and analyzed 200 datasets of 7000 individuals (the mean annual sample size in the case study). We then increased the sample sizes to 10 500 and 14 000 individuals (1.5 and 2.0 times larger, respectively) to evaluate the number of additional individuals required for mark–recapture methods to match the precision of the mark–recapture–recovery estimates based on 7000 individuals. Simulation results were summarized by comparing the mean 95% credible interval width of survival estimates. We also evaluated bias and credible interval coverage for mark–recapture–recovery and CJS methods using the analyses of 7000 individuals.

Implementation

All models were analyzed in a Bayesian framework using the software JAGS (Plummer 2003) accessed through R version 3.1.2 (R Core Team 2014), using the jagsUI package (Kellner 2015). We used independent Uniform(0, 1) priors for survival, recapture, and recovery hyperparameters and Gamma(0.1, 0.1) for the inverse variance terms. We ran three parallel MCMC simulations. Each chain contained 500 adaptation iterations, followed by 5 000 burn-in iterations, and 50 000 posterior iterations thinned by 5. Chain convergence was visually evaluated and verified using the Gelman–Rubin statistic (Gelman et al. 2013). For the simulation study, the number of posterior iterations was decreased to 35 000 to reduce runtime. We report results as posterior medians along with the 2.5 and 97.5 percentiles, which we refer to as 95% credible intervals (95% CRI). For ease of interpretation, recapture and recovery hyperparameters (μ_{p_k} and μ_{λ_k}, respectively) were back-transformed and presented as probabilities ($\bar{p}_k$ and $\bar{\lambda}_k$, respectively). R and JAGS code to run the simulation study or an example dataset are available upon request.

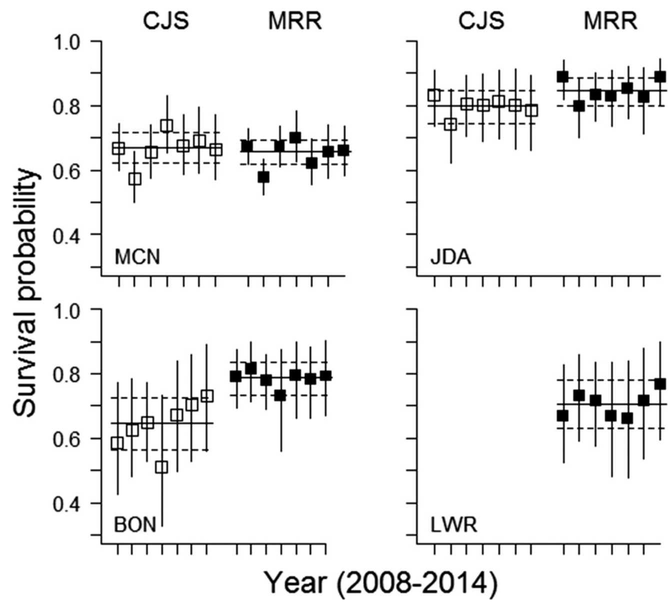
Results

Steelhead survival

A total of 49 068 juvenile steelhead were tagged and released at Rock Island Dam during 2008–2014 (Table 1). Annual sample sizes ranged from 5651 individuals (2013) to 7687 individuals (2011; Table 1). Numbers of live downstream recaptures varied by year and location but were generally <700 individuals annually recaptured at any downstream location (Table 1). Dead recoveries also varied by year and location, with the highest number of recoveries occurring in the first river reach (generally >300 recoveries per year) and in the estuary (generally >250 recoveries per year; Table 1). Numbers of dead recoveries in the estuary were 1.4–6.0 times greater than live recaptures at the Lower River trawl (Table 1).

Annual survival estimates varied by year and river reach (Fig. 3). In general, steelhead survival was lower in the McNary and Lower River reaches compared with the John Day and Bonneville reaches (Fig. 3). For instance, annual survival in the McNary reach ranged from 0.58 in 2009 (95% CRI = 0.53–0.65) to 0.69 in 2011 (95% CRI = 0.61–0.78). Comparatively, annual survival estimates in the John Day reach ranged from 0.76 in 2009 (95% CRI = 0.66–0.86) to 0.86 in 2012 (95% CRI = 0.76–0.94). Annual variation in median survival probabilities was not consistent across river reaches (Fig. 3). For example, in 2011, migration survival was above average in the McNary and John Day reaches but below average in the Bonneville and Lower River reaches (Fig. 3). Unexpectedly, CJS median survival estimates for the Bonneville reach were consistently lower than mark–recapture–recovery results (Fig. 3; see Simulation study below for possible explanation).

Fig. 3. Annual river reach survival probabilities (95% credible interval) for juvenile steelhead using mark–recapture (CJS; open square) or mark–recapture–recovery (MRR; solid square) models. Plots are separated by river reaches: Rock Island Dam to McNary Dam (MCN); McNary Dam to John Day Dam (JDA), John Day Dam to Bonneville Dam (BON), and Bonneville Dam to the Lower River trawl (LWR). Survival estimates are ordered by year from left (2008) to right (2014). Horizontal solid lines are the median survival probability across the study period (2008 – 2014; dashed lines are 95% credible intervals). CJS models cannot estimate survival in the Lower River (LWR).



Cumulative migration survival from release through the Lower River reach (Rock Island Dam to the Lower River trawl) was remarkably consistent across all 7 years, ranging from 0.27 in 2009 (95% CRI = 0.22–0.32) to 0.35 in 2014 (95% CRI = 0.27–0.43; Fig. 4). Mark–recapture–recovery methods improved precision of cumulative survival estimates, and in some cases, credible intervals were half the width of those based on mark–recapture methods (Fig. 4).

