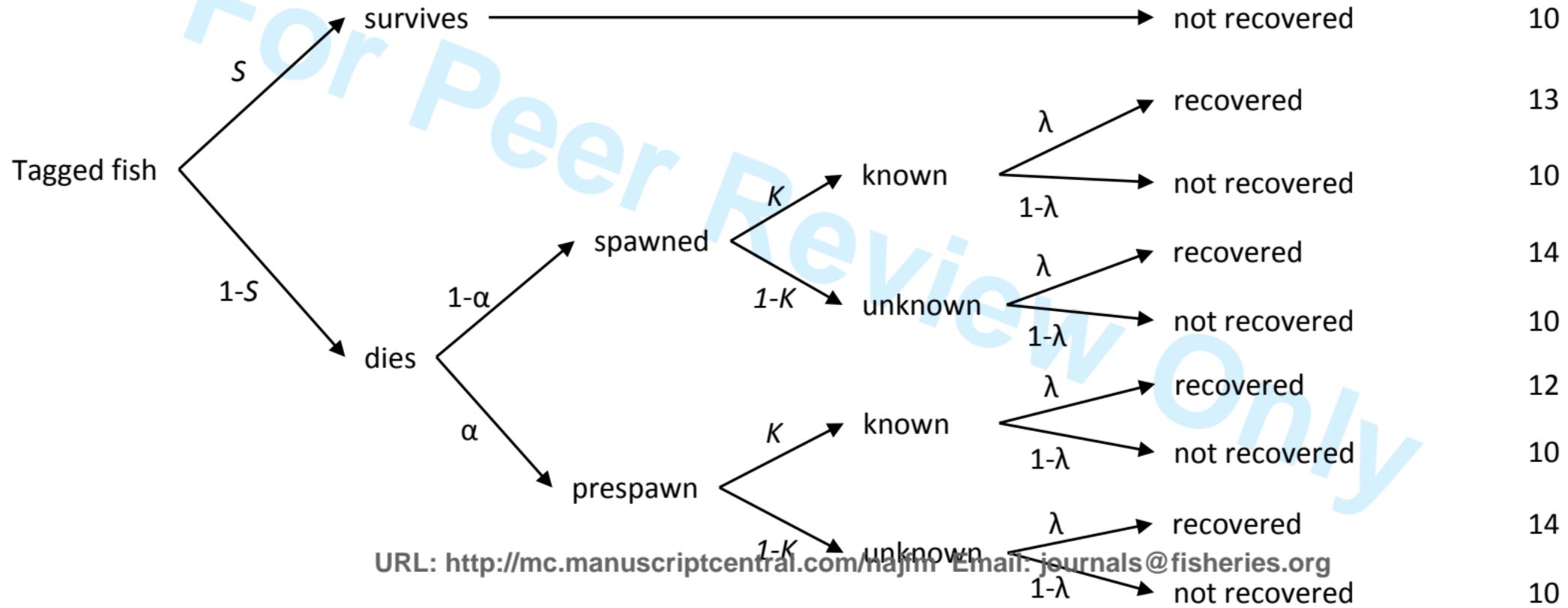


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A hidden-process model for estimating prespawn mortality using carcass survey data

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1 Abstract

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

21 <A>Introduction

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

39 One population restoration and reintroduction effort that is particularly sensitive to
40 prespawn mortality is outplanting, which involves trapping and hauling sexually mature or
41 maturing adults upstream of migration barriers or into habitats where reproduction is limited.
42 Outplanting is increasingly being used for different purposes, including to accelerate
43 recolonization of Chinook Salmon into newly available habitat following barrier removal in

44 Shitike Creek, Oregon (Baumsteiger et al. 2008); to reintroduce Chinook Salmon above high
45 head dams in the Willamette River Basin in Oregon (Keefer et al. 2010); and to allow adult Bull
46 Trout *Salvelinus confluentus* to spawn upstream of barriers (DeHaan and Bernall 2013; Al-
47 Chokhachy et al. 2015). Even moderate levels of prespawn mortality can undermine the
48 effectiveness of outplanting operations because the number of adults outplanted is limited by
49 both the number of adult fish available as well as high costs of associated infrastructure and
50 personnel time. It is also possible that outplanting operations may elevate prespawn mortality
51 through increased stress or disease transmission during holding or transport (Schreck et al. 1989;
52 Mesa et al. 2000). Outplanting can only be successful at restoring self-sustaining populations if
53 enough adults successfully spawn and produce sufficient numbers of offspring that survive
54 through subsequent life stages and return as adults to complete the life cycle (Anderson et al.
55 2014).

56 Accurately estimating prespawn mortality and identifying associated environmental
57 covariates or management practices is important for understanding spawning success and
58 mitigating negative effects if possible. The most direct and widely available source of data for
59 estimating the prevalence of prespawn mortality is collected during carcass surveys on spawning
60 grounds (e.g., Hruska et al. 2011; Scholz et al. 2011), although radiotelemetry tags that report
61 mortality can identify prespawn mortalities occurring prior to spawning season (Keefer et al.
62 2008). In populations of fish that arrive early and hold in spawning areas, fish can die prior to the
63 commencement of spawning season and any carcasses recovered during this time can be
64 classified as prespawn mortalities, regardless of sex or condition (Keefer et al. 2008). In many
65 Pacific salmon populations, fish arriving at spawning areas can commence spawning
66 immediately and only females can be used to determine spawning success. Identifying prespawn

