A TIME- AND STATE-BASED APPROACH TO ESTIMATE WINTER MOVEMENT AND SURVIVAL OF JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH)* IN FRESHWATER CREEK, CALIFORNIA

By

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ABSTRACT

A TIME- AND STATE-BASED APPROACH TO ESTIMATE WINTER MOVEMENT AND SURVIVAL OF JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH)* IN FRESHWATER CREEK, CALIFORNIA

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Accounting for life history diversity and overwinter survival of juvenile Coho Salmon is important to inform restoration and recovery efforts for this threatened species. Multiple seaward migration patterns of Coho Salmon have been identified, including spring fry migrants, fall and winter parr migrants, and spring smolt migrants. Previous studies have indicated that spring smolt migrants have low overwinter survival rates while they are rearing in upstream habitats, suggesting that freshwater overwinter survival may be one factor that limits smolt production. However, previous research did not account for the early emigration of fall and winter parr migrants from the study area, which most likely negatively biased their overwinter survival estimates. Furthermore, previous mark-recapture methods aggregated continuous detection data into course seasonal scales in order to estimate movement and survival. In an effort to refine previous methodology, I developed a multi-state model that allowed for estimation of early emigration and survival rates in space and time by having weekly time-varying occasions paired with discrete spatial states. I conducted extensive simulation trials to validate my use of the multi-state model on an existing 4-year PIT tag dataset in Freshwater Creek, California. Overwinter survival for spring smolt migrants was estimated as a function of average length at time of fall tagging for each year, and ranged from 0.87 to 0.90. Conditional on survival, early emigration estimates ranged from 0.34-0.40 annually. Results from the top model suggested that fish size during initial capture in the fall had a positive effect on overwinter survival of spring smolt migrants, and a negative effect on early emigration rates of fall and winter parr migrants. Additionally, streamflow had a positive effect on early emigration rates of fall and winter parr migrants. These results provide evidence that substantial numbers of smaller juveniles are emigrating early from upstream rearing habitat. This implies that previous estimates of low overwinter survival of Coho salmon could be due to high emigration rates to alternative rearing locations. Given the apparent diversity within the juvenile portion of the life cycle of Coho Salmon, multiple emigration patterns should be considered in the design of future research, monitoring, and restoration projects.

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INTRODUCTION

Life history diversity and overwinter survival of juvenile Coho Salmon (*Oncorhuynchus kisutch*) both have important implications for population production. Recent studies have identified multiple patterns of seaward migration, including spring fry migrants, fall and winter parr migrants, and spring smolt migrants (Miller and Sadro 2003; Koski 2009; Bennett et al. 2011; Roni et al. 2012; Craig et al. 2014; Jones et al. 2014; Rebenack et al. 2015). Previous research on juvenile spring smolt migrants found that they have low survival throughout the winter in upstream rearing habitats, implying that overwinter survival may be a limiting factor in population viability (Brakensiek and Hankin 2007). However, these overwinter survival estimates may have been biased low because they did not account for fall and winter parr migrants. Moreover, accounting for multiple migration patterns can provide insight into how alternative rearing strategies can benefit a population. For example, juvenile Coho may experience increased growth rates in the estuary (Canagaratnam 1959; Craig et al. 2014; Jones et al. 2014; Wallace et al. 2015), which will subsequently influence size at ocean entry and thereby increase marine survival rates (Holtby et al. 1990). Furthermore, early migrants can make significant contributions to adult returns, with research in Oregon documenting 20-35% of the total spawning population migrated to the estuary as sub-yearling juveniles. (Jones et al. 2014). Diversity in migration timing of juveniles may promote resiliency to environmental variation (e.g. drought) by spreading opportunity for population production throughout a dynamic landscape. In order to better plan conservation decisions and restoration actions, further research is needed to better understand mechanisms that influence overwinter survival and downstream migration into estuaries.

Coho Salmon in California have experienced dramatic declines in recent decades. Between 1940 and 1990, adult escapement estimates declined from a peak of 500,000 to less than 5,000 individuals (Brown et al. 1994). There are no recent statewide estimates of abundance, but most of the independent (i.e. self-sustaining) populations within California are at a high risk of extinction (National Marine Fisheries Service 2014). Coho Salmon are currently listed as federally threatened in the Southern Oregon/Northern California Evolutionarily Significant Unit (National Marine Fisheries Service 2014). Declines in the species are due to habitat degradation and loss, hatchery influences, overharvest, and climatic factors (Brown et al. 1994; National Marine Fisheries Service 2014). By elucidating how movement and survival rates of salmon vary in space and time, we can make more informed decisions on how to prioritize restoration that will contribute to the recovery of Coho Salmon.

Quality and quantity of habitat can affect important population parameters such as juvenile survival and production of Coho Salmon smolts. It has been suggested that loss of winter habitat, which are primarily shallow gradient pools, could be limiting smolt production (Mason 1969; Nickelson et al. 1992). Streams in the Pacific Northwest undergo a large range of streamflow conditions with the onset of rains in the fall and winter. Juvenile salmonids, including Coho Salmon, will seek velocity refuge and cover during periods of high streamflow and flood events (Taylor 1988; McMahon and Hartman 1989; Fausch 1993; Vehanen et al. 2000). Velocity refugia, in the form of backwaters and alcoves, provide shelter for juvenile Coho Salmon during high streamflows (Bell et al. 2001), and could be important to conserve energy and avoid displacement. If the quantity, and quality, of winter habitat is limited within a stream, it may be beneficial for individuals to move and seek out new habitat.

Animals make significant migrations for many reasons, and movement patterns can be correlated with biotic and abiotic factors. In a general sense, individuals tend to remain stationary if their biological needs (e.g., food, space, cover) are met, and will move if they are not (Taylor and Taylor 1977). When habitat is limited, competition for resources can facilitate movement. With Coho Salmon, downstream movement of spring fry migrants can be caused by aggressive interactions among conspecifics (Chapman 1962). This displacement of submissive fish could be a causal mechanism in the seaward migration of juveniles (Miller and Sadro 2003; Roni et al. 2012; Jones et al. 2014; Wallace et al. 2015). During periods of higher streamflow, downstream migrants are typically smaller on average (Hartman et al. 1982; Harvey 1987; Bennett et al. 2011; Rebenack et al. 2015). Downstream movement of these smaller fish may be a result of submissive behavior, displacement, or a volitional response to increased streamflow. Previous research has shown that streamflow can have a positive relationship in downstream migration of juvenile salmonids (Hartman et al. 1982; Tschaplinski and Hartman 1983; Giannico 2000), and recent studies have shown a potential correlation between streamflow and early seaward migration of juvenile Coho Salmon (Miller and Sadro 2003; Bennett et al. 2011; Rebenack et al. 2015). Although research has shown that streamflow is correlated with juvenile Coho Salmon movements, the relationship between streamflow and the probability of early emigration into estuarine rearing habitats has not yet been quantified.

One method that has been used to study the factors that affect movement and survival of juvenile Coho Salmon is to track individual movements through space and time using passive integrated transponder tags (PIT) and antennas. Each animal marked with a PIT tag can be identified by decoding the tag with either handheld antennas at a trap site, or stationary antennas in the stream. Previous research using this technology has been used to study some important demographic processes of juvenile salmon, including growth (Quinn and Peterson 1996; Roni et al. 2012), survival (Peterson et al. 1994; Ebersole et al. 2006), and migration rates (Horton et al. 2011; Armstrong et al. 2013). One study using PIT tags and antennas found that winter migration to seasonally available habitat in tributaries can increase survival and growth rates for juvenile Coho Salmon (Ebersole et al. 2006). Other studies have shown increased growth rates for individuals that migrate to estuarine habitat (Jones et al. 2014; Wallace et al. 2015). Although survival rates for the early migrants are unknown, their contributions to adult returns can be significant. Bennett et al. (2015) observed that roughly 75% of juveniles migrated in fall and winter to the ocean, and that adult returns were comprised of 0-77% of these early migrants. This wide range illustrates the importance of life history diversity within a species and could indicate a potential portfolio effect, in which variability in adult returns are buffered by alternate juvenile rearing strategies.

Mark-recapture models are used to estimate important population parameters such as survival and movement from PIT tag data. These models use unique markings of individuals to generate encounter histories over time for a subsample of the population. The frequency of observed encounter histories are the data input for a probabilistic model, which is used to estimate the parameters of interest. Previous research has used the Cormack-Jolly-Seber (CJS) model to estimate survival (Brakensiek and Hankin 2007; Welch et al. 2008; Furey et al. 2016) and emigration rates (Rebenack et al. 2015) of salmonids. However, emigration and apparent survival cannot be estimated concurrently within the same CJS model. Furthermore, previous studies estimating survival and movement of juvenile salmonids typically aggregate continuous detection data into coarse seasonal scales.