Recapture probabilities were <0.20 for 26 of the 28 annual site-specific estimates (Appendix Table B1). Recapture probabilities at the Lower River trawl were ≤0.07 in all years (Appendix Table B1). Median recovery probabilities for individuals that died in the McNary reach ranged from 0.14 in 2014 to 0.22 in 2013 (Appendix Table B1). Median recovery probabilities for individuals that died in the John Day reach ranged from 0.05 in 2012 to 0.12 in 2014, whereas recovery probabilities for individuals that died in the Bonneville river reach were all ≤0.03 (Appendix Table B1). Steelhead tags recovered on waterbird nesting colonies near McNary Dam were primarily consumed upstream of McNary Dam (Fig. 5). Recoveries on waterbird colonies located near John Day Dam were

Fig. 4. Cumulative migration survival probabilities (95% credible interval) for juvenile steelhead using mark–recapture (CJS; open square) or mark–recapture–recovery (solid square) models. Cumulative survival estimates are from release at Rock Island Dam to McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and the Lower River trawl (LWR). CJS models cannot estimate survival to the Lower River trawl.

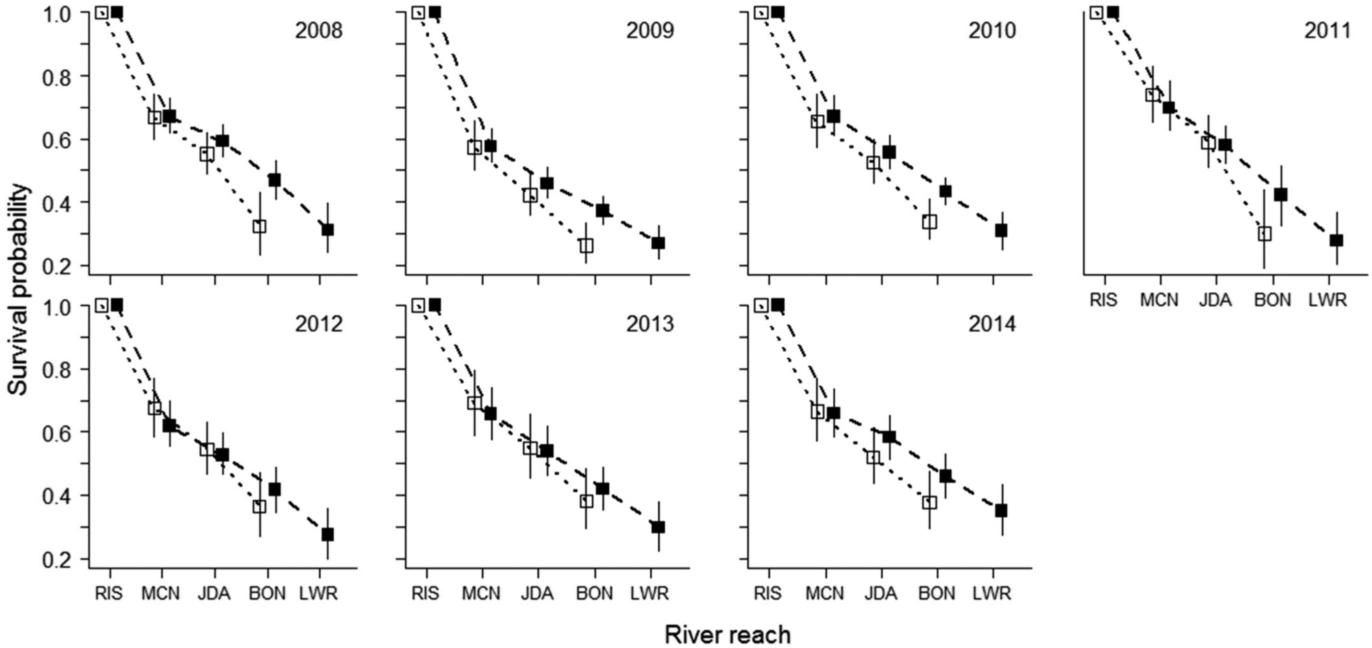
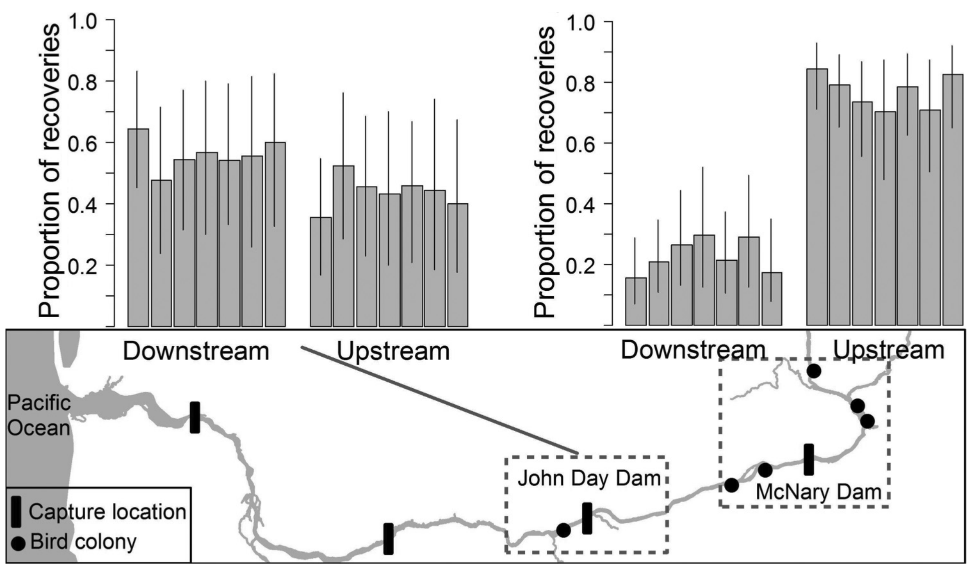


Fig. 5. Estimated proportion of recovered smolt PIT tags that were consumed by birds in the river reach upstream or downstream of the nearest recapture location (median and 95% credible interval). Dashed boxes denote the possible river reaches of mortality for each bird colony. Annual proportions are ordered from left (2008) to right (2014).



consumed both upstream and downstream of John Day Dam (Fig. 5).

Simulation study

Integrating dead recoveries reduced bias, increased precision, and improved credible interval coverage for survival estimates relative to mark–recapture methods alone (Table 2; Fig. 6). Mark–recapture–recovery methods greatly improved efficiency, requiring only half the release sample size to achieve similar precision as mark–recapture methods (Fig. 6). Mark–recapture credible intervals remained much larger in the third river reach below the release site, even after doubling the sample size (7 000 vs. 14 000 individuals; Fig. 6).