67 mortality after spawning season commences is more difficult and requires the recovery and
68 examination of female carcasses to determine the level of egg retention, where high percentages
69 may signify prespawn mortality. Uncertainties arise in using carcass survey data to estimate
70 prespawn mortality rates due to the use of egg retention to identify prespawn mortality, carcasses
71 with unknown fates, and imperfect detection. The use of egg retention estimates to identify
72 prespawn mortality in carcasses can be uncertain due to poor carcass condition and the selection
73 of a threshold above which fish are classified as prespawn mortalities. The use of a threshold
74 does not recognize that even fish above the threshold may have partially spawned and produced
75 offspring. It is common practice, however, to use a relatively high egg retention threshold such
76 as 50% (Scholz et al. 2011) or 75% (Hruska et al. 2011) to signify prespawn mortality since most
77 successful spawners are assumed to release greater than 90% of eggs under ‘normal’ conditions
78 (e.g., Major and Mighell 1969; Quinn et al. 2007). If some of these fish partially spawned and
79 successfully produced offspring, prespawn mortality and its related effects on the population
80 would be overestimated. Carcasses with unknown fates are common because spawning success
81 cannot be identified in males and many carcasses may be in poor condition due to decay or
82 scavenger damage, making determination of sex or spawning success through egg retention
83 impossible. In addition, carcass recovery at all times of the year is limited by imperfect detection
84 due to practical limits on survey effort or conditions such as high flows that limit recovery. A
85 model that accounts for imperfect detection and unknown spawning status can help make use of
86 all available information collected during carcass surveys and provide unbiased estimates of
87 prespawn mortality.

88 Given the potential for prespawn mortality to adversely affect populations, conservation
89 and recovery efforts such as outplanting can benefit from unbiased estimates of prespawn

90 mortality and an understanding of its relationships with environmental factors or management
91 practices. Since individuals handled during outplanting can be easily marked and later identified,
92 the estimation of prespawn mortality from carcass survey data can be paired with an appropriate
93 mark-recovery model to facilitate estimation. We describe the development of a hidden process
94 mark-recovery model that can be used to estimate prespawn mortality from carcass survey data
95 with marked individuals, while accounting for imperfect detection and unknown spawning
96 success. Hidden process models account for both variation in the unobserved (hidden) ecological
97 process and error due to observation methods, leading to more robust estimates of population
98 dynamics (Newman et al. 2006; Gimenez et al. 2012) or similar ecological processes. We then
99 use this model to estimate prespawn mortality of spring-run Chinook Salmon outplanted above
100 Foster Dam on the South Santiam River, Oregon, U.S.A. and to understand the effects of
101 outplanting operations on prespawn mortality.

102 <A> Methods

103 Model Development

104 We developed a hidden process mark-recovery model that enables the estimation of the
105 percentage of prespawn mortalities, while accounting for unknown fates and imperfect detection.
106 Our model was similar to a model developed by Schaub and Pradel (2004) to estimate the
107 percentage of White Storks *Ciconia ciconia* that died from power line collisions. Schaub and
108 Pradel (2004) used the more conventional maximum likelihood estimation based on a
109 summarization of the mark recovery data, which did not allow for estimation of group or
110 individual effects. We modified this model to enable us to separately estimate two known
111 spawning states (successfully spawned or prespawn mortality) from unknown states, and to
112 enable us to use all available information from individual fish mark-recovery histories.

113 The unobserved process describing the survival and fate of outplanted fish was modeled
114 with five states: 1) alive, 2) died within prior week without spawning (prespawn mortality), 3)
115 died within prior week after spawning (spawned), 4) died within prior week but spawning status
116 was unknown (unknown), and 5) dead for more than one week and unavailable for recovery
117 (dead). Fish that were either alive (state 1) or dead (state 5) were not available for recovery. We
118 assumed that salmon carcasses were unavailable for recovery after more than one week, since
119 carcasses can be quickly damaged due to scavenging or washed downstream (Cederholm and
120 Peterson 1985). While it is possible that carcasses could be recovered later than one week after
121 death (Cederholm et al. 1989), we made this simplifying assumption because we had no
122 additional information on the transition between death and recovery. If the assumption is
123 violated, estimates of weekly detection probability and survival could be biased but estimates of
124 prespawn mortality would be largely unaffected. Thus in the unobserved process model,
125 individuals that died at time t but were not recovered transitioned to state 5 (dead) and could no
126 longer be observed.

127 The observation process model had four states: unobserved (alive or unrecovered),
128 recovered prespawn mortality, recovered spawned, and recovered unknown. A transition
129 probability matrix is a convenient way to describe the model in terms of the probability of
130 transition from the current state at time t to another other state at time $t + 1$ (MacKenzie et al.
131 2009; Schaub and Pradel 2004). The transition probability matrix ϕ and associated vector of
132 recovery probabilities P are:

$$\begin{matrix} & \left[\begin{array}{ccccc} S & (1-S)(\alpha)(K) & (1-S)(1-\alpha)(K) & (1-S)(1-K) & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{array} \right] \left(\begin{array}{c} 0 \\ \lambda \\ \lambda \\ \lambda \\ 0 \end{array} \right), \quad \text{Eq. 1} \end{matrix}$$

134 where S is survival probability, α is the probability of prespawn mortality, K is the probability of
135 knowing the spawning success of a recovered fish, and λ is detection probability. Note that we
136 include only a single λ shared by all fates because preliminary simulations showed that the
137 model is not identifiable when detection probabilities are estimated separately for each fate
138 (J.T.D., unpublished data). It is possible that additional information or an alternative formulation
139 could be used to enable the estimation of multiple detection probabilities, but simulations would
140 be needed to ensure that all parameters can be identified.

