



A Hidden-Process Model for Estimating Prespawn Mortality Using Carcass Survey Data

J. Tyrell DeWeber, James T. Peterson, Cameron Sharpe, Michael L. Kent, Michael E. Colvin & Carl B. Schreck

To cite this article: J. Tyrell DeWeber, James T. Peterson, Cameron Sharpe, Michael L. Kent, Michael E. Colvin & Carl B. Schreck (2017) A Hidden-Process Model for Estimating Prespawn Mortality Using Carcass Survey Data, North American Journal of Fisheries Management, 37:1, 162-175, DOI: [10.1080/02755947.2016.1245223](https://doi.org/10.1080/02755947.2016.1245223)

To link to this article: <http://dx.doi.org/10.1080/02755947.2016.1245223>



Published online: 09 Jan 2017.



Submit your article to this journal [↗](#)



Article views: 72



View related articles [↗](#)



View Crossmark data [↗](#)

ARTICLE

A Hidden-Process Model for Estimating Prespawn Mortality Using Carcass Survey Data

J. Tyrell DeWeber*

*Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA*

James T. Peterson

*U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA*

Cameron Sharpe

Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, Oregon 97333, USA

Michael L. Kent

Department of Microbiology, Oregon State University, 220 Nash Hall, Corvallis, Oregon 97331, USA

Michael E. Colvin

*Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA*

Carl B. Schreck

*U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA*

Abstract

After returning to spawning areas, adult Pacific salmon *Oncorhynchus* spp. often die without spawning successfully, which is commonly referred to as prespawn mortality. Prespawn mortality reduces reproductive success and can thereby hamper conservation, restoration, and reintroduction efforts. The primary source of information used to estimate prespawn mortality is collected through carcass surveys, but estimation can be difficult with these data due to imperfect detection and carcasses with unknown spawning status. To facilitate unbiased estimation of prespawn mortality and associated uncertainty, we developed a hidden-process mark-recovery model to estimate prespawn mortality rates from carcass survey data while accounting for imperfect detection and unknown spawning success. We then used the model to estimate prespawn mortality and identify potential associated factors for 3,352 adult spring Chinook Salmon *O. tshawytscha* that were transported above Foster Dam on the South Santiam River (Willamette River basin, Oregon) from 2009 to 2013. Estimated prespawn mortality was relatively low ($\leq 13\%$) in most years (interannual mean = 28%) but was especially high (74%) in 2013. Variation in prespawn mortality estimates among outplanted groups of fish within each year was also very high, and some of this variation was explained by a trend toward lower prespawn mortality among fish that were outplanted later in the year. Numerous efforts are being made to monitor and, when possible, minimize prespawn mortality in salmon populations; this model can be used to provide unbiased estimates of spawning success that account for unknown fate and imperfect detection, which are common to carcass survey data.

*Corresponding author: jtdeweber@gmail.com

Received April 11, 2016; accepted October 2, 2016

It has become increasingly evident that large numbers of adult Pacific Salmon *Oncorhynchus* spp. often die without spawning successfully after they return to spawning areas; these deaths are commonly referred to as prespawn mortality. For example, beginning in the 1990s, prespawn mortality of Coho Salmon *O. kisutch* in western Washington rivers resulted in widespread concern and investigations to identify potential causes (Scholz et al. 2011; King et al. 2013). Similarly, high prespawn mortality (mean = 48%) of threatened Chinook Salmon *O. tshawytscha* in the Willamette River basin has recently been recognized as a potential threat to population persistence (Keefer et al. 2010). Although we focus primarily on prespawn mortality, mortality during migration to spawning areas (i.e., migration mortality) is closely related and may occur through similar processes. Potential factors that have been associated with prespawn and/or migration mortality include warm water temperatures (Naughton et al. 2005; Quinn et al. 2007; Keefer et al. 2008, 2010), river discharge (Rand et al. 2006; Quinn et al. 2007), pollutants (Scholz et al. 2011), infectious disease (CDFG 2004; Kocan et al. 2004; Bradford et al. 2010; Benda et al. 2015), and insufficient energy reserves to migrate and survive until spawning (Rand et al. 2006). Density dependence at very high abundance has also been associated with pre-spawn mortality (Quinn et al. 2007); however, in most recently reported cases, populations are well below historical averages, and this mechanism is unlikely.

One population restoration and reintroduction effort that is particularly sensitive to prespawn mortality is outplanting, which involves trapping and hauling sexually mature or maturing adults upstream of migration barriers or into habitats where reproduction is limited. Outplanting is increasingly being used for different purposes, including to accelerate recolonization of Chinook Salmon into newly available habitat after barrier removal in Shitike Creek, Oregon (Baumsteiger et al. 2008); to reintroduce Chinook Salmon above high-head dams in the Willamette River basin, Oregon (Keefer et al. 2010); and to allow adult Bull Trout *Salvelinus confluentus* to spawn upstream of barriers (DeHaan and Bernall 2013; Al-Chokhachy et al. 2015). Even moderate levels of prespawn mortality can undermine the effectiveness of outplanting operations because the number of adults outplanted is limited by (1) the number of adult fish available and (2) the high costs of associated infrastructure and personnel time. Outplanting operations may also elevate prespawn mortality via increased stress or disease transmission during holding or transport (Schreck et al. 1989; Mesa et al. 2000). Outplanting can only be successful at restoring self-sustaining populations if enough adults successfully spawn and produce sufficient numbers of offspring that survive through subsequent life stages and return as adults to complete the life cycle (Anderson et al. 2014).

Accurate estimation of prespawn mortality and identification of associated environmental covariates or management

practices are important for understanding spawning success and, if possible, mitigating negative effects. The most direct and widely available source of data for estimating the prevalence of prespawn mortality is collected during carcass surveys on spawning grounds (e.g., Hruska et al. 2011; Scholz et al. 2011), although radiotelemetry tags that report mortality can identify prespawn mortalities occurring prior to the spawning season (Keefer et al. 2008). In populations of fish that arrive early and hold in spawning areas, fish can die prior to the commencement of the spawning season, and any carcasses recovered during that time can be classified as prespawn mortalities, regardless of sex or condition (Keefer et al. 2008). Identification of prespawn mortality after the spawning season has begun is more difficult and requires the recovery and examination of female carcasses to determine the level of egg retention, as high percentages may signify prespawn mortality. Uncertainties arise in using carcass survey data to estimate prespawn mortality rates due to (1) the use of egg retention to identify prespawn mortality, (2) the presence of carcasses with unknown fates, and (3) imperfect detection. The use of egg retention estimates to identify prespawn mortality in carcasses can be uncertain due to poor carcass condition and the selection of a threshold above which fish are classified as prespawn mortalities. The use of a threshold does not recognize that fish with egg retention rates above the threshold may have partially spawned and produced offspring. However, it is common practice to use a relatively high egg retention threshold, such as 50% (Scholz et al. 2011) or 75% (Hruska et al. 2011), to signify prespawn mortality since most successful spawners are assumed to release more than 90% of their eggs under normal conditions (e.g., Major and Mighell 1969; Quinn et al. 2007). If some of these fish partially spawned and successfully produced offspring, then prespawn mortality and its related effects on the population would be overestimated. Carcasses with unknown fates are common because spawning success cannot be identified in males, and many carcasses may be in poor condition due to decay or scavenger damage, making it impossible to determine sex or spawning success via egg retention. In addition, carcass recovery at all times of the year is limited by imperfect detection due to practical limits on survey effort or due to conditions (e.g., high flows) that limit recovery. A model that accounts for imperfect detection and unknown spawning status can help make use of all available information collected during carcass surveys and can provide unbiased estimates of prespawn mortality.

Given the potential for prespawn mortality to adversely affect populations, conservation and recovery efforts such as outplanting can benefit from unbiased estimates of prespawn mortality and an understanding of the relationship between prespawn mortality and environmental factors or management practices. Since individuals that are handled during outplanting can be easily marked and later identified, the estimation of prespawn mortality from carcass survey data can be paired

with an appropriate mark–recovery model to facilitate estimation. We describe the development of a hidden-process mark–recovery model that can be used to estimate prespawn mortality from carcass survey data with marked individuals while accounting for imperfect detection and unknown spawning success. Hidden-process models account for variation in the unobserved (hidden) ecological process and for error due to observation methods, leading to more robust estimates of population dynamics (Newman et al. 2006; Gimenez et al. 2012) or similar ecological processes. We then use this model to estimate prespawn mortality of spring-run Chinook Salmon that were outplanted above Foster Dam on the South Santiam River, Oregon, and to understand the effects of outplanting operations on prespawn mortality.