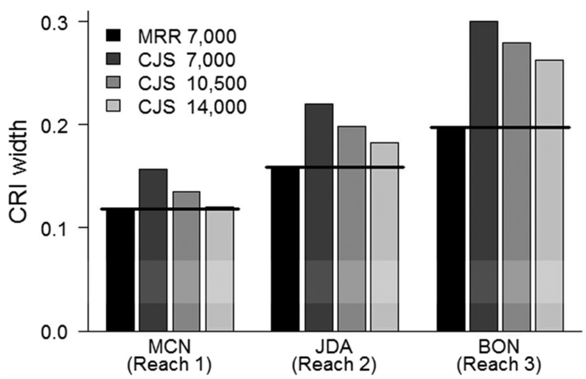
Mark–recapture survival estimates were negatively biased in the second and third river reaches (−0.06 and −0.13, respectively; Table 2). Integrating dead recovery data reduced bias in these same parameters (−0.02 and −0.04, respectively) and resulted in nominal credible interval coverage (Table 2). Recapture and recovery parameters were generally unbiased and generally achieved nominal credible interval coverage (Appendix Table A1). Biased and imprecise survival estimates likely resulted from low recapture probabilities (0.05–0.15) in conjunction with the single-release field methods where all individuals were released at a single upstream location (Appendix Tables A1 and B1; see Discussion).

Table 2. Median, bias, and credible interval coverage for estimating survival (ϕ) in the simulation study of 200 datasets with 7000 individuals.

		CJS			MRR		
Parameter	True value	Median	Bias	Coverage	Median	Bias	Coverage
ϕ_1	0.65	0.69	0.04	0.90	0.68	0.03	0.92
ϕ_2	0.80	0.74	−0.06	0.91	0.78	−0.02	0.97
ϕ_3	0.80	0.67	−0.13	0.76	0.76	−0.04	0.96
ϕ_4	0.70	—	—	—	0.66	−0.04	0.98

Note: Simulations used data generating values (True value) similar to those observed in the case study. Data were modeled using mark–recapture (CJS) or mark–recapture–recovery (MRR) models. Survival in the last occasion cannot be estimated in the CJS model.

Fig. 6. Precision (smaller is better) of mark–recapture (CJS) and mark–recapture–recovery (MRR) survival estimates as measured by mean 95% credible interval width (CRI width) across 200 simulated datasets of varying sample sizes. MRR simulations only included 7 000 individuals, whereas CJS simulations included analysis of datasets with 7 000, 10 500, or 14 000 individuals. Horizontal bars denote the mean MRR credible interval width. Survival reaches represent: Rock Island Dam to McNary Dam (MCN, Reach 1); McNary Dam to John Day Dam (JDA, Reach 2), John Day Dam to Bonneville Dam (BON, Reach 3).



Discussion

We provide a general framework for a state-space mark–recapture–recovery model to estimate survival. These methods increase the flexibility of mark–recapture–recovery models, where mortality is not restricted to the recovery occasion, state uncertainty can vary by the type of dead recovery, and mortality can be constrained to specific intervals depending on the information available from recoveries. Additionally, survival, recapture, and recovery equations are unique to each individual, allowing for individual-based models where survival, recapture, and (or) recovery probabilities can be a function of individual-level covariates or random individual-level heterogeneity. Similar to other integrated modeling approaches, we found that combining mark–recapture–recovery data not only generated more robust, accurate, and precise parameter estimates (Burnham 1993), but also estimated ecological processes that are not identifiable using independent approaches (King et al. 2009; Schaub and Abadi 2010).

The results of our simulation study showed that gains in accuracy and precision from integrating dead recovery data were not trivial when compared with standard mark–recapture methods. The integrated mark–recapture–recovery model achieved similar or improved levels of precision with only half the sample size of mark–recapture methods. Mark–recapture studies require relatively high recapture probabilities, which is often a limiting constraint in the application of these methods (Burnham et al. 1987; Hewitt et al. 2010). Common guidelines suggest encounter probabilities ≥0.20 for reliable survival estimates without unreasonable sample sizes (Hewitt et al. 2010). If increasing recapture probabilities is not possible, integrating multiple data sources can provide vital information to increase total encounter rates, increase precision of survival estimates, and possibly, reduce sample size requirements (Burnham 1993; Kendall et al. 2006; Schaub et al. 2007). The choice of data collection methods (e.g., single vs. multiple sources) is often a balance of benefits and costs. For a practitioner most interested in improving precision, we suggest considering integrated models as one of those options.

Simulation study results also supported survival differences observed in the case study, where mark–recapture survival estimates were sometimes lower than mark–recapture–recovery estimates in certain river reaches. Biased mark–recapture survival estimates are an unexpected result and likely the consequence of low PIT-tag recapture probabilities (often ≤0.15 at dams and ≤0.07 in the lower river). Single-release field methods (i.e., all individuals released at the most upstream dam) and site-specific survival and detection probabilities further exacerbate the challenge of low recaptures probabilities, as no new individuals are added to improve estimation of downstream parameters. In a separate salmonid acoustic tag study, McMichael et al. (2010) also reported lower survival probabilities (<0.60) from PIT-tag mark–recapture data compared with acoustic-tag data (>0.80) in this same river reach. Although our study integrated dead recovery data to overcome the challenge of low recapture probabilities, McMichael et al. (2010) used an alternative tag type (acoustic tags) to increase recapture probability and noticeably improve the precision of survival estimates. Together, these results support the possibility of biased CJS survival estimates under the conditions observed in this study, while also providing multiple lines of evidence that increasing encounter probabilities (e.g., integrating dead recoveries, our study; using alternative tags types, McMichael et al. 2010; or improved recapture methods, Hewitt et al. 2010) improves the reliability of mark–recapture survival estimates.