141 These transitions are summarized using a fate diagram for an outplanted individual fish in
142 Figure 1. Consider an individual that is alive at time t (row 1 in Eq. 1). This individual can either
143 remain alive with probability S , die without spawning with probability $(1-S)(\alpha)(K)$, die after
144 spawning with probability $(1-S)(1-\alpha)(K)$, or become an unknown with probability $(1-S)(1-K)$ at
145 time $t + 1$. Note that the probability of becoming an unknown is actually $(1-S)(1-K)(\alpha+(1-\alpha))$
146 because fish of unknown fates actually spawned or did not prior to dying, but $(\alpha+(1-\alpha))$ is equal
147 to 1 and is not shown in our transition matrix. A fish cannot transition from alive to dead and
148 unobservable (state 5) within one time step because carcasses are assumed available for recovery
149 for one week in our model, which is reflected by the 0 probability in the last column of row 1.
150 The last four rows are deterministic in that all individuals that are recently dead (states 2 – 4) or
151 dead (state 5) either transition to or remain dead (state 5) at time $t + 1$.

152 Outplanting Chinook Salmon as a Case Study

153 This model described above is a relatively general form that can be used to estimate
154 spawning success from carcass survey data with tagged fish, such as in outplanting operations of
155 Pacific Salmon species. We illustrate its application in the estimation of prespawn mortality of
156 outplanted Chinook Salmon in the South Santiam River, Oregon.

157 *Study region.*—

158 The South Santiam River is a major tributary to the Willamette River, with a 2,694 km²
159 watershed with elevations ranging from 67 m in the Willamette Valley to 1,744 m on the western
160 slope of the Cascade Mountains (Figure 2). Riverine habitat ranges from steep and confined
161 channels in forested, high elevation areas to low gradient reaches with broader floodplains
162 surrounded by farming and developed land cover downstream. Foster Dam is an impassable
163 barrier located at river kilometer 62 that blocks access to historic spawning locations for spring-
164 run Chinook Salmon, as well as winter-run steelhead *O. mykiss*. Chinook Salmon in the Upper
165 Willamette River, including the South Santiam population, were listed as threatened under the U.
166 S. Endangered Species Act in 1999 partially due to very limited natural reproduction (NMFS
167 1999a-b; ODFW and NMFS 2011). The loss of access to historic spawning habitat due to dams
168 was a major contributor to population declines, but habitat degradation and overharvest also
169 contributed (ODFW and NMFS 2011). Managers initially began outplanting adults above dams
170 to provide a prey base for threatened Bull Trout, but the establishment of naturally reproducing
171 populations became a primary goal after initial outplanting resulted in natural production
172 (Johnson and Friesen 2010; ODFW and NMFS 2011). Outplanting operations have included the
173 South Santiam River above Foster Dam, but also other sites in the Willamette River basin,
174 including the North Santiam River above Detroit Dam, the McKenzie River above Cougar and
175 Blue River Dams, and the Middle Fork Willamette River above Lookout Point and Fall Creek
176 Dams. Most habitat upstream of Foster Dam accessible to outplanted salmon is relatively steep
177 with a confined channel surrounded by forested land at moderate elevations.

178 *Outplanting and recovery operations.*—

179 Spring Chinook Salmon arrived at Foster Dam and entered the fish trap from May
180 through September during the 2009-2013 study period. Trapping and outplanting generally
181 occurred on a weekly basis, but varied to match the number of returning fish. In some weeks no
182 fish were outplanted, while fish were outplanted as often as 3-4 times in one week during the
183 peak return period of each year. Individuals with intact adipose fins were assumed to be wild fish
184 and were outplanted above Foster Dam, whereas fish with clipped adipose fins were of known
185 hatchery origin and were not outplanted during the study period. Some hatchery origin fish were
186 unmarked due to healed adipose fins and were thus outplanted as wild fish. Nearly all outplanted
187 fish received a single floy tag directly behind the dorsal fin above the lateral line with an
188 individual identification number. We only used fish that received and retained tags until found as
189 carcasses to estimate prespawn mortality.

190 Following tagging, fish were transferred to aerated tanks on trucks, transported upstream,
191 and outplanted at one of three locations shown in Figure 2. The location was selected by Oregon
192 Department of Fish and Wildlife (ODFW) staff to be most suitable for releasing adult salmon
193 based on water levels, water temperature, and season. The number of dead or moribund fish, if
194 any, was recorded when fish were released from the truck as transport mortalities, but these were
195 not considered prespawn mortalities in our analysis. We grouped fish that were outplanted to the
196 same site on the same date (outplant group) to identify groups that experienced a similar
197 trapping, hauling and outplanting experience, including the occurrence of transport mortality.
198 Ideally, an outplant group would only include individuals that were trapped, transported, and
199 outplanted together in the same truck, but the transport event identifier was not linked to the
200 outplanting and recapture dataset.