In contrast to CJS models, multi-state models can estimate survival and movement from mark-recapture data within the same model framework (Arnason 1973; Brownie et al. 1993; Nichols and Kendall 1995). The multi-state model can also be used to estimate survival rates in space and time by pairing time-varying occasions with discrete spatial states that animals can transition between. Recently, multi-state models have been used to estimate survival and movement of fishes in the southeast of the United States (Norman et al. 2009), as well as salmonids on both the east (Horton et al. 2011), and west coasts (Perry et al. 2010).

By applying a multi-state model to PIT tag data collected over multiple years in a watershed in Northern California, we can estimate how covariates affect survival and emigration rates, and explore how model structure can influence parameter estimates. In this study, I used a novel approach to explore factors that affect juvenile Coho Salmon movement and survival in Freshwater Creek, California. Specifically, the objectives of my study were to: 1) Determine how varying the interval length of continuous data can influence estimates of a multi-state mark-recapture model, and 2) use a multi-state model fit to juvenile Coho Salmon PIT tag data to: a) estimate early emigration rates, b) estimate overwinter survival rates, and c) examine the potential effects of fish size and streamflow on winter movement and survival in Freshwater Creek.

MATERIALS AND METHODS

Study Site

The Freshwater Creek watershed is a small coastal stream network that empties directly into Humboldt Bay in northern California (Figure 1). The watershed has a number of significant tributaries, including: Ryan Creek, Wood Creek, McCready Gulch, Cloney Gulch, Graham Gulch, Little Freshwater Creek, and South Fork Freshwater Creek. Freshwater Creek has a watershed area of roughly 79 km^2. The watershed is mostly forested, and has been extensively logged. Common riparian vegetation found throughout the watershed includes coastal redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and willow species (*Salix spp.*). Four species of salmonids consistently inhabit the basin including Coho Salmon, Chinook Salmon (*O. tshawytscha*), Steelhead Trout (*O. mykiss*), and Cutthroat Trout (*O. clarkii clarkii*). Other native fish commonly found throughout the basin include Pacific Lamprey (*Entosphenus tridentatus*), Western Brook Lamprey (*Lampetra richardsoni*), Threespine Stickleback (*Gasterosteus aculeatus*), Prickly Sculpin *(Cottus asper*), Coastrange Sculpin (*Cottus aleuticus*).

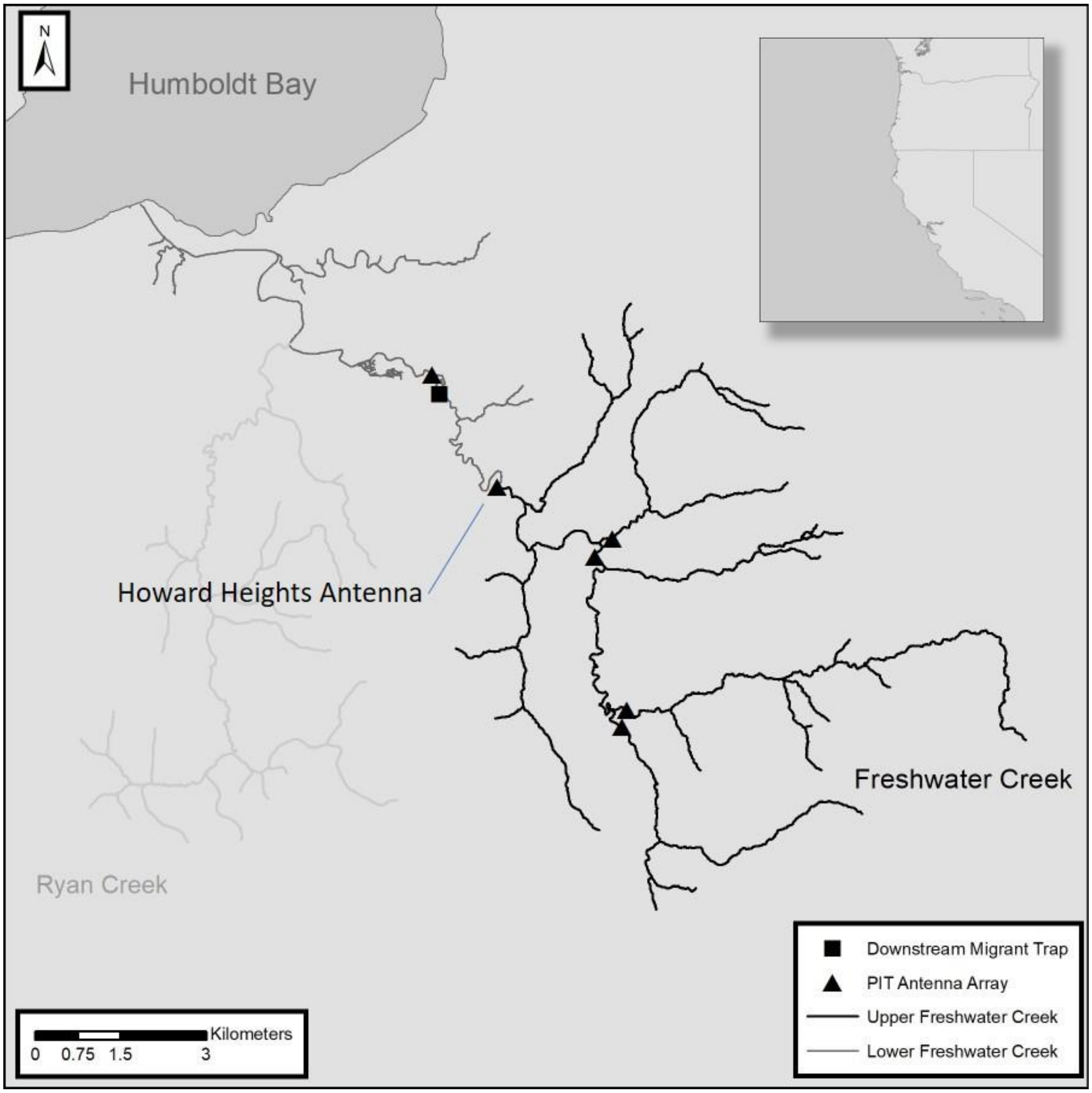

Figure 1. Freshwater Creek watershed including locations of PIT antenna arrays and the downstream migrant trap on Freshwater Creek.

The lower portions of Freshwater Creek converge with Humboldt Bay, forming estuarine habitat. The estuary is subject to a high degree of diurnal, seasonal, and annual variation in streamflow, temperature, salinity and turbidity. At periods of lower streamflow, tidal influence can change the direction of flow, and allow for saltwater intrusion. During winter freshets, brackish water in lower Freshwater Creek will recede into the bay and the creek will have negligible salinities (Wallace et al. 2015).

Humboldt State University operates a juvenile fish trap in Freshwater creek, and currently has 6 independent PIT antenna arrays installed throughout the basin (Figure 1) as part of a life cycle monitoring station. The fish trap is operated from early March to the end of June and catches are processed daily. Four antennas are located in the upper basin, and two are in lower Freshwater Creek. All of the antennas within the Freshwater Creek watershed are run from October through June, and aside from outages caused by large flow events, these antennas are monitoring continuously throughout that time.

Methods

Fish capture and processing

Juvenile Coho were captured and tagged in the fall within Freshwater Creek from 2013 through 2016. All fish capture and handling procedures were approved under Humboldt State University Institutional Animal Care and Use Committee (IACUC 11/12.F.55-A, 15/16.F.79-A). Freshwater Creek was divided into sampling reaches, with discrete upper and lower boundaries, that were consistent inter-annually. Sampling was conducted in reaches that had significant adult spawning either within or above the reach that would sufficiently seed the area sampled with juvenile Coho Salmon. Every year, the initial capture and tagging of fish was completed in October and November during periods of mostly low streamflow conditions. It was important to capture and tag fish before the onset of winter freshets, as increased streamflow could result in permanent emigration from the study area, resulting in a violation of mark-recapture model assumptions (see below). Fish were captured with beach seine nets in pools within reaches. Captured juvenile Coho Salmon were first anesthetized by immersion in a 40 mg/L solution of tricane methanesulfunate (MS-222) buffered to neutral pH. Measurements were then taken for fork length (± 1 mm) and wet weight (± 0.1 g). PIT tags (12 mm Half Duplex (HDX) tags) were then inserted into juveniles that met the National Marine Fisheries Service minimum size requirements, which was 65 mm in 2013/2014 and 70 mm in 2015/2016. Fish were allowed to recover from the effects of anesthesia before being released to the pool in which they were captured. Tagged fish were available for subsequent detection at antenna sites as well as the juvenile fish trap when operation commenced in the spring. All fish sampling in this study adhere to the guidelines of California Department of Fish and Wildlife (CDFW) Coastal Monitoring Program (CMP) regional protocol (Adams et al. 2011).