METHODS

Model Development

We developed a hidden-process mark–recovery model that enables estimation of the percentage of prespawn mortalities while accounting for unknown fates and imperfect detection. Our model was similar to that developed by Schaub and Pradel (2004) for estimating the percentage of white storks *Ciconia ciconia* that died from power line collisions. Schaub and Pradel (2004) used the more conventional maximum likelihood estimation based on a summarization of the mark–recovery data, which did not allow for estimation of group or individual effects. We modified the model in a manner that enabled us (1) to separately estimate two known spawning states (successfully spawned and prespawn mortality) from unknown states and (2) to use all available information from individual fish mark–recovery histories.

The unobserved process describing the survival and fate of outplanted fish was modeled with five states: (1) alive, (2) died within the preceding week without spawning (prespawn mortality), (3) died within the preceding week and had successfully spawned, (4) died within the preceding week but had an unknown spawning status (unknown status), and (5) died before the preceding week (i.e., had been dead for more than 7 d) and were unavailable for recovery (dead). Fish that were either alive (state 1) or dead (state 5) were not available for recovery. We assumed that after more than 1 week, Chinook Salmon carcasses would be unavailable for recovery because carcasses can be quickly damaged due to scavenging or can be washed downstream (Cederholm and Peterson 1985). Although it is possible that carcasses could be recovered more than 1 week after the mortality occurred (Cederholm et al. 1989), we made this simplifying assumption because we had no additional information on the transition between death and carcass recovery. If this assumption was violated, then the estimates of weekly detection probability and survival could be biased, but the estimates of prespawn mortality would be largely unaffected. Thus, in the unobserved-process model,

individuals that died at time t but were not recovered transitioned to state 5 (dead) and could no longer be observed.

The observation process model had four states: unobserved (alive or unrecovered/dead), recovered as a prespawn mortality, recovered as a spawned carcass, and recovered as a carcass of unknown status. A transition probability matrix is a convenient way to describe the model in terms of the probability of transitioning from the current state at time t to another state at time $t + 1$ (Schaub and Pradel 2004; MacKenzie et al. 2009). The transition probability matrix (Φ) and associated vector of recovery probabilities (P) were

$$\begin{bmatrix} S & (1-S)(\alpha)(K) & (1-S)(1-\alpha)(K) & (1-S)(1-K) & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{pmatrix} 0 \\ \lambda \\ \lambda \\ \lambda \\ 0 \end{pmatrix}, \quad (1)$$

where S is survival probability, α is the probability of prespawn mortality, K is the probability that the spawning success of a recovered fish is known, and λ is the detection probability. Note that we include only a single λ shared by all fates because preliminary simulations showed that the model was not identifiable when λ was estimated separately for each fate (J.T.D., unpublished data). Additional information or an alternative formulation could be used to enable the estimation of multiple λ values, but simulations would be needed to ensure that all parameters are identifiable.

Consider an individual that is alive at time t (row 1 in equation 1). This individual can (1) remain alive with probability S , (2) die without spawning, with probability $(1-S)(\alpha)(K)$, (3) die after spawning, with probability $(1-S)(1-\alpha)(K)$; or (4) die and become a carcass of unknown spawning status with probability $(1-S)(1-K)$ at time $t + 1$. Note that the probability of becoming an individual of unknown status is actually $(1-S)(1-K)[\alpha + (1-\alpha)]$, as fish of unknown fate actually spawned or did not spawn prior to dying, but $[\alpha + (1-\alpha)]$ is equal to 1.0 and is not shown in our transition matrix. A fish cannot transition from alive (state 1) to dead and unobservable (state 5) within one time step because in our model, carcasses are assumed to be available for recovery for 1 week, which is reflected by the 0% probability in the last column of row 1. The last four rows are deterministic, since all individuals that are recently dead (states 2–4) or dead (state 5) either transition to or remain dead (state 5) at time $t + 1$. These transitions are summarized by using a fate diagram for an outplanted individual (Figure 1).

Outplanting of Chinook Salmon as a Case Study

The model described above is a relatively general form that can be used to estimate spawning success from carcass survey data with tagged fish, such as in Pacific salmon outplanting operations. We illustrate the model's application in estimating

Capture history fragment

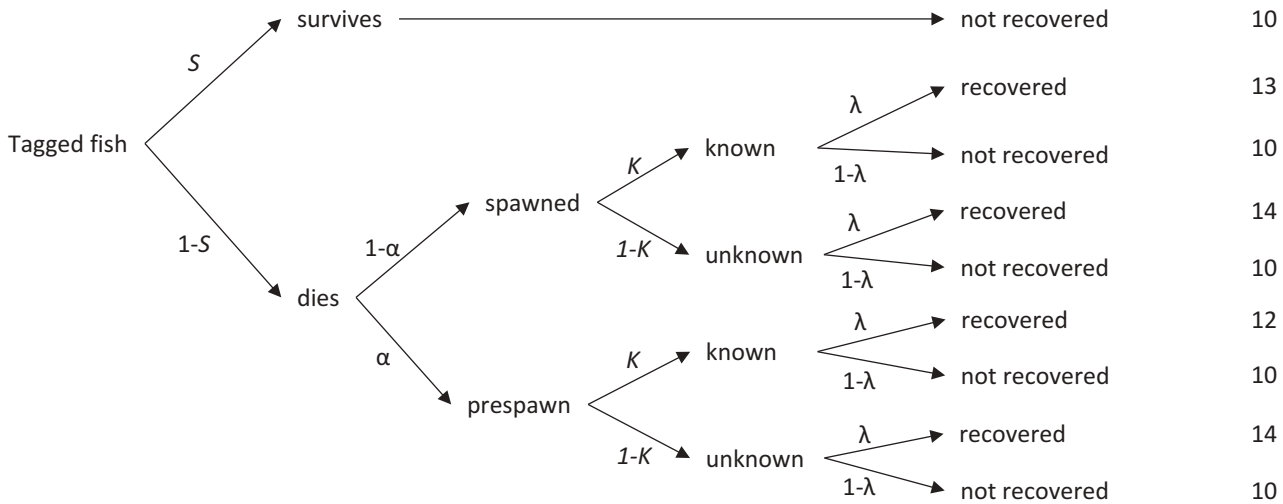


FIGURE 1. Fate diagram for individual tagged Chinook Salmon, showing possible state transitions from time t to time $t + 1$ (S = survival probability; α = probability of prespawn mortality; K = probability that spawning status is known; λ = detection probability [i.e., probability that the carcass will be recovered]). The capture history fragment records the observed state for 2 weeks resulting from each of the possible unobserved transitions in the diagram. All capture history fragments begin with the number 1 during the first week a fish is tagged (alive) and are then followed in the second week by a 0 (not recovered), 2 (prespawn), 3 (spawn), or 4 (unknown spawning status).

the prespawn mortality of outplanted Chinook Salmon in the South Santiam River, Oregon.

Study region.—The South Santiam River is a major tributary to the Willamette River. The South Santiam River has a 2,694-km² watershed, with elevations ranging from 67 m in the Willamette Valley to 1,744 m on the western slope of the Cascade Mountains (Figure 2). Riverine habitat ranges from steep, confined channels in forested, high-elevation areas to low-gradient reaches with broader floodplains surrounded by farming and developed land cover downstream. Foster Dam is located at river kilometer (rkm) 62; it is an impassable barrier that blocks spring-run Chinook Salmon and winter-run steelhead *O. mykiss* from accessing historic spawning locations. Chinook Salmon in the upper Willamette River system, including the South Santiam River population, were listed as threatened under the U.S. Endangered Species Act in 1999, partly due to very limited natural reproduction (NMFS 1999a, 1999b; ODFW and NMFS 2011). The loss of access to historic spawning habitat due to dams was a major contributor to population declines, but habitat degradation and overharvest also contributed (ODFW and NMFS 2011). Managers initially began outplanting adult Chinook Salmon above dams to provide a prey base for threatened Bull Trout, but the establishment of naturally reproducing populations became a primary goal after initial outplanting resulted in natural production (Johnson and Friesen 2010; ODFW and NMFS 2011). Outplanting operations have included the South Santiam River above Foster Dam, but also other sites in the Willamette River

basin, including the North Santiam River above Detroit Dam, the McKenzie River above Cougar Dam and Blue River Dam, and the Middle Fork Willamette River above Lookout Point Dam and Fall Creek Dam. Upstream of Foster Dam, most of the habitat that is accessible to outplanted salmon is relatively steep, with a confined channel surrounded by forested land at moderate elevations.