We present some of the first salmonid survival estimates for the lower Columbia River that use solely PIT-tag data. For decades, salmonid survival in the lower Columbia River was unknown due to a lack of PIT-tag recapture locations in the estuary (Muir et al. 2001; Welch et al. 2008; Clemens et al. 2009). Dead recoveries after the terminal recapture location (Lower River trawl), however, allow estimation of survival in the Lower River (Burnham 1993). Comparisons of our results with radio- and acoustic-tag studies suggest that steelhead smolt survival in the Lower River may be lower than other mid-Columbia river reaches, include large interannual variation, and is possibly lower than earlier migrating Chinook salmon (*O. tshawytscha*) smolts (Clemens et al. 2009; McMichael et al. 2010; this study). Steelhead survival estimates in our study (based on PIT tags) and studies based on radio and acoustic tags (Clemens et al. 2009) were often similar, with Lower River steelhead survival generally 0.70–0.85 (for run-of-the-river fish) across most years. PIT-tag survival estimates in the Lower River, however, should be considered with caution due to low recapture probabilities at the Lower River trawl and the relatively small number of steelhead that survived to the Lower River. Comparisons across radio-, acoustic-, and PIT-tag studies are also challenging because studies were conducted in different years, during different periods of the migration season, using different release and recapture locations, and using different tag types (radio, acoustic, or PIT tags; Schreck et al. 2006; Clemens et al. 2009; McMichael et al. 2010). Further investigation of the factors influencing Lower River survival will be a productive area of future research, especially given the extremely rich source of multiyear, multispecies data from thousands of PIT-tagged individuals (e.g., live recapture and dead recovery data collected annually since 1996; Collis et al. 2001).

Dead recovery data are available in many studies across a wide array of taxa (e.g., Barker 1997; Catchpole et al. 2001; Taylor et al. 2005; Kendall et al. 2006; Martins et al. 2011). Dead recovery data may arise from multiple sources, including angler and hunter surveys, designed protocols, opportunistic recoveries, and predation studies. Recoveries of fish tags on piscivorous waterbird colonies are an increasingly, and surprisingly, rich source of information with examples across multiple tag types, fish species, and predator species (e.g., Scoppettone et al. 2006; Evans et al. 2011; Frechette et al. 2012; Osterback et al. 2013). It is important to note, however, that the recovery probabilities in our paper are not predation rates. First, recovery probability is the probability of recovery given an individual died, whereas predation rates often consider the total available population at risk of predation. Second, recoveries may include scavenging of dead fish and are not adjusted for tag deposition rates (i.e., probability a consumed tag will be deposited on the bird colony; Osterback et al. 2013; Hostetter et al. 2015). Adjusting tag recoveries on bird colonies for tag deposition probabilities is comparable with "reporting rate" adjustments in fisheries and wildlife studies (Pollock et al. 1991). State-space models use three equations to separate survival, recapture, and recovery processes. It therefore seems possible to directly integrate reporting rates into the recovery probability equation as additional data or informative priors. Integrating tag reporting, tag deposition, or even fishing effort will be valuable extensions of this state-space mark–recapture–recovery model and allow investigation of hypotheses on total harvest, exploitation rates, or cause-specific mortality (Schaub and Pradel 2004).

As one reviewer noted, mark–recapture–recovery data may also be fit using a multistate or multi-event model (Lebreton et al. 1999; Pradel 2005). In a multi-event model, individuals transition between different states (e.g., alive, newly dead, dead; Lebreton et al. 1999), while accounting for imperfect detection and uncertainty in state assignment (Pradel 2005). In our study, colony-specific recoveries may be treated as events (e.g., recovered on colony A) that provide partial information on the state process (e.g., alive or dead in a specific river reach). Although not investigated as part of this study, multi-event models may provide a similarly flexible approach to model mark–recapture–recovery data.

In-river, estuarine, and early-ocean migration are critical life stages with particularly profound effects on salmonid population growth rates (Kareiva et al. 2000). In our study, cumulative steelhead survival from release to the Lower River (654 rkm) was remarkably similar across years, with median estimates ranging from 0.27 to 0.34, depending on the year. Outmigration survival estimates were also comparable with those of Snake River steelhead and Snake River yearling Chinook salmon, which migrate similar distances of approximately 460–687 rkm from Lower Granite Dam to Bonneville Dam and the Columbia River estuary (Welch et al. 2008; McMichael et al. 2010). Steelhead outmigration survival estimates (0.27–0.34), however, are noticeably higher than adult return rates (1%–3%; Evans et al. 2014), indicating substantial mortality after freshwater migration. Additionally, in the first three years of our study, juvenile outmigration survival did not account for differences in upper Columbia River steelhead adult return rates. Adult return rates for individuals released in 2008 were two to three times higher compared with releases in 2009 and 2010 (3% vs. ~1%, respectively; Evans et al. 2014), whereas juvenile outmigration survival was relatively constant across these same years.

We expected river-reach specific survival to be similarly above or below the multiyear mean within a given year (e.g., higher flows may result in collectively "good" survival years in all reaches). In our study, however, above average survival in one river reach often coincided with below average survival in other river reaches within the same year. Disentangling the relative importance of large-scale and local mortality factors is difficult and requires long-term datasets across large spatial scales. Large-scale environmental variables (e.g., river flow) obviously affect juvenile and juvenile-to-adult survival in anadromous salmonids (Petrosky and Schaller 2010; Haeseker et al. 2012); however, mortality factors at local levels (e.g., dam operations, predation) should also be considered when evaluating variation in juvenile outmigration survival.

The benefits of integrating dead recovery data in a 7-year study of upper Columbia River steelhead included improved precision of survival estimates, estimation of survival across larger spatial scales, information on where fish were consumed by birds, and, based on our simulation study, achieved equal levels of precision with only half the sample size of mark–recapture methods. State-space mark–recapture frameworks offer numerous possibilities for future developments (King 2012). For instance, additional information can be incorporated to discriminate between mortality sources, investigate assumptions about how various parameters may vary with time, age, or other covariates and can be incorporated into more extensive integrated population models to estimate multiple demographic parameters and track population dynamics (King 2012; Schaub and Abadi 2010).