Multi-state model

I used a multi-state model to estimate survival and movement of juvenile Coho Salmon within Freshwater Creek. My model consisted of two states in space, with model parameters that vary temporally. The two model states were 1) upper Freshwater Creek (hereafter upstream), and 2) lower Freshwater Creek (hereafter downstream). The upstream state consists of natal rearing habitat upstream of tidal influence. The downstream state provides non-natal rearing habitat and includes the estuary. Fish residing upstream throughout the fall and winter are defined as spring migrants, and individuals that migrate downstream before spring are defined as early migrants. Between each sampling occasion fish can either perish, survive and remain in their current state, or survive and transition to the downstream state. A detection from any antenna within a state was counted as an encounter of that individual in that particular state. The Howard Heights antenna, located approximately 0.5 km downstream of the Howard Heights Road bridge, was the furthest upstream antenna in the downstream state and the designated boundary between the upstream and downstream states. An example of some of the possible encounter histories and their interpretations are shown below in Table 1. General parameters for a multi-state model include: survival probability, transition probability, and detection probability. Each of these parameters can be allowed to vary between states and occasions to increase model complexity and improve model fit. Model notation and definitions were adopted from Cooch and White (2017), and are listed below in Table 2.

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Table 1. Example of possible encounter histories with my multi-state model, where A is defined as upstream, and B is defined as downstream. This example assumes no upstream movement (i.e., from state B to state A), as does my model.

Encounter History	Interpretation
AABBB	Individual was captured and marked in state A on occasion 1, was recaptured in state A on occasion 2, and was captured in state B on occasions 3, 4, and 5
AA0BB	Individual was captured and marked in state A on occasion 1, was recaptured in state A on occasions 2, was not captured on occasion 3, and was captured in state B on occasions 4 and 5
AAAA0	Individual was captured and marked in state A on occasion 1, was recaptured in state A on occasions 2-4, and was not recaptured on occasion 5
BBB0B	Individual was captured and marked in state B on occasion 1, was recaptured in state B on occasions 2 and 3, was not captured on occasion 4, and was recaptured in state B on occasion 5
BB0B0	Individual was captured and marked in state B on occasion 1, was recaptured in state B on occasion 2, was not captured on occasion 3, was recaptured in state B on occasion 4, and was not recaptured on occasion 5

Table 2. Multi-state model parameter notation and definitions.

Notation	Definition
S_i^r	The probability of survival in state *r* from time *i* to *i* + 1, given that the animal was present in state *r* at time *i*
ψ_i^{rs}	The probability of transition from state *r* at time *i* to state *s* at time *i* + 1, given that the animal was alive at time *i* + 1
p_i^s	The probability of detection in state *s* at time *i*

Model time interval simulations. PIT tag antennas collect detection data continuously, but multistate models operate on discrete time intervals, and it was unclear how parameter estimates could be affected by aggregating continuous detection data into discrete time intervals. I thus ran a series of multi-state model simulation trials to determine the most appropriate discrete time interval that resulted in the least amount of imposed error in the estimation of the parameters of interest (spring migrant survival, and early emigration probabilities). I define imposed error as the relative difference between the estimator and the target value (i.e., the generating model value). Additionally, as the discrete time intervals approach continuous time, parameter estimates for movement and survival will also approach the probability boundaries of 0 or 1, respectively. Close proximity of parameters to the boundaries causes numerical estimation problems for mark-recapture models (Lebreton and Cefe 2002; White et al. 2006); therefore, I varied the time step length to evaluate model performance as survival, movement and detection probabilities approach the boundary.

I conducted the simulations in the R programming language (R Core Team 2013) by generating encounter histories for a multi-state model with known parameter values. My simulation trials consisted of stochastic generating models with three variations in overwinter survival (0.3, 0.4, 0.5), winter movement (0.1, 0.2, 0.3), and sample size (500, 2000, 5000) (Table 3). Approximations were made for generating model specifications to exemplify Freshwater Creek data. I designed my simulations to have three states: 1) upstream, 2) downstream, and 3) ocean (unobservable state). I made the assumption that fish only move from the upstream state towards the ocean state, and that fish that enter the ocean have permanently emigrated from the system (Figure 2). Individuals were only marked on the first occasion, with 80% being marked in the upstream state and 20% marked in the downstream state. Data was simulated 1000 times for each generating model and each variation in sample size. Encounter history data was simulated on a daily time step for a total of 240 days.

Table 3. Generating model parameters and values for the number marked (*M*) in addition to survival (*S*), detection (*p*), and movement (*ψ*) rates. Generating model values were on a seasonal scale. State (A or B), and season (Winter or Spring) are denoted by parameter subscripts.

Parameter	Generating Model Value(s)
M	500, 2000, 5000
S_{A_Winter}	0.3, 0.4, 0.5
S_{A_Spring}	0.6
S_{B_Winter}	0.3
S_{B_Spring}	0.6
p_{A_Winter}	0.2
p_{A_Spring}	0.3
p_{B_Winter}	0.2
p_{B_Spring}	0.5
ψ_{AB_Winter}	0.1, 0.2, 0.3
ψ_{AB_Spring}	0.5
ψ_{BC_Winter}	0.2
ψ_{BC_Spring}	0.5
$\psi_{BA,}$, $\psi_{CA,}$ ψ_{AC}	0

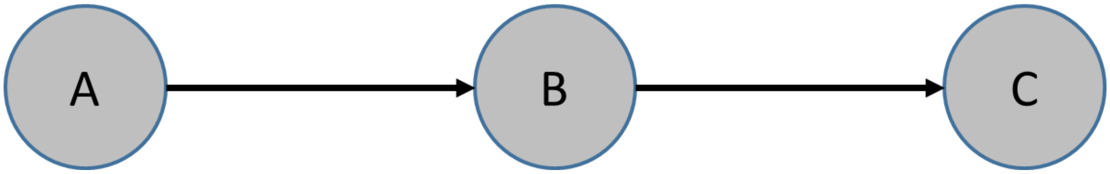

Figure 2. Illustration showing movement restrictions between states. States are defined as: A = upstream, B = downstream, and C= Ocean (unobservable state).

These encounter histories were then analyzed in multi-state model framework using RMark (Laake 2013) to estimate parameters. The multi-state model that I used consisted of two states, and thus the encounter histories only included detections in the upstream and downstream state, as the ocean state had a detection probability of 0. The simulated daily encounter histories were aggregated into 8, 15, and 24 day time intervals. The aggregated time intervals were chosen because they divide evenly into 240. For computational ease, the seasons were both 120 days in length. The multi-state model was then used to estimate parameters. Seasonal constraints for winter and spring were utilized with the purpose of simplifying model structure.

<u>Freshwater Creek model</u>. In multi-state models, the number of parameters can increase rapidly with an increasing number of occasions and states. With complex models, utilizing model constraints is an effective means to simplify model structure and reduce the number of parameters in both single and multi-state models (Lebreton et al. 1992, 2009). Given the sparse detection rate I observed in individual encounter histories, I applied temporal constraints to reduce model complexity. A conceptual diagram of my model structure is shown below in Figure 3. My two constraints were seasonal (i.e., winter and spring). Winter lasted from tagging through occasion 22 and then spring lasted for the rest of the sampling year (i.e. through occasion 39). This seasonal constraint assumes survival, transition, and detection probabilities has a constant mean value within each season (i.e., winter and spring). Although mean parameter values are constant within season, parameter estimates can vary as a function of environmental (e.g., streamflow) or individual (e.g., fork length) covariates. The cutoff between winter and

spring (occasion 22) coincided with the installation of the juvenile fish trap in March, as this will likely change the capture probability for fish that migrate downstream.