Outplanting and recovery operations.—During May–September in 2009–2013, spring Chinook Salmon arrived at Foster Dam and entered the fish trap. Trapping and outplanting generally occurred on a weekly basis but varied to match the number of returning fish. In some weeks no fish were outplanted, whereas outplanting occurred as often as three or four times in 1 week during the peak return period in each year. Individuals with intact adipose fins were assumed to be wild fish and were outplanted above Foster Dam, whereas fish with clipped adipose fins were of known hatchery origin and were not outplanted during the study period. Some hatchery-origin fish were unmarked due to healed adipose fins and were thus outplanted as wild fish. Nearly all of the outplanted fish received a single Floy tag (with an individual identification number) directly behind the dorsal fin above the lateral line. Only individuals that received and retained their Floy tags until they were discovered as carcasses were used to estimate pre-spawn mortality.

After tagging, fish were transferred to aerated tanks on trucks, transported upstream, and outplanted at one of three locations (shown in Figure 2). The most suitable location for the release of adult salmon was selected by Oregon

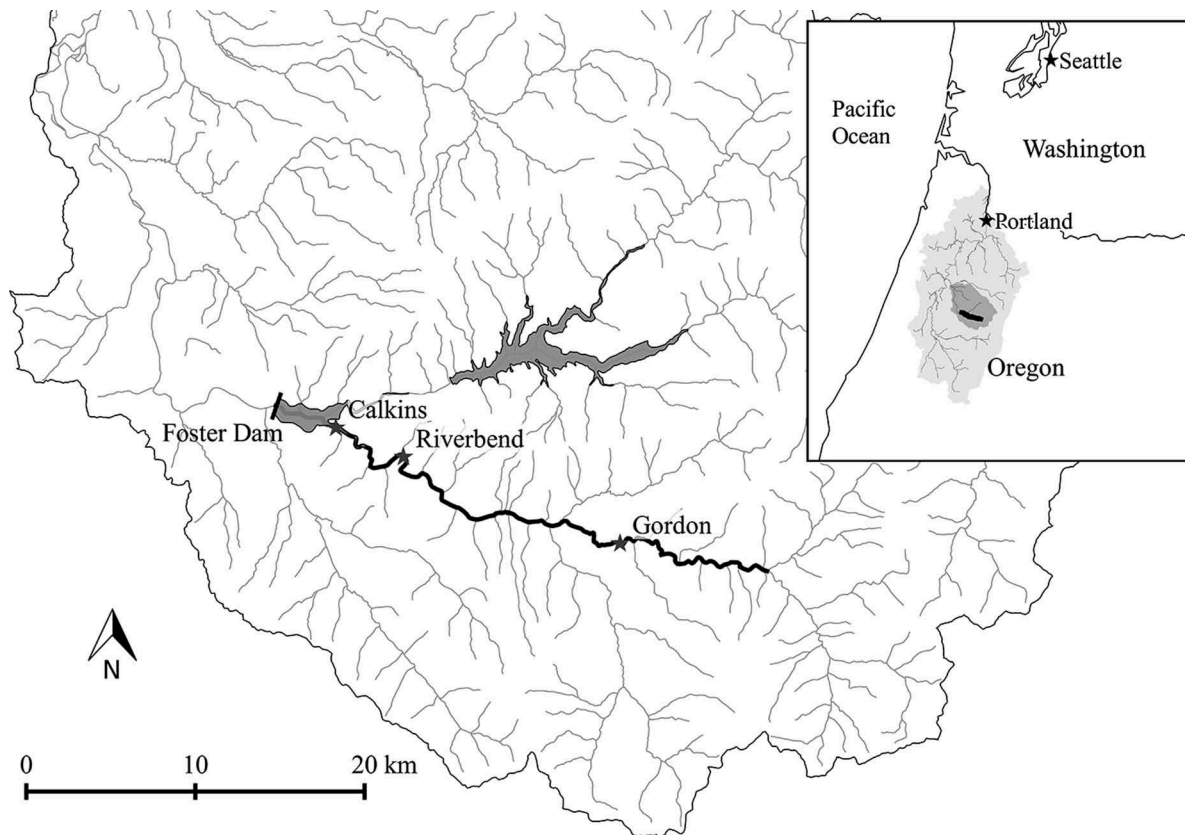


FIGURE 2. Map depicting the South Santiam River (bold line), Oregon, and the locations of Foster Dam and three Chinook Salmon release sites. Inset shows the location of the study reach (bold line) in the South Santiam River basin (dark gray shading), which is part of the Willamette River basin (light gray shading).

Department of Fish and Wildlife (ODFW) staff based on the water levels, water temperature, and season. Dead or moribund individuals (if any) were recorded as transport mortalities at the time of fish release from the truck, but those individuals were not considered prespawn mortalities in our analysis. Fish that were outplanted to the same site on the same date were classified into a single outplant group; this was done to identify groups of fish that experienced similar trapping, hauling, and outplanting conditions, including the occurrence of transport mortality. Ideally, an outplanted group would only include individuals that were trapped, transported in the same truck, and outplanted together, but the transport event identifier was not linked to the outplanting and recapture data set.

Carcass surveys by ODFW staff and volunteers began after the first group of fish was outplanted each year, and the surveys spanned from the head of the reservoir to a natural barrier waterfall at rkm 99.0. The location and length of stream surveyed varied among daily surveys, but the entire length of the main-stem South Santiam River that was available to spawning fish was surveyed on a weekly basis. All recovered carcasses were examined for Floy tags and were identified as one of the following: prespawn mortality females

(>50% of eggs remaining), successfully spawned females (<50% of eggs remaining), males, and unknown spawning status (too much damage or decay to be identifiable). The 50% threshold was used because in most years, survey data only recorded whether egg retention was below or above this value. During the 2013 surveys, when egg retention was estimated in quartiles, most of the fish that were classified as prespawn mortalities (43 of 47) had 75–100% of eggs remaining. This finding suggests that (1) most of the fish that were recovered as pre-spawn mortalities in our study either did not spawn or released less than 25% of their eggs, and (2) the use of a 50% threshold was unlikely to affect our results. The recovery location of each carcass also was recorded as belonging to one of nine main-stem survey reaches, which were delineated by tributaries or landmarks and ranged in size from 2.5 to 7.5 km. Recovered carcasses were chopped to ensure that those individuals would not be recorded during subsequent surveys.

Model implementation.—We used the general form of the hidden-process model presented above to estimate the fates of Chinook Salmon in the outplanted groups. The ecological and observation processes were modeled at a weekly time step, which provided sufficient temporal resolution to depict the

underlying process and corresponded to the timing of salmon carcass surveys. We classified all fish that died prior to week 35 of each year (i.e., the beginning of September) as prespawn mortalities because Chinook Salmon do not normally spawn prior to September in the South Santiam River. The unknown state included carcasses that were damaged or decayed beyond recognition as well as all males that died after the spawning season began, since it was impossible to determine from carcass surveys whether males had successfully spawned.

In addition, we prepared a matrix with known information about the unobserved process to assist in convergence, as discussed by Kery and Schaub (2012). For each recovered carcass, it was known that the individual was alive from the time of release until the period prior to recovery, after which it died, was recovered in the observed state, and subsequently entered the dead state. The known matrix was used so that the unobserved states of all recovered fish did not have to be estimated. This was not required but did increase the speed of model convergence.

We modeled the annual probabilities S_y , K_y , and λ_y as constant within a year y , where each annual estimate was independent from those of other years. We recognize that each of these parameters could be modeled as random deviations from a normal distribution with an interannual mean and SD, but we did not pursue this approach because it greatly increased computational time and did not improve inference in preliminary comparisons (J.T.D., unpublished data). We constrained survival in the last week of each year to be zero because it was unlikely that any individuals survived past the end of the spawning season in late October.

One of our primary objectives was to estimate how the prespawn mortality rate varied among years and among outplant groups and to estimate potential covariate effects. The probability of prespawn mortality for outplant group g in year y (α_{gy}) can be modeled as a logit-linear function of the intercept, an annual deviation (γ_y), a group deviation (ε_g), and the effect b of outplant group covariate X_g ,

$$\text{logit}(\alpha_{gy}) = \mu_{\bullet} + bX_{gy} + \gamma_y + \varepsilon_g, \quad (2)$$

where $\gamma_y \sim N(0, \sigma_y^a)$ and $\varepsilon_g \sim N(0, \sigma_y^a)$.