201 Carcass surveys by ODFW staff and volunteers began after the first group of fish was
202 outplanted each year, and spanned from the head of the reservoir to a natural barrier waterfall at
203 river kilometer 99.0. The location and length of stream surveyed varied among daily surveys, but
204 the entire length of the South Santiam River mainstem available to spawning fish was surveyed
205 on a weekly basis. All recovered carcasses were examined for floy tags and were identified as
206 one of the following: prespawn mortality females (>50% of eggs remaining), successfully
207 spawned females (<50% of eggs remaining), males, and unknown (too much damage or decay to
208 be identifiable). The 50% threshold was used because survey data only recorded if egg retention
209 was below or above this value in most years. Based on 2013 surveys when egg retention was
210 estimated in quartiles, most fish classified as prespawn mortalities (43 of 47) had 75-100% of
211 eggs remaining. This suggests that most prespawn mortalities in our study either did not spawn
212 or released less than 25% of eggs, and that the use of a 50% threshold did not likely affect
213 results. The recovery location of each carcass also was recorded as belonging to one of 9
214 mainstem survey reaches, which were delineated by tributaries or landmarks and ranged in size
215 from 2.5 – 7.5 km. Recovered carcasses were chopped to ensure that fish would not be recorded
216 during subsequent surveys.

217 *Model implementation.*—

218 We used the general form of the hidden process model presented above to estimate the
219 fates of Chinook Salmon outplanted in groups. The ecological and observation processes were
220 modeled at a weekly time step, which provided sufficient temporal resolution to depict the
221 underlying process and corresponded to the timing of salmon carcass surveys. We classified all
222 fish that died prior to week 35 of each year (beginning of September) as prespawn mortalities
223 because Chinook Salmon do not normally spawn prior to September in the South Santiam River.

224 The unknown state included carcasses that were damaged or decayed beyond recognition, as well
225 as all males that died after the spawning season began, since it was impossible to determine from
226 carcass surveys if males had successfully spawned.

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

233 We modeled survival (S_y), knowing spawning status (K_y), and detection (λ_y) probabilities
234 as constant within a year, where each annual estimate was independent from other years. We
235 recognize that these parameters could be modeled as random deviations from normal
236 distributions with interannual means and standard deviations, but did not pursue this approach
237 because it greatly increased computational time and did not improve inference in preliminary
238 comparisons (J.T. DeWeber, unpublished data). We constrained survival in the last week of each
239 year to be 0 because it was unlikely that any individuals survived past the end of spawning
240 season in late October.

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

246
$$\text{logit}(\alpha_{gy}) = \mu_0 + b * X_{gy} + \gamma_y + \varepsilon_g, \text{ where } \gamma_y \sim N(0, \sigma_\gamma^\alpha) \text{ and } \varepsilon_g \sim N(0, \sigma_\varepsilon^\alpha) \text{ Eq. 2}$$

247 Without covariates, the model is a two level hierarchical model with annual and group
248 level deviations that stem from normal distributions with a mean of 0 and standard deviations of
249 σ_x^α and σ_y^α , respectively. When covariates are included, the deviations ε_g allow for additional
250 variation in outplant groups, respectively, that is not accounted for by covariate effects.

251 *Potential Covariates.*—

252 We developed a set of covariates that may influence the prespawn mortality probability
253 of fish in outplant groups. Covariates included the week of the year during which a group was
254 outplanted (outweek), whether a death occurred during transport for a given outplant group
255 (death), and the outplant location (site). Outweek ranged from 19 to 43, with an average of 28.9
256 and standard deviation of 5.3. The prevalence of a transport death was 26%, and the three
257 outplant locations shown in Figure 2 were the three levels of the site covariate. We expected
258 outweek to have a negative effect because other studies have found that fish outplanted later in
259 the season had lower prespawn mortality rates (Keefer et al. 2010). A transport death was
260 expected to be associated with increased prespawn mortality probability because all fish in the
261 transport vessel could have been influenced by the stressor or pathogen causing the mortality,
262 which could result in latent mortality in the outplanted fish that survived transport (Schreck et al.
263 1989). We included outplant location because a closely related analysis found a significant effect
264 on transport mortality (M. Colvin, unpublished data) and there are immediate management
265 implications that would stem from higher prespawn mortality at a given site. The death covariate
266 was uncertain because outplant groups included all fish outplanted to a site on the same day, and
267 two to three transport groups were included in one outplant group on 19 dates. For outplant
268 groups that included multiple transport groups, we recorded a death if it occurred during

269 transport of any fish on that site and day. All correlation coefficients among outplant group
270 covariates were less than ± 0.5 .

271 The full model was modified from the generic model shown in Eq. 2 to include the
272 effects $b_{outweek}$, b_{death} , b_{gordon} and $b_{riverbend}$ of the covariates outweek (O), death (D) and indicator
273 variables for the sites Gordon (G) and Riverbend (R):

274
$$\text{logit}(a_{gy}) = \mu_0 + b_{outweek} * O_{gy} + b_{death} * D + b_{gordon} * G + b_{riverbend} * R + \gamma_y + \varepsilon_g,$$

275 where $\gamma_y \sim N(0, \sigma_y^\alpha)$ and $\varepsilon_g \sim N(0, \sigma_g^\alpha)$ Eq. 3

276 We used forward stepwise selection to identify covariates that were important predictors
277 of prespawn mortality. We first began by fitting a null model that did not include any covariates
278 of prespawn mortality. We then fit three models with one covariate each to determine if covariate
279 effects were supported by the data. If the 80% credible intervals of a given covariate effect did
280 not include 0, that covariate was selected for inclusion in the model. We recognize that 80% is
281 not conservative and may result in the inclusion of spurious predictors in our results, but we
282 think that this is a reasonable level of support given the high amount of variation in our dataset.
283 Since the choice of this value is ultimately subjective, we also report the credible intervals plus
284 the percentage of posterior distributions that are below (above) 0 and suggest a negative
285 (positive) effect for any supported covariate effects. If two or more covariates were supported,
286 we fit models that included all supported covariates plus two way interactions.