Acknowledgements

We thank J. Adkins, T. Lawes, P. Loschl, J. Tennyson, and numerous technicians for their help with fieldwork and logistics. We thank M. Cove, K. Pollock, T.S. Sillett, T. Simons, and D. Hewitt for comments on earlier drafts. Fish tagged at Rock Island Dam were part of a project previously funded by Grant County Public Utility District (GPUD) No. 2, with additional support from the U.S. Army Corps of Engineers (USACE) Walla Walla District, Bonneville Power Administration (BPA), the USACE Portland District, and the Bureau of Reclamation. We especially thank C. Dotson (GPUD), D. Trachtenbarg (USACE), S. Dunmire (USACE), P. Schmidt (USACE), J. Skidmore (BPA), and D. Roberts (BPA). We also thank the Chelan County Public Utility District, particularly S. Hemstrom, B. Keesee, and L. Keller, for providing access to Rock Island Dam. We thank the Pacific States Marine Fisheries Commission for providing and maintaining a publically accessible repository of PIT tag release, recapture, and recovery data. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. All handling of live fish as part of this study followed protocols approved by the Institutional Animal Care and Use Committee at Oregon State University.

References

Anderson, C.D., Roby, D.D., and Collis, K. 2004. Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. Can. J. Zool. **82**(4): 541–554. doi:10.1139/z04-019.

Anderson, S.K., Roby, D.D., Lyons, D.E., and Collis, K. 2007. Relationship of Caspian tern foraging ecology to nesting success in the Columbia River estuary, Oregon, USA. Estuar. Coastal Shelf Sci. **73**(3–4): 447–456. doi:10.1016/j.ecss.2007.02.006.

Barker, R.J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics, **53**(2): 666–677. doi:10.2307/2533966.

Berggren, T.J., and Filardo, M.J. 1993. An analysis of variables influencing the migration of juvenile Salmonids in the Columbia River basin. N. Am. J. Fish. Manage. **13**(1): 48–63. doi:10.1577/1548-8675(1993)013<0048:AAOVIT>2.3.CO;2.

Besbeas, P., Freeman, S.N., Morgan, B.J.T., and Catchpole, E.A. 2002. Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics, **58**(3): 540–547. doi:10.1111/j.0006-341X.2002.00540.x. PMID:12229988.

Brownie, C., Anderson, D.R., Burnham, K.P., and Robson, D.S. 1985. Statistical inference from band recovery data: a handbook. 2nd ed. Fish and Wildlife Service, U.S. Department of the Interior.

Burnham, K. 1993. A theory for combined analysis of ring recovery and recapture data. *In* Marked individuals in the study of bird populations. *Edited by* J. Lebreton and P. North. Birkhauser Verlag. pp. 199–213.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., and Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5, Bethesda, Md.

Catchpole, E.A., Freeman, S.N., Morgan, B.J.T., and Harris, M.P. 1998. Integrated recovery/recapture data analysis. Biometrics, **54**(1): 33–46. doi:10.2307/2533993.

Catchpole, E.A., Freeman, S.N., Morgan, B.J.T., and Nash, W.J. 2001. Abalone I: Analyzing mark-recapture-recovery data incorporating growth and delayed recovery. Biometrics, **57**(2): 469–477. doi:10.1111/j.0006-341X.2001.00469.x. PMID:11414571.

Clemens, B.J., Clements, S.P., Karnowski, M.D., Jepsen, D.B., Gitelman, A.I., and Schreck, C.B. 2009. Effects of transportation and other factors on survival estimates of juvenile salmonids in the unimpounded lower Columbia River. Trans. Am. Fish. Soc. **138**(1): 169–188. doi:10.1577/T07-090.1.

Collis, K., Roby, D.D., Craig, D.P., Ryan, B.A., and Ledgerwood, R.D. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River Estuary: vulnerability of different salmonid species, stocks, and rearing types. Trans. Am. Fish. Soc. **130**(3): 385–396. doi:10.1577/1548-8659(2001)130<0385:CWPOJS>2.0.CO;2.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika, **51**(3–4): 429–438.

Evans, A.F., Roby, D.D., Collis, K., Cramer, B.M., Sheggeby, J.A., Adrean, L.J., Battaglia, D.S., and Lyons, D.E. 2011. Recovery of coded wire tags at a Caspian tern colony in San Francisco Bay: a technique to evaluate impacts of avian predation on juvenile salmonids. N. Am. J. Fish. Manage. **31**(1): 79–87. doi:10.1080/02755947.2011.562429.

Evans, A.F., Hostetter, N.J., Roby, D.D., Collis, K., Lyons, D.E., Sandford, B.P., Ledgerwood, R.D., and Sebring, S. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Trans. Am. Fish. Soc. **141**(4): 975–989. doi:10.1080/00028487.2012.676809.

Evans, A.F., Hostetter, N.J., Collis, K., Roby, D.D., and Loge, F.J. 2014. Relationship between juvenile fish condition and survival to adulthood in steelhead. Trans. Am. Fish. Soc. **143**(4): 899–909.

Evans, A.F., Payton, Q., Turecek, A., Cramer, B., Collis, K., Roby, D.D., Loschl, P.J., Sullivan, L., Skalski, J., Weiland, M., and Dotson, C. 2016. Avian predation on juvenile salmonids: spatial and temporal analysis based on acoustic and passive integrated transponder tags. Trans. Am. Fish. Soc. **145**(4): 860–877. doi:10.1080/00028487.2016.1150881.

Frechette, D., Osterback, A.-M.K., Hayes, S.A., Bond, M.H., Moore, J.W., Shaffer, S.A., and Harvey, J.T. 2012. Assessing avian predation on juvenile salmonids using passive integrated transponder tag recoveries and mark–recapture methods. N. Am. J. Fish. Manage. **32**(6): 1237–1250. doi:10.1080/02755947.2012.728171.

Gelman, A., Calin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. 2013. Bayesian data analysis. 3rd ed. Chapman and Hall/CRC, Boca Raton, Fla.

Good, T.P., Waples, R.S., and Adams, P. (*Editors*). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66.

Haeseker, S.L., McCann, J.A., Tuomikoski, J., and Chockley, B. 2012. Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River spring–summer Chinook salmon and steelhead. Trans. Am. Fish. Soc. **141**(1): 121–138. doi:10.1080/00028487.2011.652009.

Hausch, S.J., and Melnychuk, M.C. 2012. Residualization of hatchery steelhead: a meta-analysis of hatchery practices. N. Am. J. Fish. Manage. **32**(5): 905–921. doi:10.1080/02755947.2012.711269.