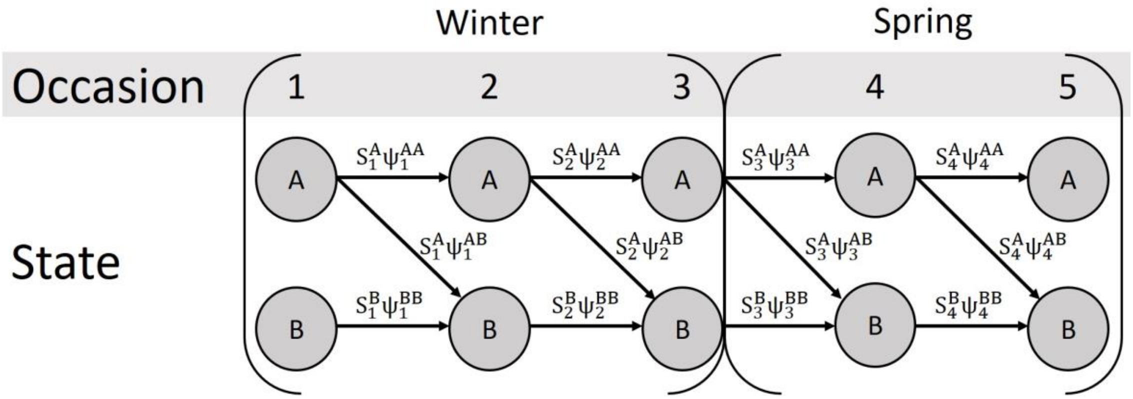

Figure 3. Conceptual diagram of a multi-state model with five time-varying occasions constrained to two seasons. The states are defined as: ‘A’ upper Freshwater Creek, and ‘B’ lower Freshwater Creek.

Before running an *a priori* candidate model set, I ran a set of models without covariates to evaluate model convergence and estimate goodness of fit (Appendix A). In this model run, I included a range of models from the least complex model that still included meaningful parameters, up to the most complex model that I thought that the data would support. Upstream movement was fixed to 0 for all models. Using an all combinations approach, I ran a set of nine models in R (R Core Team 2013) with the package “RMark” (Laake 2013). The general model was chosen by selecting the most complex model that properly converged. Goodness of fit was assessed by using the median ĉ approach in Program Mark with models that included group covariates (i.e. year and reach) (White and Burnham 1999). The median ĉ approach is unable to incorporate individual covariates (i.e. length) so I could not include any of those models in the goodness of fit candidate model set. Median ĉ was used to account for over dispersion, correct parameter variance estimates, and to calculate the Quasi-Akaike’s Information Criterion corrected for sample size ($QAIC_c$) used for model selection (Symonds and Moussalli 2011).

After assuring the goodness of fit was reasonable, I designed multi-state models that incorporated group, individual, and environmental covariates (Table 4). I selected each of these covariates with *a priori* hypotheses regarding how biological and physical conditions would affect early migration and winter survival rates. Season was used as a covariate for survival, movement, and detection probabilities to account for differences between the two emigration patterns for both early migrants and spring migrants. The use of season as a covariate for movement was essential in separating the two emigration patterns. Furthermore, I hypothesized that season could affect survival, as there are inherent seasonal differences within Freshwater Creek (e.g., streamflow, turbidity, temperature). I also hypothesized that there were seasonal differences in detection probability, as increased streamflow in the winter could reduce detection probability by causing outages at antenna sites. Additionally, higher streamflow would increase the space that a fish can occupy, and could increase their chances of swimming outside of the detection range of the antenna. I also included year and reach as covariates to model detection probability as a function of when and where fish were tagged. Year was included to account for any annual variation in detection. Reach was included because some reaches had more antennas that fish would encounter during emigration; thus, these fish would be expected to have a higher detection probability. Length was used as a covariate for survival because previous research has shown a positive relationship between survival and length (Quinn and Peterson 1996; Brakensiek and Hankin 2007). However, these models did not account for emigration, which is why I also included length as a covariate for movement. Weekly average streamflow was also used as a covariate for movement, as previous research has shown this to be an important factor in downstream migration (Hartman et al. 1982; Tschaplinski and Hartman 1983; Giannico 2000).

Table 4. Covariates used in the multi-state model, and their descriptions.

Covariate	Covariate Description
Length	Fork length (mm) at time of fall tagging
Flow	Average weekly streamflow (cfs) of Little River
Year	Year of fall tag group
Season	Temporal constraint of either winter or spring
Reach	Survey reach of tagged fish at time of fall tagging

Most covariate data was recorded on initial fish capture. Covariate data for individual length, year, and reach were obtained at the time of tagging in the fall, and uploaded to the CDFW database. Survey reaches were delineated in relation to the nearest downstream antenna. There is no streamflow gage on Freshwater Creek, so I used the Little River gage as a proxy. Little River is larger, but is the closest gauged watershed of comparable size with a watershed area of 119 km^2. Streamflow data was obtained for Little River gage by using the R package "dataRetrieval" (Hirsch and De Cicco 2015).

Although the multi-state model was run on a short discrete time intervals within a season, I was most interested in estimating survival and movement probabilities on a seasonal scale, thus, I converted the discrete time interval parameter estimates and confidence intervals into seasonal estimates by bootstrapping. I sampled from a normal distribution (n=10000) using beta parameter estimates and standard errors output on the discrete time interval output from RMark. These values were then converted from the logit scale to the probability scale. Winter survival was calculated by taking the product of all the probability estimates within the season. Winter movement estimates were calculated by:

$$\psi_{Winter} = 1 - \prod_{1}^{21}(1 - \psi_t)$$

where ψ_{Winter} is the probability of having moved in any time interval within a winter, and ψ_t is the probability for movement during a given time interval within a winter. Winter estimates and confidence intervals were obtained by taking the median and 95% quantile values from the bootstrap samples.

As with all mark-recapture models, multi-state models make a number of assumptions, some of which are violated by the PIT tag data in this study. The major assumptions of multi-state models are (Williams et al. 2002):

1. Every marked animal present in state *r* at sampling period *i* has the same probability of being recaptured;
2. Every marked animal in state *r* immediately following sampling in period *i* has the same probability of surviving until period *i* + 1.
3. Marks are neither lost nor overlooked, and are recorded correctly.
4. Sampling periods are instantaneous (or relatively short periods), and recaptured animals are released immediately.
5. The fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

In this study, the assumption of equal recapture probability is the most likely assumption to be violated. Proximity of individuals to antennas will likely influence individual detection probability. Furthermore, the number of antennas downstream of an individual's initial tagging location may also affect detection rates. However, bias in survival estimates caused by heterogeneity in capture probabilities has been shown to be negligible (Williams et al. 2002). I accounted for some of the variation in detection probability by incorporating group covariates for reach and year tagged.

RESULTS

Estimation of Survival and Movement

Model time interval simulations

Using simulated data, I found that the relative amount of imposed error was lowest for the smallest time step (8 days) and that precision increased proportional to sample size (Figure 4 and Figure 5). Point estimates were obtained by taking the median from the distribution of the generating model estimates, and 95% confidence intervals were calculated by taking the lower 0.025 and upper 0.975 quantile values. Imposed error was calculated by taking the difference between the log-odds of the real parameter estimate and the log-odds of the generating model probability. A value of zero for imposed error would indicate that there is no difference between the real parameter estimate and the target probability of the generating model. Estimates with a positive value for imposed error would indicate that they are higher than the generating model probability, and negative values are lower than the generating model probability. Broadly, the simulations indicate that a smaller time step length reduces the amount of imposed error, and precision increases with an increasing sample size. Finally, all confidence intervals for both parameters overlapped zero with the eight-day time step, demonstrating that this formulation of the multi-state model could theoretically generate reliable parameter estimates for the two parameters I was most interested in: 1) winter survival of spring migrants, and 2) early migration rates.