287 All models were fit in JAGS software (Plummer 2003) implemented in the R2Jags
288 package (Su and Yajima 2015) of the R Statistical environment (R Core Team 2015). The model
289 code is available upon request from J.T.D. All model priors were uninformative, uniform
290 distributions ranging from 0 and 1. We used three chains and fit models for 500,000 iterations,
291 discarding the first 50,000. Due to high autocorrelation, we kept every 50th draw for a total of

292 27,000 posterior samples. We analyzed trace plots and density plots of posterior distributions,
293 and considered models to be converged when mixing was thorough and the Gelman-Rubin
294 diagnostic was less than or equal to 1.05 for all parameters. The estimation of parameters in this
295 model is not trivial and convergence for models described here with our dataset typically
296 required greater than two weeks running in parallel on three 3.60 gigahertz processors.
297 Computation time can be greatly reduced if prespawn mortality is estimated using a fixed effects
298 structure or if the dataset includes more information (i.e., more recovered prespawn mortalities).

299 *Simulations.*—

300 Since the reliability of our model was unknown, we compared parameter estimates with
301 known values from simulated data to determine the reliability of our model estimates. We
302 simulated outplanting groups of 100 individual fish on 10 occasions for a single year, followed
303 by recapture events on 12 occasions beginning after the first outplant occasion with known
304 values for (S , α_g , K , λ). We simulated datasets to represent situations with relatively low and high
305 values for survival, detection, and knowing spawning status probabilities shown in Table 1. For
306 each of the 6 combinations of survival, detection, and knowing spawning status probabilities, we
307 randomly drew the 10 outplant group prespawn mortality probabilities (α_g) from a uniform
308 distribution between 0 and 1 (Table 1). Survival was set to 0 during the last time interval since
309 Pacific salmon do not survive after spawning season. For each combination of known values, we
310 simulated 30 datasets and estimated all parameters using a model with all probabilities as fixed
311 effects, ensuring that estimates converged with Gelman-Rubin diagnostic less than or equal to
312 1.05 for all parameters. We then compared estimates to true values to identify potential biases.

313 <A> Results

314 Simulation Results

315 Estimates of S , K , and λ from the 30 simulations for all combinations of parameters were
316 very precise ($SD < 7\%$) and unbiased, with mean values much less than 1 SD from true values
317 (Table 1). Nearly all mean estimates of α_g from the 30 simulations for most combinations of (S ,
318 K , λ) were within 1 SD of the true values, and the remaining 10 values were within 2 SD. For the
319 combination ($S = 60\%$, $K = 30\%$, $\lambda = 5\%$), 5 mean estimates of α_g were within 2 SD of the true
320 values and the other 5 were 3 SD. This last combination involved both low probabilities of
321 detection and knowing, resulting in the fewest known prespawn mortalities and the least
322 information for estimation. When we ran the same simulation and increased the number of fish
323 outplanted from 100 to 500 fish, there were more known prespawn mortalities in simulated
324 datasets and all mean estimates of α_g were within 1.5 SD of the true values.

325 Case Study Results

326 A total of 4,381 Chinook Salmon adults were outplanted above Foster Dam during the
327 study period, of which 3,453 received floy tags and could be used in model estimation. Fish were
328 outplanted from May through October, and the average number of outplant groups and
329 individuals per year was 20.4 and 691, respectively. A smaller number of outplant groups (10)
330 and individuals (223) were used in 2009 because many outplanted fish did not receive tags, and
331 this smaller sample greatly decreased precision in 2009 estimates as discussed below. The
332 number of individuals per outplant group varied from 1 to 110 and averaged 33.9. The most fish
333 were released at Riverbend (1,667), followed by Gordon (1,186) and Calkins (499), and there
334 were differences in the choice of release site among years and throughout the season. No fish
335 used in analyses were released at Calkins in 2009, for example, and most fish released later in
336 the season in all years were released at Gordon, the furthest upstream site (Figure 2; Table 2).

337 A total of 904 carcasses with and without tags were recovered during the study period;
338 113 and 289 of these were known prespawn and spawned females, respectively. In addition, 28
339 male carcasses were recovered in July and August prior to spawning season (September 1) and
340 were considered prespawn mortalities. The naïve prespawn mortality rate (i.e., uncorrected for
341 imperfect detection) calculated as the percentage of all recovered carcasses that were known
342 prespawn females or early male deaths was 15.6% overall. The annual naïve prespawn mortality
343 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
344 females were considered, the naïve prespawn mortality rate based on all recovered female
345 carcasses was 28% overall and 14.8% in 2009, 5.6% in 2010, 24.8% in 2011, 14.5% in 2012, and
346 65.9% in 2013. The naïve tag retention rate calculated as the percentage of all recovered fish
347 found with tags (530) averaged 59%, and ranged from 50% in 2013 to 71% in 2009. Of the 904
348 carcasses recovered, 530 were recovered with tags and 433 were included in the model as
349 recoveries (the remaining recoveries were not included because the death covariate was not
350 available). Of these 433, there were 54 prespawn and 175 spawned mortalities, while all others
351 had unknown fates (Table 2). Prespawn mortalities were recovered throughout the year, with 32
352 recovered during the typical spawning season in September after week 35.