Without covariates, the model is a two-level hierarchical model with annual and group-level deviations that stem from normal distributions with a mean of zero and SDs of σ_{\bullet}^a and σ_y^a , respectively. When covariates are included, the deviations ε_g allow for additional variation in outplant groups that is not accounted for by covariate effects.

Potential covariates.—We developed a set of covariates that might influence the probability of prespawn mortality for fish in outplant groups. Covariates included the week of the year during which a group was outplanted (hereafter, “outweek”), whether a death occurred during transport for a given outplant group (transport death), and the outplant

location (site). Outweek ranged from 19 to 43 and averaged 28.9 (SD = 5.3). The prevalence of transport death was 26%, and the three outplant locations shown in Figure 2 served as the three levels of the site covariate. We expected outweek to have a negative effect because other studies have found that fish outplanted later in the season exhibited lower prespawn mortality rates (Keefer et al. 2010). We included outplant location because a closely related analysis found a significant effect on transport mortality (M.E.C., unpublished data), and there are immediate management implications that would stem from higher prespawn mortality at a given site. A transport death was expected to be associated with an increased probability of prespawn mortality because all fish in the transport vessel could have been influenced by the stressor or pathogen that caused the transport mortality, potentially resulting in latent mortality of the outplanted fish that survived transport (Schreck et al. 1989). The transport death covariate was uncertain because outplant groups included all fish that were outplanted to a given site on the same day, and two to three transport groups were included in a single outplant group on 19 dates. For outplant groups that included multiple transport groups, we recorded a transport death if mortality occurred during transport for any fish taken to that site on that day. All r^2 values among outplant group covariates were less than ± 0.50 .

The full model was modified from the generic model shown in equation (2) to include the effects (b_{outweek} , $b_{\text{transport_death}}$, b_{Gordon} , and $b_{\text{Riverbend}}$) of the covariates outweek (O), transport death (D), and indicator variables for the Gordon (G) and Riverbend (R) sites,

$$\text{logit}(\alpha_{gy}) = \mu_{\bullet} + b_{\text{outweek}}O_{gy} + b_{\text{transport_death}}D + b_{\text{Gordon}}G + b_{\text{Riverbend}}R + \gamma_y + \varepsilon_g, \quad (3)$$

where $\gamma_y \sim N(0, \sigma_y^a)$ and $\varepsilon_g \sim N(0, \sigma_y^a)$.

We used forward stepwise selection to identify covariates that were important predictors of prespawn mortality. We first began by fitting a null model that did not include any covariates of prespawn mortality. We then fitted three models with one covariate each to determine whether covariate effects were supported by the data. If the 80% credible intervals (CIs) of a given covariate effect did not include zero, that covariate was selected for inclusion in the model. We recognize that an 80% CI is not conservative and may have led to the inclusion of spurious predictors in our results, but we think that this is a reasonable level of support given the high amount of variation in our data set. Since the choice of CI is ultimately subjective, we report the CIs plus the percentage of posterior distributions that are below (or above) zero and thereby lend support for a negative (or positive) effect for any included covariates. If two or more covariates were supported, we fitted models that included all supported covariates plus two-way interactions.

All models were fitted in JAGS software (Plummer 2003), which was implemented in the R2Jags package (Su and Yajima 2015) of the R statistical environment (R Core Team 2015). The model code is available upon request from J.T.D. All model priors were uninformative, with uniform distributions ranging from 0 and 1 for all probabilities and normal distributions with a mean of 0 and a standard deviation of 1 for covariate effects. We used three chains and fitted models for 500,000 iterations, discarding the first 50,000 iterations. Due to high autocorrelation, we kept every 50th draw, resulting in a total of 27,000 posterior samples. We analyzed trace plots and density plots of posterior distributions, and we considered models to have converged when mixing was thorough and when the Gelman–Rubin diagnostic was less than or equal to 1.05 for all parameters. The estimation of parameters for this model is not trivial: convergence for models described here with our data set typically required over 2 weeks running in parallel on three 3.60-gigahertz processors. Computation time can be greatly reduced if prespaw mortality is estimated by using a fixed-effects structure or if the data set includes more information (i.e., more recovered prespaw mortalities).

Simulations.—Since the reliability of our model was unknown, we compared parameter estimates with known values from simulated data to determine the reliability of our model estimates. We simulated the outplanting of groups of 100 individual fish on 10 occasions for a single year, followed by recapture events on 12 occasions beginning after the first outplant occasion, with known values for S , α_g , K , and λ . We simulated data sets to represent situations with relatively low

and high values for S , K , and λ , as shown in Table 1. For each of the six combinations of S , K , and λ , we randomly drew the 10 outplant group prespaw mortality probabilities (α_g) from a uniform distribution between 0 and 1 (Table 1). Survival was set to zero during the last time interval because Pacific salmon do not survive after the spawning season. For each combination of known values, we simulated 30 data sets and estimated all parameters by using a model with all probabilities as fixed effects, ensuring that estimates converged (Gelman–Rubin diagnostic ≤ 1.05 for all parameters). We then compared the estimates to the true values to identify potential biases.

RESULTS

Simulation Results

Estimates of S , K , and λ from the 30 simulations for all parameter combinations were very precise (SD < 7%) and unbiased, with mean values much less than 1 SD from true values (Table 1). Nearly all mean estimates of α_g from the 30 simulations for combinations 1–5 of S , K , and λ were within 1 SD of the true values, and the remaining 10 values were within 2 SDs. For combination 6, in which S was 60%, K was 30%, and λ was 5%, five mean estimates of α_g were within 2 SDs of the true values, and the other five were within 3 SDs. This last combination involved both low λ and low K , resulting in the fewest known prespaw mortalities and the least information for estimation. When we ran the same

TABLE 1. Simulation results summarizing the mean estimates for six combinations of known true values for the probability of survival (S), the probability that spawning status is known (K), detection probability (λ), and the probability of prespaw mortality for Chinook Salmon outplant group y (α_y). For each combination of known values, we estimated parameters based on 30 simulated mark–recapture data sets, where 100 fish were outplanted in 10 groups of fish with differential α_y . “True” is the known true value, and “mean (SD)” is the estimated mean (with SD in parentheses) from the 30 simulations. All values are probabilities.

Parameter	Combination 1		Combination 2		Combination 3		Combination 4		Combination 5		Combination 6	
	True	Mean (SD)	True	Mean (SD)	True	Mean (SD)	True	Mean (SD)	True	Mean (SD)	True	Mean (SD)
S	0.30	0.3 (0.01)	0.30	0.3 (0.01)	0.30	0.3 (0.01)	0.60	0.6 (0.01)	0.60	0.6 (0.01)	0.60	0.6 (0.01)
K	0.60	0.6 (0.02)	0.30	0.3 (0.02)	0.60	0.6 (0.07)	0.60	0.59 (0.03)	0.60	0.58 (0.05)	0.30	0.3 (0.07)
λ	0.30	0.3 (0.01)	0.30	0.3 (0.02)	0.05	0.05 (0.01)	0.30	0.3 (0.01)	0.05	0.05 (0.01)	0.05	0.05 (0.01)
α_1	0.07	0.12 (0.07)	0.62	0.58 (0.14)	0.76	0.61 (0.15)	0.08	0.13 (0.07)	0.33	0.38 (0.17)	0.06	0.34 (0.13)
α_2	0.12	0.17 (0.06)	0.61	0.56 (0.12)	0.67	0.63 (0.16)	0.83	0.79 (0.09)	0.76	0.61 (0.15)	0.64	0.54 (0.14)
α_3	0.39	0.45 (0.1)	0.11	0.17 (0.08)	0.97	0.75 (0.11)	0.85	0.82 (0.06)	0.46	0.48 (0.17)	0.97	0.68 (0.11)
α_4	0.03	0.08 (0.04)	0.72	0.68 (0.14)	0.53	0.43 (0.16)	0.82	0.77 (0.06)	0.62	0.5 (0.15)	0.77	0.59 (0.13)
α_5	0.11	0.16 (0.06)	0.46	0.52 (0.15)	0.26	0.38 (0.17)	0.33	0.34 (0.09)	0.72	0.7 (0.14)	0.98	0.66 (0.12)
α_6	0.22	0.23 (0.09)	0.00	0.1 (0.04)	0.42	0.47 (0.19)	0.97	0.93 (0.03)	0.59	0.52 (0.17)	0.74	0.56 (0.14)
α_7	0.03	0.08 (0.05)	0.66	0.62 (0.14)	0.20	0.3 (0.13)	0.86	0.83 (0.08)	0.85	0.69 (0.12)	0.29	0.44 (0.14)
α_8	0.35	0.35 (0.09)	0.33	0.36 (0.11)	0.53	0.51 (0.15)	0.48	0.45 (0.14)	0.04	0.25 (0.11)	0.98	0.7 (0.11)
α_9	0.06	0.09 (0.05)	0.44	0.51 (0.16)	0.31	0.43 (0.16)	0.73	0.68 (0.11)	0.90	0.74 (0.14)	0.97	0.64 (0.13)
α_{10}	0.05	0.1 (0.05)	0.59	0.58 (0.14)	0.86	0.72 (0.13)	0.34	0.36 (0.09)	0.42	0.46 (0.17)	0.76	0.63 (0.13)

simulation and increased the number of outplanted fish from 100 to 500 individuals, there were more known prespawn mortalities in the simulated data sets, and all mean estimates of α_g were within 1.5 SD of the true values.