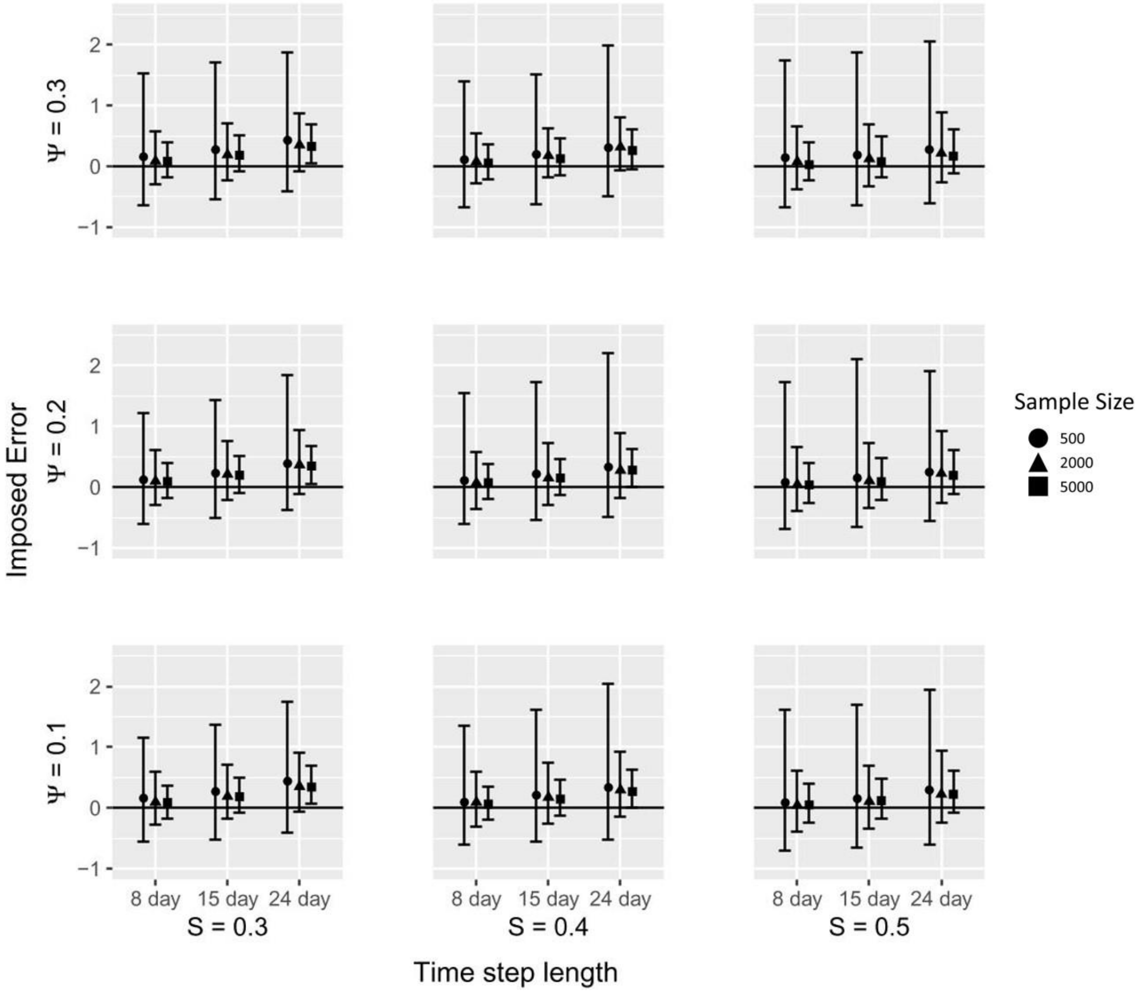

Figure 4. Imposed error for winter survival in the upstream state as a function of time step length for 9 generating model values. Each error bar and point represent the median and 95% quantile values for 1000 model iterations.

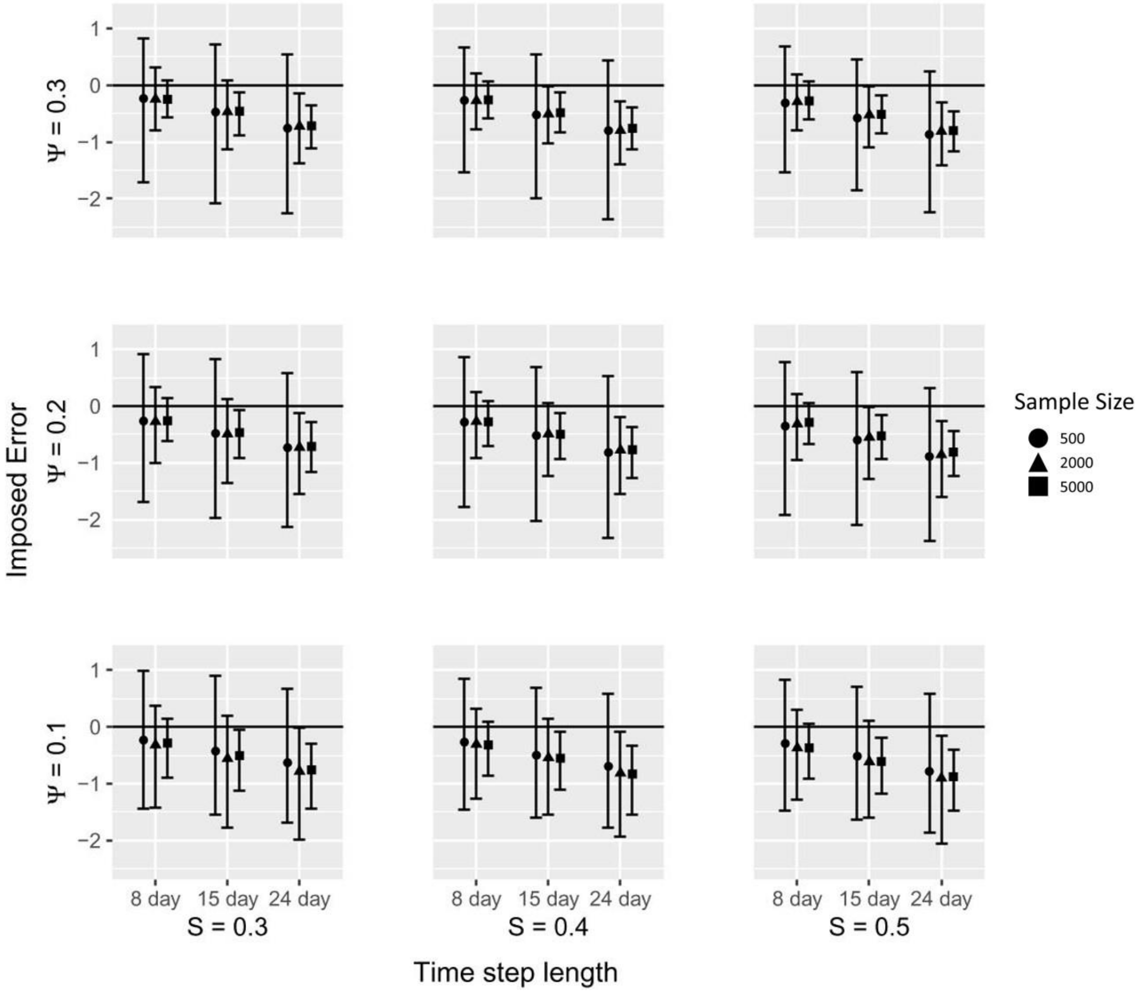

Figure 5. Imposed error for winter movement from upper Freshwater Creek to lower Freshwater Creek as a function of time step length for 9 generating model values. Each error bar and point represent the median and 95% quantile values for 1000 model iterations.

I also calculated unexpected error for overwinter survival and winter movement, by taking the relative difference between the model estimate, and the expected value. Discretization of continuous data violates the assumption of instantaneous sampling periods. Thus, for overwinter survival, an individual need only survive until the beginning of the last winter occasion. The expected value for overwinter survival is defined as:

$$S_E = S_{Daily}{}^\wedge DLO$$

Where S_E is the expected overwinter survival rate, S_{Daily} is the daily survival rate in the generating model, and DLO is the number of days until the beginning of the last occasion. As shown below in Figure 6, a large amount of the amount of unexpected error in survival appears to be accounted for, in that the median values are relatively centered on 0. Considering the expected value for overwinter movement, an individual can move between the beginning of the first occasion up until the beginning of the last occasion, and is thus defined as

$$\psi_E = (1 - (\psi_{Daily})^\wedge DLO) - (1 - (\psi_{Daily})^\wedge DFO)$$

Where ψ_E is the expected winter movement rate, ψ_{Daily} is the daily movement rate in the generating model, DLO is the number of days until the last occasion, and DFO is the number of days in the first occasion. As shown below in Figure 7, it appears that there some unexpected error in movement that remains unaccounted for. While there appears to be little to no unexpected error when the generating values for winter movement are

0.3, and overwinter survival is 0.3, the amount of unexpected error seems to increase with decreasing movement and increasing survival rates.