353 The average prespawn mortality probability from the intercept-only model for the entire
354 study period was 28%, and interannual and among group variation were both high (Table 3;
355 Figure 3). The variation among groups was especially high in 2009 when relatively few fish were
356 outplanted and the years 2010 and 2012 when average annual prespawn mortality probabilities
357 were below 10%. High interannual and among group variability was driven by the estimation of
358 comparatively high prespawn mortality in one year (2013) or in a few outplant groups within a
359 year (Figure 3). Estimates of prespawn mortality for outplant groups were often imprecise

360 (Figure 3), especially in groups with few outplants or recovered carcasses. Average probability
361 of detection ranged from 5% to 17% among years, and detection was substantially lower in 2010
362 than in all other years (Table 3).

363 Model selection suggested that a negative effect of outweek was supported by the data, as
364 80% credible intervals did not overlap 0. The probability of a negative effect was 94% based on
365 the percentage of posterior draws below 0. This effect predicted that the probability of prespawn
366 mortality was higher for groups of fish outplanted earlier in the season (Table 4). The 80%
367 credible intervals for the effects of death and site widely overlapped zero and suggested that
368 these covariates were not supported by the data.

369 <A> Discussion

370 We were able to successfully estimate prespawn mortality probabilities while accounting
371 for imperfect detection and the fact that many carcasses had unknown fates through the use of a
372 hidden process model. Simulations showed that the model provided unbiased estimation of
373 parameters across a reasonable range of parameter values, and were especially precise for the
374 probabilities of survival, detection and knowing spawning status. Estimates of prespawn
375 mortality were imprecise when few prespawn mortalities were available due to low simulated
376 detection and knowing spawning status probabilities, which is not surprising since little
377 information is available in such cases to inform estimates. Situations with few prespawn
378 mortalities can arise from small outplant groups, a low prevalence of prespawn mortality, low
379 detection probability, or a large number of unknowns. In such cases, model estimates of
380 prespawn mortality will likely provide unbiased estimates with low precision. This lack of
381 precision was reflected in the wide credible intervals for many years and outplant groups in our
382 case study application when data was limited (Figure 3).

383 We estimated that prespawn mortality occurred in relatively few fish ($\leq 13\%$) in years
384 2009-2012 and outplant groups, but was highly variable and occurred in an average of 74% of
385 fish in 2013 and 87% in one outplant group. The annual naïve prespawn mortality rate based on
386 the proportion of all carcasses recovered (including those without tags) were also low ($\leq 12\%$) for
387 2009-2012 and was relatively high in 2013 (36%), though lower than model estimates. This
388 comparison shows that model estimates capture general trends in naïve estimates, while also
389 providing reliable uncertainty estimates that account for process and sampling error. Differences
390 in 2013 estimates are likely due to tag loss or differential detection throughout the season, which
391 are important limitations of our dataset that we discuss further below. Comparably high
392 variability was also found in a recent study using radio-tagged outplants in the nearby Middle
393 Fork Willamette River, where prespawn mortality (defined in that study as fish that did not
394 survive past September 1) averaged 48% but varied from 0% to 93% among outplant groups
395 (Keefer et al. 2010). It is important to note that our definition of prespawn mortality includes
396 individuals that may have partially spawned based on the 50% egg retention threshold, and these
397 fish may successfully produce offspring. Because almost all (43 of 47) prespawn mortalities in
398 2013 had greater than 75% egg retention and even moderately high egg retention may be
399 detrimental to reintroduction efforts, we think that it is reasonable to classify these fish as
400 prespawn mortalities.

401 We estimated prespawn mortality based on the percentage of all carcasses recovered
402 (both male and female) because spring-run Chinook Salmon in the South Santiam arrive to
403 spawning areas early, and prespawn mortality may occur prior to and during the spawning
404 season. Because both males and females that die prior to the spawning season are known
405 prespawn mortalities and early death of either sex is of concern to managers, we think that this

406 definition best characterizes prespawn mortality for the studied population. In 2013, for example,
407 8 of 28 known prespawn mortalities used in the modeling dataset were early male deaths that
408 occurred in July and August, and we did not want to exclude these from the analysis. Although
409 prespawn mortality in females may be a primary concern of some managers because numerical
410 production is limited by egg deposition, premature male deaths may have negative consequences
411 through the loss of genetic diversity. Our definition of prespawn mortality as the percentage of
412 all fish is common in estimates of migration mortality (Macdonald et al. 2010) and in studies
413 considering prespawn mortality prior to the spawning season such as Keefer et al. (2010). In
414 contrast, most studies conducted using carcass surveys in spawning areas report prespawn
415 mortality as the percentage of female carcasses (e.g., Quinn et al. 2007; Scholz et al. 2011),
416 presumably because spawning can occur when fish arrive in these populations and males always
417 have unknown spawning success. Since our estimate of prespawn mortality is calculated based
418 on the total number of recovered carcasses, it will be an underestimate when compared to studies
419 that use only the percentage of females. The general hidden process model can be used to
420 estimate prespawn mortality as defined by any of these definitions, or could be modified to
421 separately estimate mortality occurring prior to and after the commencement of spawning
422 season.