Case Study Results

In total, 4,381 Chinook Salmon adults were outplanted above Foster Dam during the study period, of which 3,453 received Floy tags and could be used in model estimation. Fish were outplanted during May–October; the average number of outplant groups per year was 20.4, and the average number of individuals outplanted per year was 691. Smaller numbers of outplant groups (10) and individuals (223) were used in 2009 because many of the outplanted fish did not receive tags, and this smaller sample greatly decreased precision in the 2009 estimates, as discussed below. The number of individuals per outplant group varied from 1 to 110 and averaged 33.9. The most fish were released at Riverbend (1,667), followed by Gordon (1,186) and Calkins (499), and there were differences in the choice of release site among years and throughout the season. None of the fish used in analyses was released at Calkins in 2009, for example, and most of the fish that were released later in the season in all years were released at Gordon, the furthest upstream site (Figure 2; Table 2).

Overall, 904 carcasses with and without tags were recovered during the study period; 113 were known prespawn females, and 289 were known spawned females. In addition,

28 male carcasses were recovered in July and August prior to the spawning season (September 1) and were therefore considered to be prespawn mortalities. The naive prespawn mortality rate (i.e., uncorrected for imperfect detection), which was calculated as the percentage of all recovered carcasses that were known prespawn females or early male deaths, was 15.6% overall. The annual naive prespawn mortality rate was 6.2% in 2009, 2.7% in 2010, 12.2% in 2011, 8.6% in 2012, and 35.8% in 2013. If only females were included in the calculation, the naive prespawn mortality rate based on all recovered female carcasses was 28% overall and was 14.8% in 2009, 5.6% in 2010, 24.8% in 2011, 14.5% in 2012, and 65.9% in 2013. The naive tag retention rate (calculated as the percentage of all recovered fish that were found with tags; $n = 530$) averaged 59% and ranged from 50% in 2013 to 71% in 2009. Of the 904 carcasses that were recovered, 530 were recovered with tags and 433 were included in the model as recoveries; the remaining recoveries were not included because the death covariate was not available. Of these 433 fish, there were 54 prespawn mortalities and 175 spawned mortalities, whereas all others had unknown fates (Table 2). Prespawn mortalities were recovered throughout the year, with 32 recovered during the typical spawning season in September after week 35.

The average probability of prespawn mortality from the intercept-only model for the entire study period was 28%; inter-annual variation and among-group variation were both high (Table 3; Figure 3). The variation among groups was especially

TABLE 2. Number of Chinook Salmon that were outplanted and recovered in the South Santiam River, Oregon; number of recovered carcasses that were designated as prespawn mortalities, successfully spawned fish, or having an unknown spawning status; number of transport occasions during which a transport death occurred; and the minimum (min), maximum (max), and mean week of outplanting (outweek). Data are summarized by year and site and include only those used in model development (NA = no fish were outplanted at the specified site during that year).

Year	Site	Number outplanted	Number recovered	Recovered carcasses				Outweek		
				Prespawn mortality	Spawned	Unknown status	Transport death	Min	Max	Mean
2009	Calkins	95	4	0	0	4	0	29	34	31.4
	Gordon	128	23	0	8	15	0	30	40	37
	Riverbend	NA	NA	NA	NA	NA	NA	NA	NA	NA
2010	Calkins	108	1	0	1	0	0	28	29	28.3
	Gordon	163	11	0	7	4	1	32	38	33.9
	Riverbend	342	19	0	11	8	0	20	29	27
2011	Calkins	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Gordon	348	80	7	29	44	4	30	40	34.9
	Riverbend	655	90	7	41	42	6	25	30	27.6
2012	Calkins	157	10	1	4	5	1	25	34	29.1
	Gordon	108	17	2	5	10	1	24	38	32.7
	Riverbend	577	81	6	49	26	4	19	29	25.7
2013	Calkins	139	10	3	1	6	4	25	31	28.6
	Gordon	439	61	21	14	26	5	24	39	32.3
	Riverbend	93	10	4	1	5	1	19	24	22.6

TABLE 3. Summaries of parameter estimates from a hidden-process model without covariates for adult Chinook Salmon that were outplanted above Foster Dam on the South Santiam River during 2009–2013 (S_y = probability of survival in year y ; K_y = probability that spawning status in year y is known; λ_y = detection probability in year y ; μ_{\cdot} = interannual mean prespawn mortality; σ_{\cdot} = variance of μ_{\cdot} ; μ_y = mean prespawn mortality in year y ; σ_y = intra-annual variance). The mean, SD, and 90% credible interval (CI) are summaries of 30,000 draws from the posterior distribution. The rate parameters are reported as probabilities, whereas variances are reported on the logit scale.

Parameter	Mean	SD	90% CI
S_{2009}	0.20	0.02	0.16, 0.24
S_{2010}	0.33	0.02	0.31, 0.36
S_{2011}	0.57	0.01	0.55, 0.59
S_{2012}	0.59	0.01	0.57, 0.60
S_{2013}	0.42	0.01	0.40, 0.45
K_{2009}	0.31	0.08	0.18, 0.45
K_{2010}	0.61	0.08	0.47, 0.74
K_{2011}	0.49	0.04	0.43, 0.56
K_{2012}	0.62	0.05	0.54, 0.69
K_{2013}	0.53	0.05	0.44, 0.61
λ_{2009}	0.12	0.02	0.09, 0.16
λ_{2010}	0.05	0.01	0.04, 0.07
λ_{2011}	0.17	0.01	0.15, 0.19
λ_{2012}	0.13	0.01	0.11, 0.15
λ_{2013}	0.13	0.01	0.11, 0.15
μ_{\cdot}	0.28	0.22	0.03, 0.73
σ_{\cdot}	4.89	2.31	1.74, 9.18
μ_{2009}	0.10	0.21	0.00, 0.63
μ_{2010}	0.01	0.03	0.00, 0.06
μ_{2011}	0.13	0.06	0.04, 0.23
μ_{2012}	0.09	0.06	0.01, 0.19
μ_{2013}	0.74	0.13	0.52, 0.93
σ_{2009}	4.79	2.89	0.43, 9.45
σ_{2010}	2.77	2.35	0.21, 7.88
σ_{2011}	1.35	0.95	0.16, 3.11
σ_{2012}	2.17	1.53	0.28, 5.62
σ_{2013}	1.90	1.01	0.72, 3.81

high in 2009, when relatively few fish were outplanted, and in 2010 and 2012, when average annual prespawn mortality probabilities were below 10%. High interannual variability and among-group variability were driven by the estimation of comparatively high prespawn mortality in one year (2013) or in a few outplant groups within a year (Figure 3). Estimates of prespawn mortality for outplant groups were often imprecise (Figure 3), especially when groups had few outplants or few recovered carcasses. Average λ ranged from 5% to 17% among years, and detection was substantially lower in 2010 than in all other years (Table 3).

Model selection suggested that a negative effect of outweek was supported by the data, as 80% CIs did not overlap zero. The probability of a negative effect was 94% based on the percentage of posterior draws below zero.

This effect predicted that the probability of prespawn mortality was higher for groups of fish that were outplanted earlier in the season (Table 4). The 80% CIs for the effects of transport death and site widely overlapped zero and suggested that these covariates were not supported by the data.