Hewitt, D.A., Janney, E.C., Hayes, B.S., and Shively, R.S. 2010. Improving inferences from fisheries capture-recapture studies through remote detection of PIT tags. Fisheries, **35**(5): 217–231. doi:10.1577/1548-8446-35.5.217.

Hostetler, J.A., and Chandler, R.B. 2015. Improved state-space models for inference about spatial and temporal variation in abundance from count data. Ecology, **96**(6): 1713–1723. doi:10.1890/14-1487.1.

Hostetter, N.J., Evans, A.F., Roby, D.D., Collis, K., Hawbecker, M., Sandford, B.P., Thompson, D.E., and Loge, F.J. 2011. Relationship of external fish condition to pathogen prevalence and out-migration survival in juvenile steelhead. Trans. Am. Fish. Soc. **140**(5): 1158–1171. doi:10.1080/00028487.2011.613303.

Hostetter, N.J., Evans, A.F., Cramer, B.M., Collis, K., Lyons, D.E., and Roby, D.D. 2015. Quantifying avian predation on fish populations: integrating predator-specific deposition probabilities in tag recovery studies. Trans. Am. Fish. Soc. **144**(2): 410–422. doi:10.1080/00028487.2014.988882.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika, **52(1**/2): 225–247. doi:10.2307/2333826. PMID:14341276.

Kareiva, P., Marvier, M., and McClure, M. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. Science, **290**(5493): 977–979. doi:10.1126/science.290.5493.977. PMID:11062128.

Kellner, K. 2015. jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version 1.

Kendall, W.L., Conn, P.B., and Hines, J.E. 2006. Combining multistate capture-recapture data with tag recoveries to estimate demographic parameters. Ecology, **87**(1): 169–177. doi:10.1890/05-0637. PMID:16634308.

Kéry, M., and Schaub, M. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

King, R. 2012. A review of Bayesian state-space modelling of capture–recapture–recovery data. Interface Focus, **2**(2): 190–204. doi:10.1098/rsfs.2011.0078. PMID:23565333.

King, R., Morgan, B.J.T., Gimenez, O., and Brooks, S.P. 2009. Bayesian analysis for population ecology. 1st ed. Chapman and Hall/CRC, Boca Raton, Fla.

Lebreton, J.-D., Almeras, T., and Pradel, R. 1999. Competing events, mixtures of information and multistratum recapture models. Bird Study, **46**: S39–S46. doi:10.1080/00063659909477230.

Ledgerwood, R.D., Ryan, B.A., Dawley, E.M., Nunnallee, E.P., and Ferguson, J.W. 2004. A surface trawl to detect migrating juvenile salmonids tagged with passive integrated transponder tags. N. Am. J. Fish. Manage. **24**(2): 440–451. doi:10.1577/M0-071.1.

Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., Lapointe, M.F., English, K.K., and Farrell, A.P. 2011. Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). Global Change Biol. **17**(1): 99–114. doi:10.1111/j.1365-2486.2010.02241.x.

McClure, M.M., Holmes, E.E., Sanderson, B.L., and Jordan, C.E. 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. Ecol. Appl. **13**(4): 964–989. doi:10.1890/1051-0761(2003)13[964:ALMSAA]2.0.CO;2.

McMichael, G.A., Eppard, M.B., Carlson, T.J., Carter, J.A., Ebberts, B.D., Brown, R.S., Weiland, M.A., Ploskey, G.R., Harnish, R.A., and Deng, Z.D. 2010. The juvenile salmon acoustic telemetry system: a new tool. Fisheries, **35**(1): 9–22. doi:10.1577/1548-8446-35.1.9.

Morris, W.F., and Doak, D.F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. 1st ed. Sinauer Associates, Sunderland, Mass.

Muir, W.D., Smith, S.G., Williams, J.G., Hockersmith, E.E., and Skalski, J.R. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the Lower Snake and Lower Columbia rivers, 1993-1998. N. Am. J. Fish. Manage. **21**(2): 269–282. doi:10.1577/1548-8675(2001)021<0269:SEFMYC>2.0.CO;2.

National Oceanic and Atmospheric Administration (NOAA). 2008. Biological opinion, Endangered Species Act section 7(a)(2) consultation: consultation on remand for operation of the federal Columbia River power system, 11 Bureau of Reclamation projects in the Columbia basin and ESA section 10(a)(1)(A) permit for juvenile fish transportation program. NOAA National Marine Fisheries Service. Available from www.salmonrecovery.gov/Files/BiologicalOpinions/2008/2008%20BiOp.pdf.

Osterback, A.-M.K., Frechette, D.M., Shelton, A.O., Hayes, S.A., Bond, M.H., Shaffer, S.A., and Moore, J.W. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere, **4**(9): art116. doi:10.1890/ES13-00100.1.

Petrosky, C.E., and Schaller, H.A. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. Ecol. Freshw. Fish, **19**(4): 520–536. doi:10.1111/j.1600-0633.2010.00425.x.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *In* Proceedings of the 3rd International Workshop on Distributed Statistical Computing, 20–22 March, Vienna, Austria. *Edited by* K. Hornik, F. Leisch, and A. Zeileis.

Pollock, K.H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. J. Am. Statist. Assoc. **86**(413): 225–238. doi:10.2307/2289733.

Pollock, K.H., Hoenig, J.M., and Jones, C.M. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. *In* Creel and angler surveys in fisheries management. Vol. 12. American Fisheries Society Symposium, Bethesda, Md. pp. 423–434.

Pradel, R. 2005. Multievent: an extension of multistate capture–recapture models to uncertain states. Biometrics, **61**(2): 442–447. doi:10.1111/j.1541-0420.2005.00318.x. PMID:16011690.

Prentice, E.F., Flagg, T.A., McCutcheon, C.S., and Brastow, D.F. 1990. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Am. Fish. Soc. Symp. **7**: 323–334.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J.A., and Dorazio, R.M. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press.

Royle, J.A., and Kéry, M. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology, **88**(7): 1813–1823. doi:10.1890/06-0669.1. PMID:17645027.

Ryan, B.A., Smith, S.G., Butzerin, J.M., and Ferguson, J.W. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River Estuary, 1998–2000. Trans. Am. Fish. Soc. **132**: 275–288. doi:10.1577/1548-8659(2003)132<0275:RVTAPO>2.0.CO;2.