423 Variability in the prevalence of prespawn mortality could be due to a number of factors,
424 and we were able to explain some of this variation. The outweek effect suggested that prespawn
425 mortality was lower for groups that were outplanted later in a given year, though this effect was
426 largely driven by high mortalities in 2013. Keefer et al. (2010) also found lower prespawn
427 mortality in groups of fish that were outplanted later in the season. One potential explanation is
428 that fish outplanted later had higher fitness, perhaps because these individuals entered the river

429 system later and therefore spent less time exposed to pathogens and thermal stress. It is also
430 possible that the fish with poorer condition had already died during migration or while holding
431 downstream of the dam, and that fish available for outplanting later in the year were thus more
432 likely to survive. We cannot compare these two hypotheses here because we do not have
433 information tracking individual fish from time of freshwater entry and do not know if fish
434 outplanted later spent more or less time in the river system. A third hypothesis is that handling
435 and transport stress led to immunosuppression and increased infection (Schreck 1996; Mesa et al.
436 2000), which had greater time to develop and lead to prespawn mortality in earlier outplants that
437 had longer to survive until commencement of spawning. We do not have information available to
438 further explore these hypotheses, but future studies could be designed to determine their
439 plausibility. Interestingly, two recent studies in the South Santiam and nearby McKenzie River
440 found that fish outplanted earlier produce as many or more juveniles and returning adults
441 compared to those outplanted later in some years (Evans et al. 2015, Sard et al. 2015). The
442 seeming contradiction between higher prespawn mortality and greater reproductive success in
443 early outplants may be due to a lack of prespawn mortality in fish outplanted during these two
444 studies. Based on data from earlier carcass survey for 2007-2008 (C. Sharpe, unpublished data)
445 and data used in the current study for 2009-2010, prespawn mortality was likely low (<8%)
446 during the years of adult outplanting analyzed in these two studies. The single exception was
447 2011 when prespawn mortality was moderately higher, but Sard et al. (2015) did not identify an
448 effect of outplant timing in 2011. Future integrated research that includes genetic analyses of
449 offspring across a range of prespawn mortality events could help us better understand the link
450 between outplant timing, spawning success, and offspring production.

451 We expected that a death during transport would result in higher prespawn mortality in
452 the group, because previous studies have shown that transported fish often have common fates
453 due to shared exposure to stressors and pathogens (Specker and Schreck 1980; Schreck et al.
454 1989). The current analysis did not support this hypothesis, however, perhaps because we could
455 not accurately link the occurrence of a transport death to outplanted fish. An equally plausible
456 alternative explanation is that transport mortality did not have a latent effect on outplanted fish
457 and that prespawn mortality is due to separate mechanisms. The current evidence suggested that
458 prespawn mortality rates did not differ among outplanting locations, but correlation between
459 outplant site and week of release in our dataset made this difficult to determine. Similarly, Evans
460 et al. (2015) also found that there was no effect of release location on the number of returning
461 adults produced by fish outplanted in the South Santiam in 2009 as determined by genetic
462 parentage analysis.

463 Prespawn mortality was estimated to occur in 73.5% of fish in 2013, which was
464 substantially higher than in the other four years. Variability in prespawn mortality among years
465 within a single population is expected, but may be driven by differences among years (Hinch et
466 al. 2012). However, very high flows following a storm event in late September, 2013 during the
467 peak spawning season likely reduced the number of spawned recoveries, resulting in an
468 overestimated prespawn mortality rate. In most years a large percentage of recoveries occurred in
469 October, and few prespawn mortalities were observed among these fish. For example, 96 of 201
470 (47.8 %) carcasses recoveries in 2009 occurred in October, and only 5 were prespawn mortalities
471 compared with 31 spawned fish (the remaining 60 recovered carcasses were either males or had
472 unknown fates due to damage or decay). In contrast, only 6 of 109 (5.5%) carcass recoveries in
473 2013 occurred in October (none were prespawn mortalities), suggesting that detection probability

474 was greatly reduced due to high flows. Thus, it is likely that a greater number of successfully
475 spawned carcasses would have been found if recovery had not been hampered by high flows in
476 late September and October, resulting in a lower estimated prespawn mortality rate. While it is
477 likely based on available data that the 2013 prespawn mortality rate may was much higher than
478 in other years, it is possible that the actual rate was lower than estimated here. This potential for
479 biased estimates in 2013 is a good reminder that estimates from any model reflect upon sampling
480 data, and that the validity of model assumptions should always be investigated prior to estimates
481 being trusted.

482 We estimated a relatively lower level of prespawn mortality compared to the 48%
483 average of Keefer et al. (2010) for radiotagged fish outplanted in the Middle Fork Willamette.
484 Transport mortality was much more prevalent in outplanting operations at Dexter Dam in the
485 Middle Fork than at Foster Dam, and was associated with longer times spent waiting at the trap
486 and related exposure to thermal stress, longer handling times, and transportation at higher
487 densities at Dexter (M. Colvin, unpublished data). This suggests that prespawn mortality
488 differences among populations could at least partly be due to greater stress during trapping and
489 outplanting of fish, but other factors may include differences in migratory route and fitness
490 levels. It is also possible that Keefer et al. (2010) found higher rates due to the potential adverse
491 effects of radio-tagging on survival because they were limited to the use of relatively poor
492 condition fish for their study. Although we expect that prespawn mortality differences among
493 populations and years in the Willamette River basin are at least partly related to altered river
494 conditions and outplanting operations, high variability in egg retention and prespawn mortality
495 is common (Hinch et al. 2012) and may be unrelated to any of these factors.