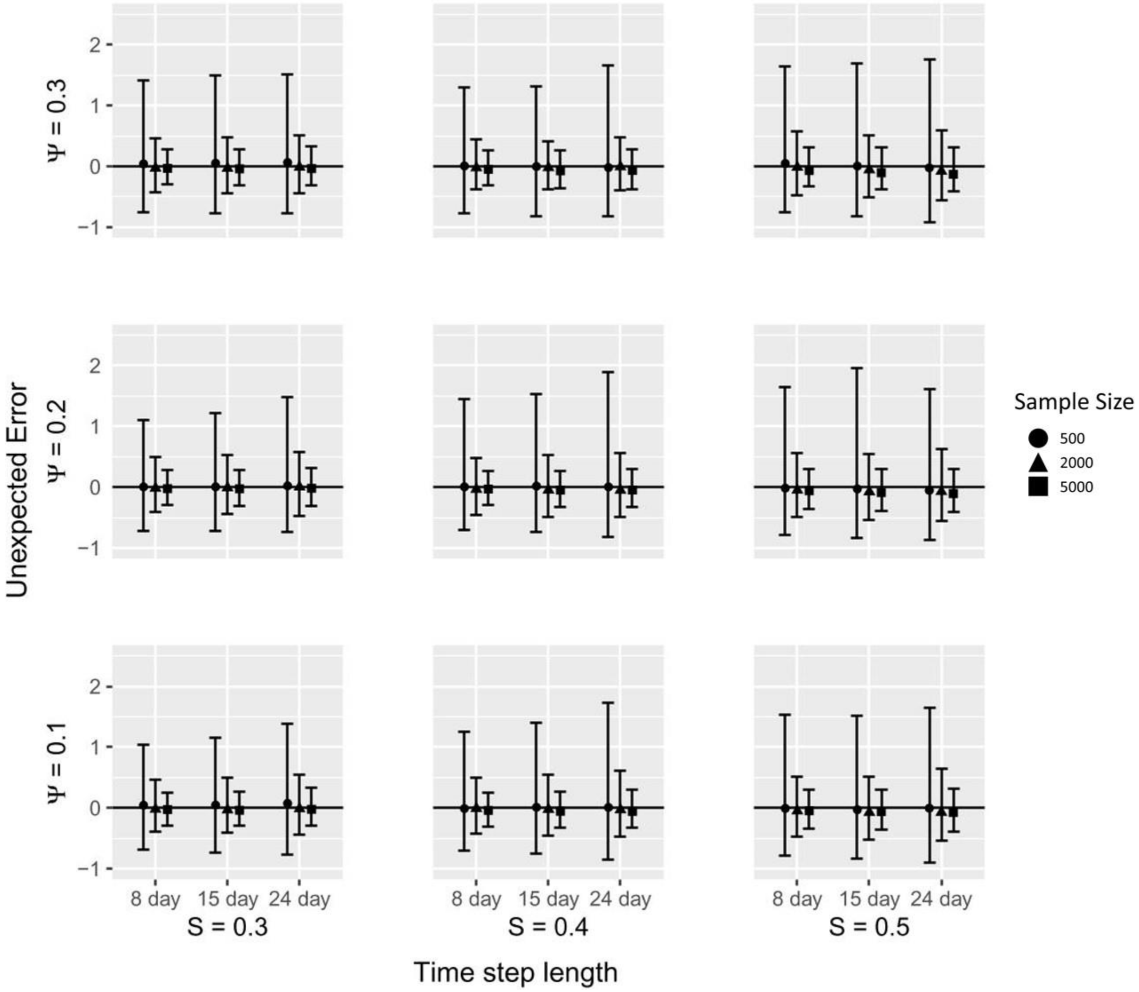

Figure 6. Unexpected error for winter survival in the upstream state as a function of time step length for 9 generating model values. Each error bar and point represent the median and 95% quantile values for 1000 model iterations.

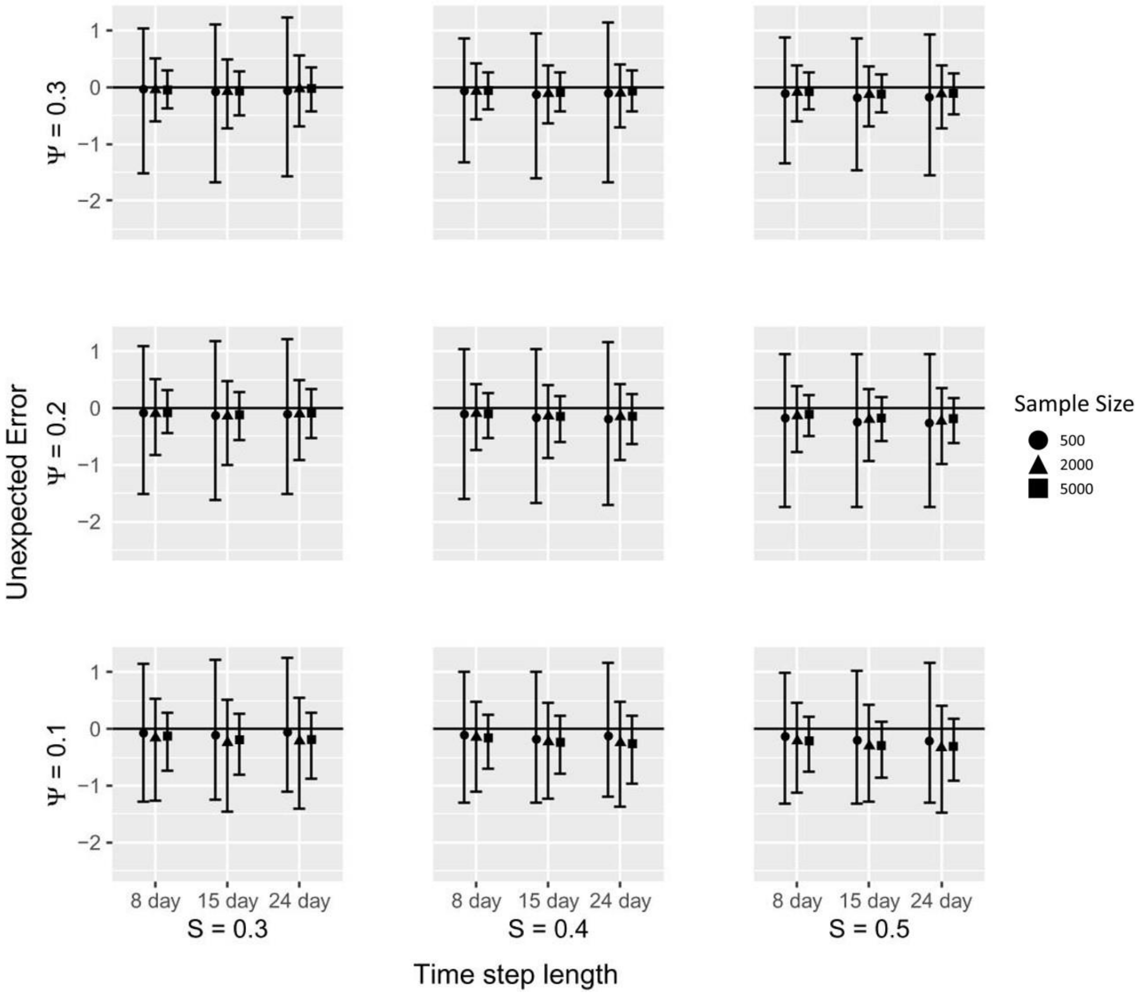

Figure 7. Unexpected error for winter movement from upper Freshwater Creek to lower Freshwater Creek as a function of time step length for 9 generating model values. Each error bar and point represent the median and 95% quantile values for 1000 model iterations.

Freshwater Creek model

Based on the results of my simulations, I used a weekly time interval for the Freshwater Creek multi-state model. This resulted in an encounter history with 39 occasions. Continuous stationary antenna data and daily trap recaptures were aggregated into the weekly time intervals and all tagging and detection data hereafter will be summarized by week.

Over the four-year period of the study, 2003 juvenile Coho Salmon were tagged in the fall throughout Freshwater Creek (Table 5). In each year, the number of tagged fish ranged from 245-610 individuals in the upstream state, and 60-97 individuals in the downstream state. Although fall tagging took place over multiple weeks each year, for modeling purposes I considered it to have occurred only during the last week fish were tagged and released each year.

Table 5. Total number of fish tagged in fall. Date fall tagging ended varied annually.