Schaub, M., and Abadi, F. 2010. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. **152**(1): 227–237. doi:10.1007/s10336-010-0632-7.

Schaub, M., and Pradel, R. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. Ecology, **85**(4): 930–938. doi:10.1890/03-0012.

Schaub, M., Gimenez, O., Sierro, A., and Arlettaz, R. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. Conserv. Biol. **21**(4): 945–955. doi:10.1111/j.1523-1739.2007.00743.x. PMID:17650245.

Schreck, C.B., Stahl, T.P., Davis, L.E., Roby, D.D., and Clemens, B.J. 2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and estuary, 1992-1998: evidence for delayed mortality? Trans. Am. Fish. Soc. **135**(2): 457–475. doi:10.1577/T05-184.1.

Scoppettone, G., Rissler, P., Withers, D., and Fabes, M. 2006. Fish tag recovery from the American white pelican nesting colony on Anaho Island, Pyramid Lake, Nevada. Great Basin Birds, **8**: 6–10. doi:10.3133/ofr20151242.

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika, **52**(1–2): 249–259. doi:10.1093/biomet/52.1-2.249. PMID:14341277.

Skalski, J.R., Steig, T.W., and Hemstrom, S.L. 2012. Assessing compliance with fish survival standards: a case study at Rock Island Dam, Washington. Environ. Sci. Pol. **18**: 45–51. doi:10.1016/j.envsci.2012.01.001.

Taylor, M.K., Laake, J., McLoughlin, P.D., Born, E.W., Cluff, H.D., Ferguson, S.H., Rosing-Asvid, A., Schweinsburg, R., and Messier, F. 2005. Demography and viability of a hunted population of polar bears. Arctic, **58**(2): 203–214.

Welch, D.W., Rechisky, E.L., Melnychuk, M.C., Porter, A.D., Walters, C.J., Clements, S., Clemens, B.J., McKinley, R.S., and Schreck, C. 2008. Survival of migrating salmon smolts in large rivers with and without dams. PLoS Biol. **6**(10): e265. doi:10.1371/journal.pbio.0060265. PMID:18959485.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations. Academic Press, San Diego.

Appendix A. Simulation study results

Table A1. Complete simulation results for estimating survival (ϕ), recapture ($\overline{p}$), and recovery ($\overline{\lambda}$) probabilities and temporal variance in recapture and recovery probabilities (σ_p and σ_λ, respectively, on the logit scale).

		CJS			MRR		
Parameter	True value	Median	Bias	Coverage	Median	Bias	Coverage
ϕ_1	0.65	0.69	0.04	0.90	0.68	0.03	0.92
ϕ_2	0.80	0.74	−0.06	0.91	0.78	−0.02	0.97
ϕ_3	0.80	0.67	−0.13	0.76	0.76	−0.04	0.96
ϕ_4	0.70	—	—	—	0.66	−0.04	0.98
$\overline{p}_1$	0.15	0.15	0.00	0.98	0.15	0.00	0.99
$\overline{p}_2$	0.15	0.16	0.01	0.98	0.15	0.00	0.98
$\overline{p}_3$	0.15	0.20	0.05	0.82	0.16	0.01	0.99
$\overline{p}_4$	0.05	—	—	—	0.06	0.01	0.96
$\overline{\lambda}_1$	0.15	—	—	—	0.18	0.03	0.98
$\overline{\lambda}_2$	0.05	—	—	—	0.05	0.00	1.00
$\overline{\lambda}_3$	0.05	—	—	—	0.05	0.00	0.99
σ_{p1}	0.39	0.45	0.06	0.98	0.44	0.05	0.99
σ_{p2}	0.39	0.43	0.04	0.95	0.43	0.04	0.96
σ_{p3}	0.39	0.44	0.05	0.99	0.44	0.05	0.98
σ_{p4}	0.42	—	—	—	0.48	0.06	0.98
$\sigma_{\lambda1}$	0.39	—	—	—	0.46	0.06	0.98
$\sigma_{\lambda2}$	0.42	—	—	—	0.49	0.07	0.98
$\sigma_{\lambda3}$	0.42	—	—	—	0.53	0.10	0.98

Note: Mark–recapture (CJS) and mark–recapture–recovery (MRR) models were evaluated by comparing median, bias, and credible interval coverage in a simulation study of 200 datasets with 7000 individuals. All data generating values (True value) and sample sizes are similar to the steelhead study presented herein. Em dashes denote parameters that cannot be estimated in the CJS model. The size of weekly release cohorts were n_w = (450, 800, 1500, 1500, 1500, 800, 450), which were similar to sample sizes observed in the steelhead case study.

Appendix B. Recapture and recovery probabilities

Table B1. Posterior medians (95% credible interval) for logit-scale recapture (μ_p), recovery (μ_λ), and temporal variance in recapture and recovery parameters (σ_p and σ_λ, respectively) from PIT-tagged steelhead annually released at Rock Island Dam.