DISCUSSION

By using a hidden-process model, we were able to successfully estimate the probability of prespawn mortality in Chinook Salmon while accounting for imperfect detection and for the fact that many carcasses had unknown fates. Simulations showed that the model provided unbiased estimation of parameters across a reasonable range of parameter values and were especially precise for the probabilities of survival (S), detection (λ), and known spawning status (K). When few carcasses representing prespawn mortalities were available, the estimates of prespawn mortality were imprecise due to low simulated λ and K , which is not surprising since little information was available to inform estimates in such cases. Situations with few prespawn mortalities could arise from small outplant groups, a low prevalence of prespawn mortality, low λ , or a large number of individuals with unknown spawning status. In such cases, model estimates of prespawn mortality are likely to provide unbiased estimates with low precision. This lack of precision was reflected in the wide CIs for many years and outplant groups in our case study application when data were limited (Figure 3).

We estimated that prespawn mortality occurred in relatively few Chinook Salmon ($\leq 13\%$) and few outplanted groups during 2009–2012, but it was highly variable and affected an average of 74% of the outplanted fish in 2013 and 87% of individuals in one outplant group. The annual naive prespawn mortality rates based on the proportion of all carcasses recovered (including those without tags) were also low ($\leq 12\%$) for 2009–2012 and relatively high in 2013 (36%), although lower than model estimates. This comparison shows that model estimates captured the general trends in naive estimates while also providing reliable uncertainty estimates that accounted for process error and sampling error. Differences in the 2013 estimates were likely attributable to tag loss or differential detection throughout the season, which are important limitations of our data set that we discuss further below. Comparably high variability was also reported in a recent study that used radio-tagged outplants in the nearby Middle Fork Willamette River, where prespawn mortality (defined in that study as fish that did not survive past September 1) averaged 48% but varied from 0% to 93% among outplant groups (Keefer et al. 2010). It is important to note that our definition of prespawn mortality included individuals that might have partially spawned (i.e., 50% egg retention threshold), and those fish may have successfully produced offspring. Because almost all (43 of 47) prespawn mortalities in 2013

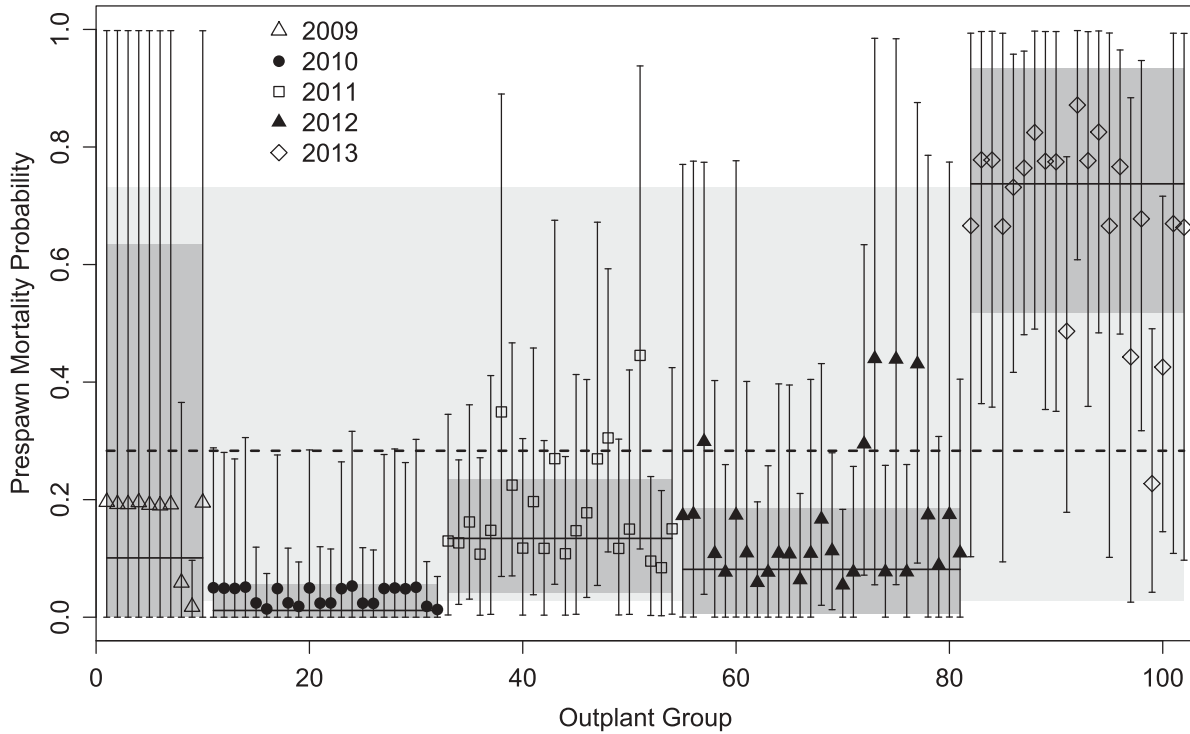


FIGURE 3. Estimates of prespawn mortality probability are shown for the 102 groups of Chinook Salmon that were outplanted above Foster Dam on the South Santiam River, presented in order of outplanting date from 2009 to 2013. Each estimate is accompanied by 90% credible intervals (CIs); the horizontal lines and dark-gray boxes show the annual means and 90% CIs, respectively, for each corresponding year. The bold dashed line and light-gray shaded area depict the mean prespawn mortality for the entire study period and the corresponding 90% CI, respectively.

had more than 75% egg retention and because even moderately high egg retention may be detrimental to reintroduction efforts, we think that it is reasonable to classify those fish as prespawn mortalities.

We estimated prespawn mortality based on the percentage of all carcasses recovered (both males and females) because spring-run Chinook Salmon in the South Santiam River arrive to spawning areas early, and prespawn mortality may occur

prior to and during the spawning season. Because both males and females that die prior to the spawning season are known prespawn mortalities and because the early death of either sex is of concern to managers, we think that this definition best characterizes prespawn mortality for the studied population. In 2013, for example, 8 of 28 known prespawn mortalities used in the modeling data set were early male deaths that occurred in July and August, and we did not want to exclude them from the analysis. Although prespawn mortality in females may be a primary concern of some managers because numerical production is limited by egg deposition, premature deaths of males may have negative consequences via the loss of genetic diversity. Our definition of prespawn mortality as the percentage of all fish is common in estimates of migration mortality (Macdonald et al. 2010) and in studies that consider prespawn mortality prior to the spawning season (e.g., Keefer et al. 2010). In contrast, most studies based on carcass surveys in spawning areas have reported prespawn mortality as the percentage of female carcasses (e.g., Quinn et al. 2007; Scholz et al. 2011), presumably because (1) spawning can occur when fish arrive in these populations and (2) males always have unknown spawning success. Since our estimate of prespawn mortality was calculated based on the total number of recovered carcasses, it is an underestimate relative to studies that use only the percentage of females. The general hidden-

TABLE 4. Summary of the estimated effects of potential covariates for within-year variability in prespawn mortality of Chinook Salmon that were outplanted above Foster Dam on the South Santiam River during 2009–2013 (CI = credible interval). “Transport death” denotes the occurrence of one or more transport mortalities, “outweek” is the week during which fish were outplanted, and “site” is the location of outplanting. Asterisks denote covariates that were considered supported (i.e., the 80% CI did not overlap zero). Site is a categorical variable, with Gordon and Riverbend effects estimated as deviations from prespawn mortality at the third site, Calkins.

Covariate	Mean	80% CI
Transport death	0.35	-0.51, 1.19
Outweek*	-0.75	-1.36, -0.13
Site		
Gordon	-0.94	-2.78, 0.83
Riverbend	-1.18	-2.96, 0.57

process model can be used to estimate prespawn mortality as defined by any of these criteria, or it could be modified to separately estimate mortality that occurs prior to and after the commencement of the spawning season.