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

514 Tag loss was a potential source of bias in our study, as 40.6% of carcasses recovered
515 during the study period no longer had tags and were not included in analyses because they could
516 not be identified. Our estimates of detection probability must thus be viewed as underestimates
517 because we were implicitly estimating the probability of finding a carcass given that it still had a
518 tag. It is possible that tag loss could bias our estimates of prespawn mortality if the tag loss rate

519 differed between fates, but we have no reason to believe that this was the case. The naïve
520 estimate of prespawn mortality based solely on recovered individuals with tags and a known fate
521 was slightly lower (mean = 15.4%, N = 207) than that for all individuals of known fate with or
522 without tags (mean = 21.5%, N = 402). However, these point estimates are not widely different
523 and it does not seem likely that prespawn fish have greater rates of tag loss given that all
524 individuals are in a similar environment and experience similar processes prior to recovery.
525 Similarly, it is possible that the outweek effect estimates could be biased if tag loss was not
526 constant across weeks in each year, but we have no information to know if this is the case.
527 Different tagging technologies that have lower tag loss could help reduce potential biases, and
528 ODFW switched to using passive integrated transponder tags for all individuals outplanted in the
529 South Santiam in 2014 (ODFW; C. Sharpe, personal communication).

530 Our hidden process model provided a useful framework for estimating the fate of
531 recovered individuals when fates cannot always be determined, which is common to carcass
532 surveys and many other mark-recovery applications. This modeling framework is convenient for
533 estimating prespawn mortality using carcass survey data for a few reasons. First, outplanting
534 operations are often reasonably directed towards minimizing the time that fish wait in a trap to
535 minimize stress and not on statistical estimation. This can lead to highly unbalanced data that is
536 best addressed in a hierarchical framework where estimates for individual outplant groups or
537 years with very limited information could ‘borrow’ information from all other outplant groups in
538 the year as well as across all years. Second, we were able to partition variation among years and
539 outplant groups, with covariates introduced at the appropriate levels of the model. The model
540 could be extended to estimate prespawn mortality probability for individuals based on covariates
541 or to allow survival or detection probability to vary throughout the season. Numerous efforts are

542 being made to reestablish self-sustaining salmon populations and carcass surveys are commonly
543 used to evaluate spawning success, and this model can be used to provide unbiased estimates that
544 account for unknown fate and imperfect detection.

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Table 1 – Simulation results are summarized to show the mean estimates for six combination of known true values for the probabilities of survival (S), knowing spawning status (K), detection probability (λ), and prespawning mortality for group y (α_y). For each combination of known values, we estimated parameters based on 30 simulated mark recapture datasets where 100 fish were outplanted in 10 groups of fish with differential α_y . The results are summarized in pairs of sequential columns, where True records the known true value and Mean (SD) records the estimated mean (standard deviation) from the 30 simulations. All values are reported as probabilities.

Parameter	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)

Table 2 – The number of Chinook Salmon outplanted (Outplants) and recovered (Recovered), the number of prespawn carcasses (Prespawn), spawned carcasses (Spawn), and unknown carcasses (Unknown) recovered, the number of transport occasions during which a death occurred (Deaths) and the minimum, maximum and mean of the week of outplanting (Min, Max, and Mean outweek, respectively) are summarized by year and site from the data used in model development. NA means that the value could not be observed because no fish were outplanted at the site in the year specified.

Year	Site	Outplanted	Recovered	Prespawn	Spawn	Unknown	Deaths	Min Outweek	Max Outweek	Mean Outweek
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 outplanted above Foster Dam in the years 2009 – 2013. The parameters $\mu.$ and $\sigma.$ are the interannual mean prespawn mortality and associated variance, respectively, and those for each year y are the probabilities of survival (S_y), having a known spawning status (K_y), detection (λ_y), annual mean prespawn mortality (μ_y), and intrannual variance (σ_y). The mean, standard deviation (SD) and 90% Credible Intervals (C.I.) were summaries of 30,000 draws from the posterior distribution. Note that rate parameters are reported as probabilities, whereas variances are reported on the logit scale.

Parameter	Mean	SD	90% C.I.
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)
$\mu.$	0.28	0.22	(0.03, 0.73)
$\sigma.$	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)

Table 4 –A summary of the estimated effects of potential covariates of within year variability of prespawn mortality in Chinook Salmon outplanted above Foster Dam in the years 2009 – 2013. Death denoted the occurrence of one or more transport mortalities, outweek was the week during which fish were outplanted, and site was the location of outplanting. Asterisks denote covariates that were considered supported because the C.I. did not overlap 0. Note that Site was a categorical variable with Gordon and Riverbend effects estimated as a deviation from prespawn mortality at the third site, Calkins.

Covariate	Mean	80% C.I.
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)

Figure 1 – Fate diagram of an individual tagged fish showing possible state transitions from time t to time $t + 1$. S is the survival probability, α is the probability of successfully spawning, K is the probability of knowing the spawning success, and λ is the probability of recovering a carcass. The Capture history fragment shows the state resulting from each of the possible transitions.

Figure 2 – The South Santiam River (bold river line) and location of Foster Dam and three Chinook Salmon release sites. Inset shows the location of the study reach (bold river) in the South Santiam River Basin (darker grey shading), which is a tributary of the Willamette River Basin (light grey shading) in Oregon, U.S.A.

Figure 3 – Estimates of prespawn mortality are shown for each of the 102 groups of Chinook Salmon in order of date outplanted above Foster Dam from 2009 – 2013. Error bars around each group estimate show 90% credible intervals, with the horizontal lines and dark grey boxes showing annual means and 90% credible intervals for each corresponding year. The bold, dashed line and light grey shaded area shows the mean prespawn mortality for the entire study period and corresponding 90% credible intervals, respectively.