	Year						
Parameter	2008	2009	2010	2011	2012	2013	2014
Recapture							
$\bar{p}_{MCN}$	0.14 (0.10–0.19)	0.17 (0.11–0.25)	0.08 (0.06–0.11)	0.08 (0.05–0.14)	0.10 (0.07–0.15)	0.10 (0.06–0.18)	0.09 (0.06–0.14)
$\bar{p}_{JDA}$	0.18 (0.14–0.24)	0.14 (0.08–0.25)	0.08 (0.05–0.14)	0.23 (0.17–0.3)	0.15 (0.10–0.21)	0.07 (0.05–0.11)	0.07 (0.04–0.11)
$\bar{p}_{BON}$	0.14 (0.09–0.22)	0.17 (0.13–0.23)	0.29 (0.22–0.37)	0.06 (0.03–0.11)	0.14 (0.09–0.24)	0.18 (0.11–0.29)	0.17 (0.12–0.25)
$\bar{p}_{LWR}$	0.04 (0.02–0.09)	0.06 (0.04–0.09)	0.05 (0.03–0.07)	0.04 (0.02–0.06)	0.06 (0.03–0.09)	0.07 (0.04–0.13)	0.07 (0.04–0.13)
$\mu_{p_{MCN}}$	−1.82 (−2.18–1.44)	−1.61 (−2.07–1.09)	−2.49 (−2.81–2.14)	−2.44 (−2.95–1.85)	−2.16 (−2.56–1.71)	−2.18 (−2.69–1.50)	−2.36 (−2.77–1.85)
$\mu_{p_{JDA}}$	−1.49 (−1.82–1.18)	−1.79 (−2.39–1.12)	−2.44 (−3.00–1.79)	−1.21 (−1.57–0.87)	−1.74 (−2.15–1.34)	−2.55 (−2.97–2.12)	−2.54 (−3.07–2.06)
$\mu_{p_{BON}}$	−1.84 (−2.29–1.28)	−1.60 (−1.93–1.23)	−0.89 (−1.26–0.54)	−2.78 (−3.38–2.07)	−1.81 (−2.32–1.18)	−1.53 (−2.09–0.89)	−1.57 (−1.99–1.07)
$\mu_{p_{LWR}}$	−3.18 (−3.82–2.37)	−2.76 (−3.20–2.31)	−3.02 (−3.43–2.59)	−3.27 (−3.76–2.71)	−2.82 (−3.33–2.25)	−2.60 (−3.20–1.92)	−2.66 (−3.15–1.93)
$\sigma_{p_{MCN}}$	0.42 (0.23–0.85)	0.55 (0.31–1.13)	0.39 (0.21–0.78)	0.64 (0.38–1.28)	0.41 (0.21–0.95)	0.54 (0.27–1.32)	0.50 (0.27–1.04)
$\sigma_{p_{JDA}}$	0.34 (0.19–0.70)	0.74 (0.43–1.48)	0.78 (0.47–1.45)	0.37 (0.21–0.76)	0.39 (0.20–0.87)	0.34 (0.17–0.86)	0.50 (0.24–1.21)
$\sigma_{p_{BON}}$	0.53 (0.26–1.13)	0.33 (0.17–0.73)	0.40 (0.21–0.82)	0.70 (0.36–1.46)	0.56 (0.27–1.26)	0.52 (0.23–1.35)	0.45 (0.23–0.97)
$\sigma_{p_{LWR}}$	0.67 (0.28–1.61)	0.34 (0.17–0.86)	0.36 (0.18–0.84)	0.37 (0.18–0.90)	0.38 (0.18–0.98)	0.43 (0.19–1.43)	0.49 (0.21–1.23)
Recovery							
$\bar{\lambda}_{MCN}$	0.17 (0.11–0.26)	0.16 (0.12–0.22)	0.16 (0.12–0.23)	0.16 (0.11–0.27)	0.13 (0.09–0.20)	0.16 (0.07–0.35)	0.05 (0.03–0.08)
$\bar{\lambda}_{JDA}$	0.05 (0.02–0.10)	0.05 (0.03–0.07)	0.05 (0.03–0.08)	0.05 (0.03–0.09)	0.03 (0.02–0.04)	0.06 (0.03–0.14)	0.09 (0.05–0.14)
λ_{BON}	0.03 (0.02–0.06)	0.03 (0.02–0.07)	0.02 (0.01–0.04)	0.02 (0.01–0.03)	0.02 (0.01–0.04)	0.02 (0.01–0.12)	0.03 (0.01–0.06)
$\mu_{\lambda_{MCN}}$	−1.62 (−2.08–1.02)	−1.67 (−2.01–1.29)	−1.63 (−2.02–1.20)	−1.64 (−2.07–0.99)	−1.88 (−2.29–1.37)	−1.69 (−2.55–0.63)	−2.99 (−3.49–2.38)
$\mu_{\lambda_{JDA}}$	−3.02 (−3.83–2.16)	−3.00 (−3.37–2.61)	−2.96 (−3.51–2.42)	−2.91 (−3.45–2.28)	−3.55 (−3.98–3.09)	−2.80 (−3.62–1.85)	−2.35 (−2.92–1.78)
$\mu_{\lambda_{BON}}$	−3.46 (−4.04–2.80)	−3.39 (−4.08–2.58)	−3.89 (−4.49–3.28)	−4.13 (−4.79–3.38)	−3.89 (−4.62–3.07)	−3.88 (−5.14–1.97)	−3.48 (−4.19–2.68)
$\sigma_{\lambda_{MCN}}$	0.50 (0.23–1.16)	0.35 (0.19–0.75)	0.33 (0.17–0.78)	0.41 (0.19–1.02)	0.38 (0.19–0.93)	0.81 (0.28–2.21)	0.43 (0.20–1.07)
$\sigma_{\lambda_{JDA}}$	0.90 (0.46–2.08)	0.37 (0.19–0.84)	0.58 (0.27–1.35)	0.61 (0.32–1.28)	0.35 (0.18–0.85)	0.63 (0.22–2.37)	0.55 (0.24–1.36)
$\sigma_{\lambda_{BON}}$	0.41 (0.18–1.11)	0.57 (0.22–1.67)	0.45 (0.20–1.16)	0.42 (0.19–1.15)	0.47 (0.20–1.37)	0.80 (0.23–4.48)	0.51 (0.20–1.50)
r_{MCN}	0.20 (0.18–0.24)	0.20 (0.18–0.23)	0.21 (0.19–0.26)	0.20 (0.16–0.26)	0.15 (0.13–0.18)	0.22 (0.19–0.28)	0.14 (0.11–0.17)
r_{JDA}	0.07 (0.05–0.10)	0.07 (0.05–0.09)	0.07 (0.05–0.09)	0.06 (0.04–0.08)	0.05 (0.03–0.07)	0.08 (0.06–0.12)	0.12 (0.09–0.16)
r_{BON}	0.03 (0.02–0.05)	0.03 (0.02–0.05)	0.02 (0.01–0.03)	0.01 (0.01–0.03)	0.02 (0.01–0.03)	0.02 (0.01–0.04)	0.03 (0.02–0.05)

Note: Back-transformed recapture and recovery probabilities ($\bar{p}$ and $\bar{\lambda}$, respectively) and probability of recovery conditional on mortality in a specific river reach (r) are also provided for reference.