Year	Total Tagged	Tagged in State A	Tagged in State B	Last Fall Tagging Occasion
2013	707	610	97	1
2014	509	443	66	2
2015	329	245	84	3
2016	458	398	60	6
Total	2003	1696	307	NA

PIT tag antennas and the downstream migrant trap detected juveniles as they moved throughout Freshwater Creek. In the upstream state, there were 381 unique weekly detections, of which 127 were observed during the fall and winter, and 254 were observed during the spring. In the downstream state, there were 1057 unique weekly detections, of which 198 were observed during the winter, and 859 were observed during the spring (Figure 8). Only 3 fish were detected moving from the downstream state to the upstream state. Given that the sample size was too small to estimate upstream movement, I fixed the upstream transition probability to zero. I censored the 3 fish that were observed moving upstream in the occasion during which they were detected in the upstream state, so they did not affect any subsequent parameter estimates. Fish that were detected in both states during a week were assigned to the downstream state in the encounter history.

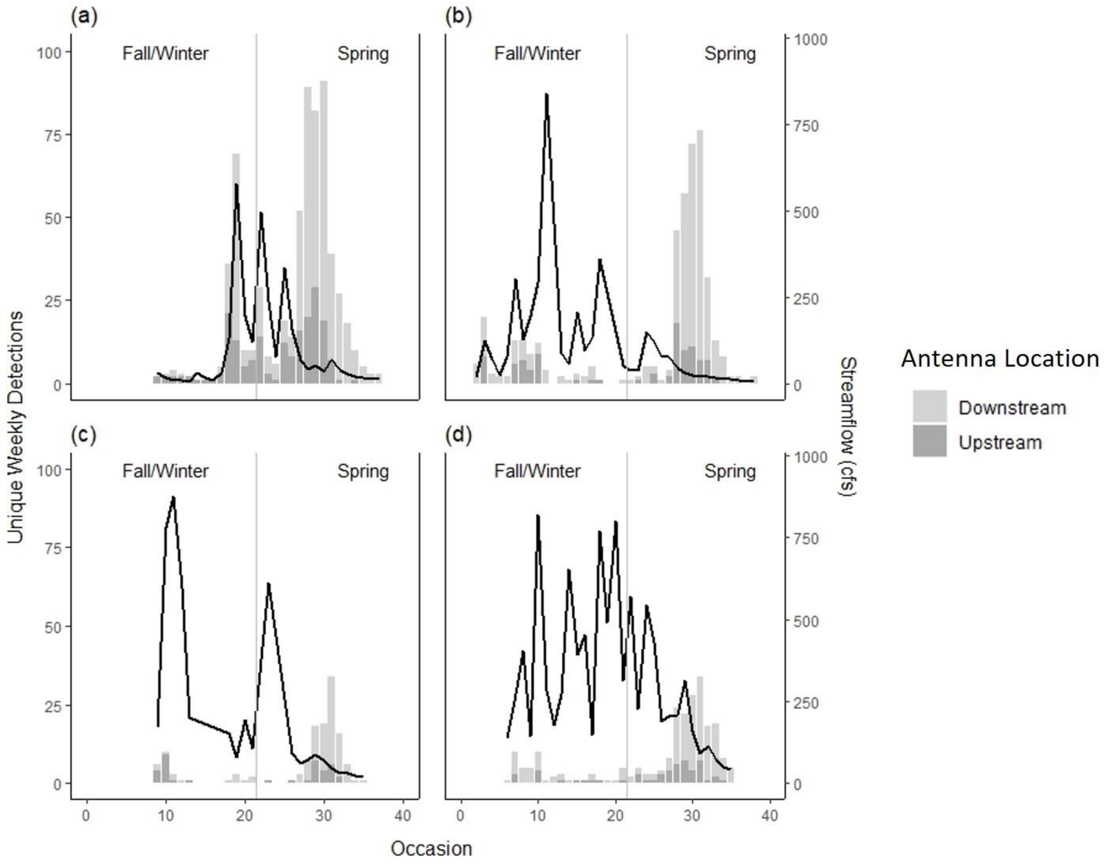

Figure 8. Unique weekly detections (vertical bars) and Little River average weekly streamflow (black line) for each occasion in: (a) 2013-2014, (b) 2014-2015, (c) 2015-2016, and (d) 2016-2017. Detections are for all antennas as well as the juvenile fish trap. The thin grey vertical line represents the break between winter and spring.

Goodness of fit was evaluated in Program Mark by estimating the overdispersion parameter median ĉ. The global model I used to assess goodness of fit was: S(Season*Stratum*Year) ψ(Season*Year) p(Season*Stratum*Year+Reach). This was the most complex model that converged for all parameters of interest. The global model was estimated to have a median ĉ value of 1.5, indicating an acceptable level of overdispersion (Cooch and White 2017). This median ĉ value was used to calculate the QAICc values to select the most parsimonious model (Table 6). Median ĉ was also used to adjust the standard errors and 95% confidence intervals for all model parameters.

An assortment of individual, environmental, and group covariates were incorporated into the candidate model set. Fork length of fish tagged in the fall was used as an individual covariate in the survival and movement models. Size of tagged fish ranged from 65-125 mm fork length with a mean of 74 mm and standard deviation of 9.5 mm. Average weekly streamflow was used as an environmental covariate in the movement model. Streamflow measurements on Little River ranged from 3.11-5690 cfs, with a mean of 165.19 cfs and standard deviation of 281.32 cfs. Group covariates for 6 reaches and 4 years for time at fall tagging were used in the detection model. These group covariates were not used for survival or movement models, as I was more interested in individual and environmental covariate effects.

Table 6. Candidate model set for survival (*S*) and movement (ψ) probabilities. All models used the global model for detection (*p*) probability: p(Season*Year*Strata+Reach)

Model	Num. Par	QAICc	Delta QAICc	Weight	QDeviance
S(Season*Strata+Length) ψ (Season*Length*Flow)	33	9388.54	0	0.63	9321.87
S(Season*Strata+Length) ψ (Season*Length+Season * Flow)	31	9389.59	1.05	0.37	9327.00
S(Season*Strata) ψ (Season)	28	9408.87	20.33	2.42E-05	9408.87
S(Season*Strata) ψ (Season*Length+Season*Flow)	30	9420.26	31.73	8.11E-08	9359.71
S(Season*Strata) ψ (Season*Length*Flow)	32	9420.58	32.05	6.91E-08	9355.95

I selected the most parsimonious model from my candidate set using QAICc model selection, by selecting the simplest model within two QAICc units of the best fitting model. Based on my selection criteria, the model I used for inference was: S(Season*Strata+Length) ψ (Season*Length*Flow) p(Season*Year*Strata+Reach). Although the chosen model had less support than the top ranked model, it had fewer parameters, and a delta QAICc difference of only 1.05. Overwinter survival for spring smolt migrants was estimated as a function of average length at time of fall tagging for each year, and ranged from 0.87 (95% CI 0.78-0.92) to 0.90 (95% CI 0.81-0.94) (Table 7). Without accounting for permanent emigration, early migrant survival during the winter was estimated as a function of average length at time of fall tagging for each year, and ranged from 0.59 (95% CI 0.54-0.64) to 0.65 (95% CI 0.60-0.69) (Table 7). The results for the top model suggest that fish length at time of tagging has a positive effect on overwinter survival (Figure 9), given a beta estimate of 0.341 (SE 0.068). Early emigration rates were estimated independently for each of the four years, as it used environmental covariate for streamflow, and ranged from 0.34 (95% CI 0.32-0.36) to 0.40 (95% CI 0.38-0.43) (Table 7. Yearly Overwinter survival and early migration rates, streamflow (cfs) at Little River gauging station, and mean fork length at time of fall tagging. Mean weekly streamflow was used as an environmental covariate to predict emigration rates. Fish length had a negative relationship with estimates of early migration rates (beta value = -0.265, SE = 0.104), and thus smaller fish were more likely to migrate downstream (Figure 10). Estimates for early emigration rates used the average sized fish when calculating weekly movement. Results from the top model also suggest that early migration rates were positively affected by streamflow (beta value = 0.182, SE = 0.118; Figure 11).