Variability in the prevalence of prespawn mortality could be due to several factors, and we were able to explain some of this variation. The outweek effect suggested that prespawn mortality was lower for groups that were outplanted later in a given year, although this effect was largely driven by the high mortalities that occurred in 2013. Keefer et al. (2010) also reported lower prespawn mortality among groups of fish that were outplanted later in the season. One potential explanation is that fish outplanted later had higher fitness, perhaps because they entered the river system later and therefore had a shorter period of exposure to pathogens and thermal stress. Furthermore, fish in poorer condition might have already died during migration or while holding downstream of Foster Dam, meaning that fish available for outplanting later in the year were thus more likely to survive. We cannot compare these two hypotheses here because we do not have information with which to track individual fish from the time of freshwater entry and we do not know whether fish that were outplanted later spent more or less time in the river system. A third hypothesis is that handling and transport stress led to immunosuppression and increased infection (Schreck 1996; Mesa et al. 2000), which had greater time to develop and lead to prespawn mortality in earlier outplants because they had to survive longer before spawning commenced. Information to further explore these hypotheses is not available, but future studies could be designed to determine their plausibility. Interestingly, two recent studies in the South Santiam River and the nearby McKenzie River determined that in some years, individuals that were outplanted earlier produced an equivalent or greater number of juveniles and returning adults than fish that were outplanted later (Evans et al. 2015; Sard et al. 2015). The seeming contradiction between higher prespawn mortality and greater reproductive success in early outplants may be due to a lack of prespawn mortality in fish that were outplanted during those two studies. Based on data from an earlier carcass survey for 2007–2008 (C. S., unpublished data) and data used in the current study for 2009–2010, prespawn mortality was likely low (<8%) during the years of adult outplanting analyzed in the two studies. The single exception was 2011, when prespawn mortality was moderately higher, but Sard et al. (2015) did not identify an effect of outplant timing in 2011. Future integrated research that includes genetic analyses of offspring across a range of prespawn mortality events could enhance our understanding of the link between outplant timing, spawning success, and offspring production.

We expected that a death during transport would be associated with higher prespawn mortality in the corresponding outplant group, as previous studies have shown that transported fish often have common fates due to shared exposure

to stressors and pathogens (Specker and Schreck 1980; Schreck et al. 1989). However, the current analysis did not support this hypothesis, perhaps because we could not accurately link the occurrence of a transport death to outplanted fish. An equally plausible alternative explanation is that transport mortality did not have a latent effect on outplanted fish and that prespawn mortality is due to separate mechanisms. The current evidence suggests that prespawn mortality rates did not differ among outplanting locations, but the correlation between outplant site and outweek in our data set made this difficult to determine. Similarly, Evans et al. (2015) conducted genetic parentage analysis and determined that there was no effect of release location on the number of returning adults produced by Chinook Salmon outplanted in the South Santiam River during 2009.

Prespawn mortality was estimated to affect 73.5% of outplanted fish in 2013, which was substantially higher than in the other four study years. Variability in prespawn mortality among years within a single population is expected but may be driven by differences among years (Hinch et al. 2012). However, very high flows after a storm event in late September 2013 during the peak of the spawning season likely reduced the number of spawned fish recoveries, resulting in overestimation of the prespawn mortality rate. In most years, a large percentage of recoveries occurred in October, and few prespawn mortalities were observed among those fish. For example, 96 (47.8%) of 201 carcass recoveries in 2009 were found in October; only 5 of the 96 carcasses were prespawn mortalities, whereas 31 carcasses were fish that had spawned (the remaining 60 recovered carcasses were either males or had unknown fates due to damage or decay). In contrast, only 6 (5.5%) of 109 carcass recoveries in 2013 occurred in October, and none were prespawn mortalities, suggesting that λ was greatly reduced due to high flows. Thus, if carcass recovery had not been hampered by high flows in late September and October 2013, a greater number of carcasses from successful spawners would have been found, resulting in a lower estimated prespawn mortality rate for 2013. Although it is likely based on available data that the 2013 pre-spawn mortality rate was much higher than that in other years, the actual rate was probably lower than estimated here. The potential for biased estimates in 2013 is a good reminder that estimates from any model reflect upon the sampling data and that the validity of model assumptions should always be investigated prior to acceptance of the estimates.

We estimated a lower level of prespawn mortality than the 48% average reported by Keefer et al. (2010) for radio-tagged fish that were outplanted in the Middle Fork Willamette River, Oregon. Transport mortality was much more prevalent in outplanting operations at Dexter Dam in the Middle Fork Willamette River than at Foster Dam and was associated with longer times spent waiting at the Dexter Dam fish trap and related exposure to thermal stress, longer handling times, and transportation at higher densities (M.E.C., unpublished

data). This suggests that differences in prespawn mortality among populations could be due at least partially to greater stress during trapping and outplanting; however, other factors may include differences in migratory route and fitness level. Keefer et al. (2010) may have observed higher rates due to the potential adverse effects of radio-tagging on survival because those authors were limited to using fish that were in relatively poor condition. Although we expect that prespawn mortality differences among Willamette River basin populations and among years are at least partly related to altered river conditions and outplanting operations, high variability in egg retention and pre-spawn mortality is common (Hinch et al. 2012) and may be unrelated to any of these factors.

Even the relatively low prespawn mortality rates estimated during most years in this study could adversely affect efforts to establish self-sustaining Chinook Salmon populations upstream of barriers in the South Santiam River basin. Our results indicate that the outplanting of fish later in the season could result in lower prespawn mortality, which could lead to increased production of juvenile salmonids and larger returns in the future. Such a finding seems to suggest that holding adult fish under controlled conditions and outplanting them later in the season may constitute an effective strategy (Benda et al. 2015). The potential effect of outplanting timing in our study should be accepted with caution, however, because fish were not randomly assigned to outplant dates as would be required to more robustly test for this effect. In addition, other recent studies have reported that earlier outplants may exhibit greater reproductive success (Evans et al. 2015; Sard et al. 2015). The practice of holding adults and conducting outplanting operations may select for fish that are ill equipped to survive under natural riverine conditions, which could undermine the establishment of a locally adapted, self-sustaining population. It is also important to consider other potential bottlenecks that may limit recovery efforts (Anderson et al. 2014). In the South Santiam River, one additional bottleneck is the poor downstream passage for juveniles, resulting in delayed out-migration and reduced survival (Keefer et al. 2013). Despite poor passage, Evans et al. (2015) found that outplanted adults produced sufficient numbers of offspring to achieve or exceed population replacement, which illustrates the potential benefits for population reintroduction.

Tag loss was a potential source of bias in our study, as 40.6% of carcasses that were recovered during the study period no longer had tags and were not included in analyses because they could not be identified. Estimated values of λ must therefore be viewed as underestimates because we were implicitly estimating the probability of finding a carcass given that it still had a tag. Tag loss could have biased our estimates of prespawn mortality if the tag loss rate differed between fish of different fates, but we have no reason to believe that this was the case. The naive estimate of prespawn mortality based solely on recovered individuals with tags and known fates was

slightly lower (mean = 15.4%; $N = 207$) than that for all individuals of known fate with or without tags (mean = 21.5%; $N = 402$). However, these point estimates are not widely different, and it does not seem likely that prespawn fish would have greater rates of tag loss given that all individuals are in a similar environment and experience similar processes prior to recovery. The outweek effect estimates could be biased if tag loss was not constant across weeks in each year, but we have no information to determine whether this is the case. Different tagging technologies that have lower tag loss could help to reduce potential biases, and ODFW switched to using PIT tags for all individuals that were outplanted in the South Santiam River during 2014 (C. S., personal observation).

Our hidden-process model provides a useful framework for estimating the fate of recovered individuals when fates cannot always be determined, which is common to carcass surveys and many other mark-recovery applications. This modeling framework is convenient for estimating pre-spawn mortality via carcass survey data for a few reasons. First, outplanting operations are often reasonably directed toward minimizing the time that fish wait in a trap (i.e., to minimize stress) and are not focused on statistical estimation. This can lead to highly unbalanced data that are best addressed in a hierarchical framework wherein estimates for individual outplant groups or years with very limited information could “borrow” information from all other outplant groups in the year as well as across all years. Second, we were able to partition the variation among years and among outplant groups, with covariates introduced at the appropriate levels of the model. The model could be extended to estimate the probability of prespawn mortality for individuals based on covariates or to allow survival or λ to vary throughout the season. Numerous efforts are being made to re-establish self-sustaining salmon populations, and carcass surveys are commonly used to evaluate spawning success; the model presented here can be used to provide unbiased estimates that account for unknown fates and imperfect detection.

ACKNOWLEDGMENTS

Staff of the ODFW collected and provided access to outplanting, transport mortality, and spawning survey data. Funding for this study was provided by the U.S. Army Corps of Engineers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The Oregon Cooperative Fish and Wildlife Research Unit is jointly sponsored by the U.S. Geological Survey, U.S. Fish and Wildlife Service, ODFW, Oregon State University, and Wildlife Management Institute. We thank Marc Johnson, two anonymous reviewers, and the editorial staff for helpful comments on previous versions of this manuscript.

REFERENCES

- Al-Chokhachy, R., S. Moran, and P. A. McHugh. 2015. Consequences of actively managing a small Bull Trout population in a fragmented landscape. *Transactions of the American Fisheries Society* 144:515–531.
- Anderson, J., G. Pess, R. Carmichael, M. Ford, T. Cooney, C. Baldwin, and M. McClure. 2014. Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management* 34:72–93.
- Baumsteiger, J., D. Hand, D. Olson, R. Spateholts, G. FitzGerald, and W. Arden. 2008. Use of parentage analysis to determine reproductive success of hatchery-origin spring Chinook Salmon outplanted into Shitike Creek, Oregon. *North American Journal of Fisheries Management* 28:1472–1485.
- Benda, S. E., M. L. Kent, C. C. Caudill, C. B. Schreck, and G. P. Naughton. 2015. Cool, pathogen free refuge lowers pathogen associated prespawn mortality of Willamette River Chinook Salmon (*Oncorhynchus tshawytscha*). *Transactions of the American Fisheries Society* 144:1159–1172.
- Bradford, M. J., J. Lovy, D. A. Patterson, D. J. Speare, W. R. Bennett, A. R. Stobbart, and C. P. Tovey. 2010. *Parvicapsula minibicornis* infections in gill and kidney and the premature mortality of adult Sockeye Salmon (*Oncorhynchus nerka*) from Cultus Lake, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 67:673–683.
- CDFG (California Department of Fish and Game). 2004. September 2002 Klamath River fish-kill: final analysis of contributing factors and impacts. CDFG, Sacramento.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of Coho Salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1347–1355.
- Cederholm, C. J., and N. P. Peterson. 1985. The retention of Coho Salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1222–1225.
- DeHaan, P. W., and S. R. Bernall. 2013. Spawning success of Bull Trout transported above main-stem Clark Fork River dams in Idaho and Montana. *North American Journal of Fisheries Management* 33:1269–1282.
- Evans, M. L., M. A. Johnson, D. Jacobson, J. Wang, M. Hogansen, and K. G. O'Malley. 2015. Evaluating a multi-generational reintroduction program for threatened salmon using genetic parentage analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1–9.
- Gimenez, O., J. Lebreton, and J. Gaillard. 2012. Estimating demographic parameters using hidden process dynamic models. *Theoretical Population Biology* 82:307–316.
- Hinch, S. G., S. J. Cooke, A. P. Farrell, K. M. Miller, M. Lapointe, and D. A. Patterson. 2012. Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River Sockeye Salmon *Oncorhynchus nerka*. *Journal of Fish Biology* 81:576–599.
- Hruska, K. A., S. G. Hinch, D. A. Patterson, and M. C. Healey. 2011. Egg retention in relation to arrival timing and reproductive longevity in female Sockeye Salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 68:250–259.
- Johnson, M. A., and T. A. Friesen. 2010. Spring Chinook Salmon hatcheries in the Willamette basin: existing data, discernible patterns and information gaps. Final Report of the Oregon Department of Fish and Wildlife, Corvallis to U.S. Army Corps of Engineers, Portland District, Task Order NWPPM-09-FH-05, Portland, Oregon.
- Keefer, M., G. Taylor, D. Garletts, G. Gauthier, T. Pierce, and C. Caudill. 2010. Prespawn mortality in adult spring Chinook Salmon outplanted above barrier dams. *Ecology of Freshwater Fish* 19:361–372.
- Keefer, M., G. Taylor, D. Garletts, C. Helms, G. Gauthier, T. Pierce, and C. Caudill. 2013. High-head dams affect downstream passage timing and survival in the Middle Fork Willamette River. *River Research and Applications* 29:483–492.
- Keefer, M. L., C. A. Peery, and M. J. Heinrich. 2008. Temperature-mediated en route migration mortality and travel rates of endangered Snake River Sockeye Salmon. *Ecology of Freshwater Fish* 17:136–145.
- Kery, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts.
- King, K., C. Grue, J. Grassley, and J. Hearsey. 2013. Pesticides in urban streams and prespawn mortality of Pacific Coho Salmon. *Archives of Environmental Contamination and Toxicology* 65:546–554.
- Kocan, R., P. Hershberger, and J. Winton. 2004. Ichthyophoniasis: an emerging disease of Chinook Salmon in the Yukon River. *Journal of Aquatic Animal Health* 16:58–72.
- Macdonald, J. S., D. A. Patterson, M. J. Hague, and I. C. Guthrie. 2010. Modeling the influence of environmental factors on spawning migration mortality for Sockeye Salmon fisheries management in the Fraser River, British Columbia. *Transactions of the American Fisheries Society* 139:768–782.
- MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutierrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.
- Major, R. L., and J. L. Mighell. 1969. Egg-to-migrant survival of spring Chinook Salmon (*Oncorhynchus tshawytscha*) in the Yakima River, Washington. U.S. National Marine Fisheries Service Fishery Bulletin 67:347–359.
- Mesa, M. G., A. G. Maule, and C. B. Schreck. 2000. Interaction of infection with *Renibacterium salmoninarum* and physical stress in juvenile Chinook Salmon: physiological responses, disease progression, and mortality. *Transactions of the American Fisheries Society* 129:158–173.
- Naughton, G., C. Caudill, and M. Keefer. 2005. Late-season mortality during migration of radio-tagged adult Sockeye Salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 62:30–47.
- Newman, K., S. Buckland, S. Lindley, L. Thomas, and C. Fernández. 2006. Hidden process models for animal population dynamics. *Ecological Applications* 16:74–86.
- NMFS (National Marine Fisheries Service). 1999a. Endangered and threatened species; threatened status for three Chinook Salmon evolutionarily significant units (ESUs) in Washington and Oregon, and endangered status for one Chinook Salmon ESU in Washington. *Federal Register* 64:56(24 March 1999):14308–14328.
- NMFS (National Marine Fisheries Service). 1999b. Endangered and threatened species; threatened status for two ESUs of steelhead in Washington and Oregon. *Federal Register* 64:57(25 March 1999):14517–14528.
- ODFW (Oregon Department of Fish and Wildlife) and NMFS (National Marine Fisheries Service). 2011. Upper Willamette River conservation and recovery plan for Chinook Salmon and steelhead. ODFW, Salem and NMFS, Silver Spring, Maryland.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Available: mcmc-jags.sourceforge.net/. (September 2015).
- Quinn, T., D. Eggers, J. Clark, and H. Rich. 2007. Density, climate, and the processes of prespawning mortality and egg retention in Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 64:574–582.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rand, P., S. Hinch, J. Morrison, M. Foreman, M. MacNutt, J. Macdonald, M. Healey, A. Farrell, and D. Higgs. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River Sockeye Salmon. *Transactions of the American Fisheries Society* 135:655–667.
- Sard, N. M., K. G. O'Malley, D. P. Jacobson, M. J. Hogansen, M. A. Johnson, M. A. Banks, and M. Krkosek. 2015. Factors influencing spawner success in a spring Chinook Salmon (*Oncorhynchus tshawytscha*) reintroduction program. *Canadian Journal of Fisheries and Aquatic Sciences* 72:1390–1397.
- Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85:930–938.

- Scholz, N., M. Myers, S. McCarthy, J. Labenia, J. McIntyre, G. Ylitalo, L. Rhodes, C. Laetz, C. Stehr, B. French, B. McMillan, D. Wilson, L. Reed, K. Lynch, S. Damm, J. Davis, and T. Collier. 2011. Recurrent die-offs of adult Coho Salmon returning to spawn in Puget Sound lowland urban streams. PLOS (Public Library of Science) ONE [online serial] 6:e28013.
- Schreck, C. B. 1996. Immunomodulation: endogenous factors. Pages 311–337 in G. Iwama and T. Nakanishi, editors. The fish immune system: organism, pathogen, and environment fish physiology series. Academic Press, San Diego, California.
- Schreck, C. B., M. F. Solazzi, S. L. Johnson, and T. E. Nickelson. 1989. Transportation stress affects performance of Coho Salmon, *Oncorhynchus kisutch*. Aquaculture 82:15–20.
- Specker, J. L., and C. B. Schreck. 1980. Stress responses to transportation and fitness for marine survival in Coho Salmon (*Oncorhynchus kisutch*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 37:765–769.
- Su, Y., and M. Yajima. 2015. R2jags: using R to run JAGS (R package version 0.5-7). Available: CRAN.R-project.org/package=R2jags. (September 2015).