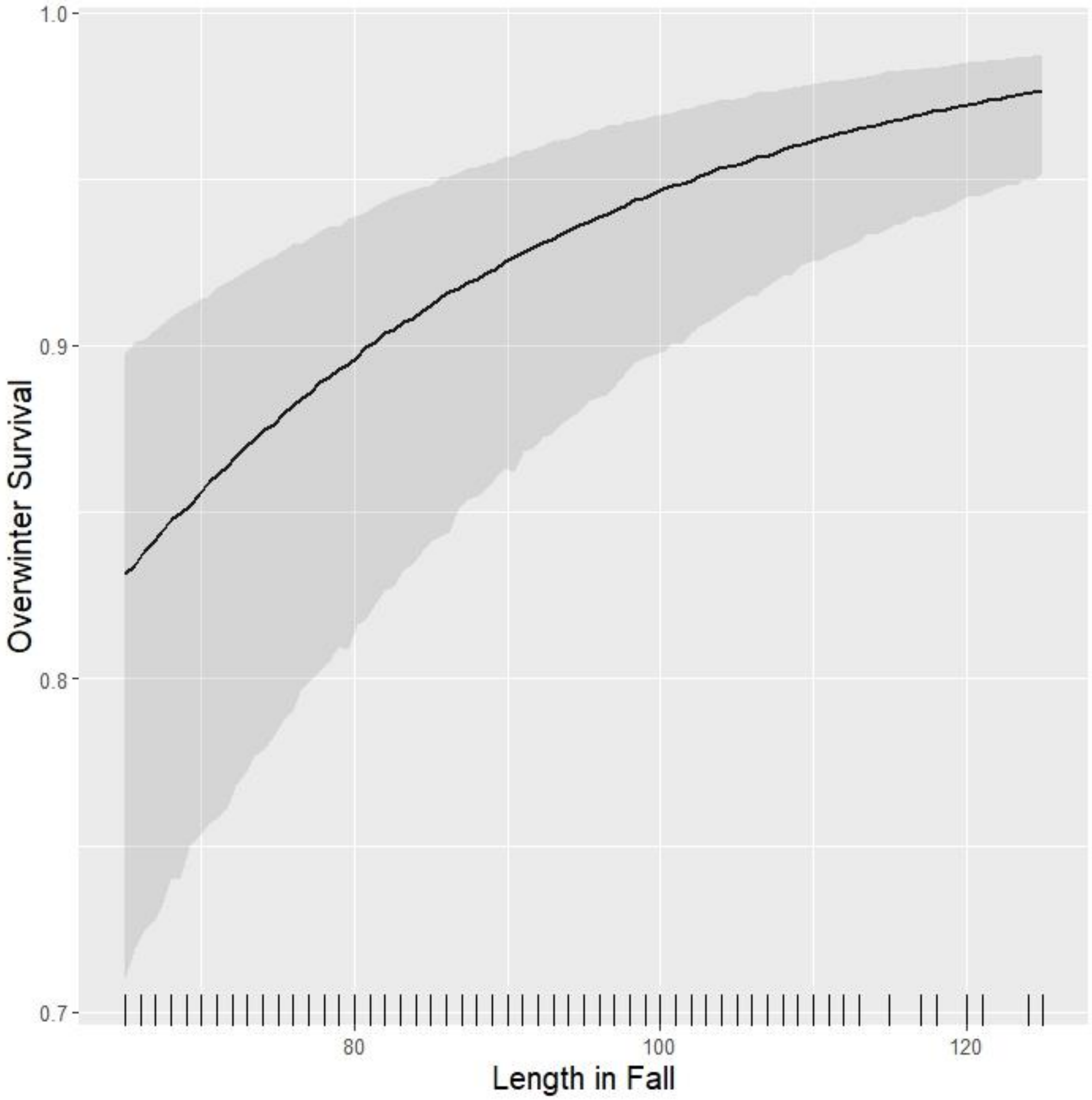

Figure 9. Overwinter survival rate (95% confidence interval is shaded in grey) of spring smolt migrants in the upstream state as a function of fish fork length. A rug plot along the x-axis displays the distribution of fish fork lengths when fish were originally tagged in October or November.

Table 7. Yearly Overwinter survival and early migration rates, streamflow (cfs) at Little River gauging station, and mean fork length at time of fall tagging. Mean weekly streamflow was used as an environmental covariate to predict emigration rates.

Years	Spring Smolt Migrant Overwinter Survival (95% CI)	Early Migrant Overwinter Survival (95% CI)	Early Migration (95% CI)	Mean Winter Streamflow (range)	Mean Fork Length in Fall
2013-2014	0.87 (0.78-0.92)	0.59 (0.54-0.64)	0.36 (0.34-0.38)	61 (8-576)	73.8
2014-2015	0.89 (0.80-0.93)	0.63 (0.59-0.68)	0.35 (0.33-0.38)	170 (5-838)	78.1
2015-2016	0.89 (0.80-0.93)	0.63 (0.58-0.68)	0.38 (0.35-0.41)	248 (3-874)	77.4
2016-2017	0.90 (0.81-0.94)	0.65 (0.60-0.70)	0.38 (0.35-0.41)	341 (5-817)	79.6

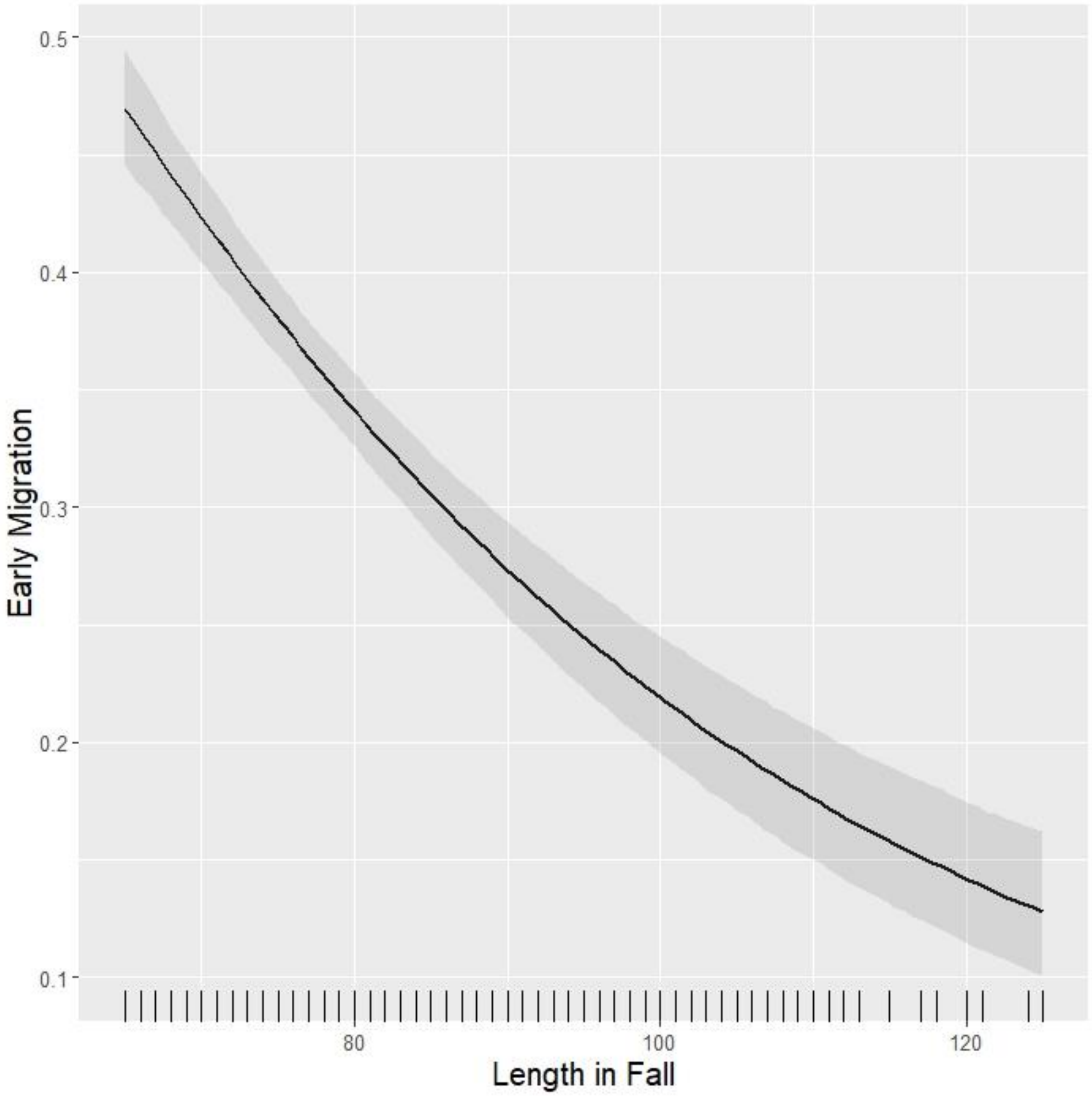

Figure 10. Early migration rate (95% confidence interval is shaded in grey) of juvenile Coho Salmon from the upstream state to the downstream state during the winter months as a function of fish fork length. A rug plot along the x-axis displays the distribution of fish fork lengths when fish were originally tagged in October or November.

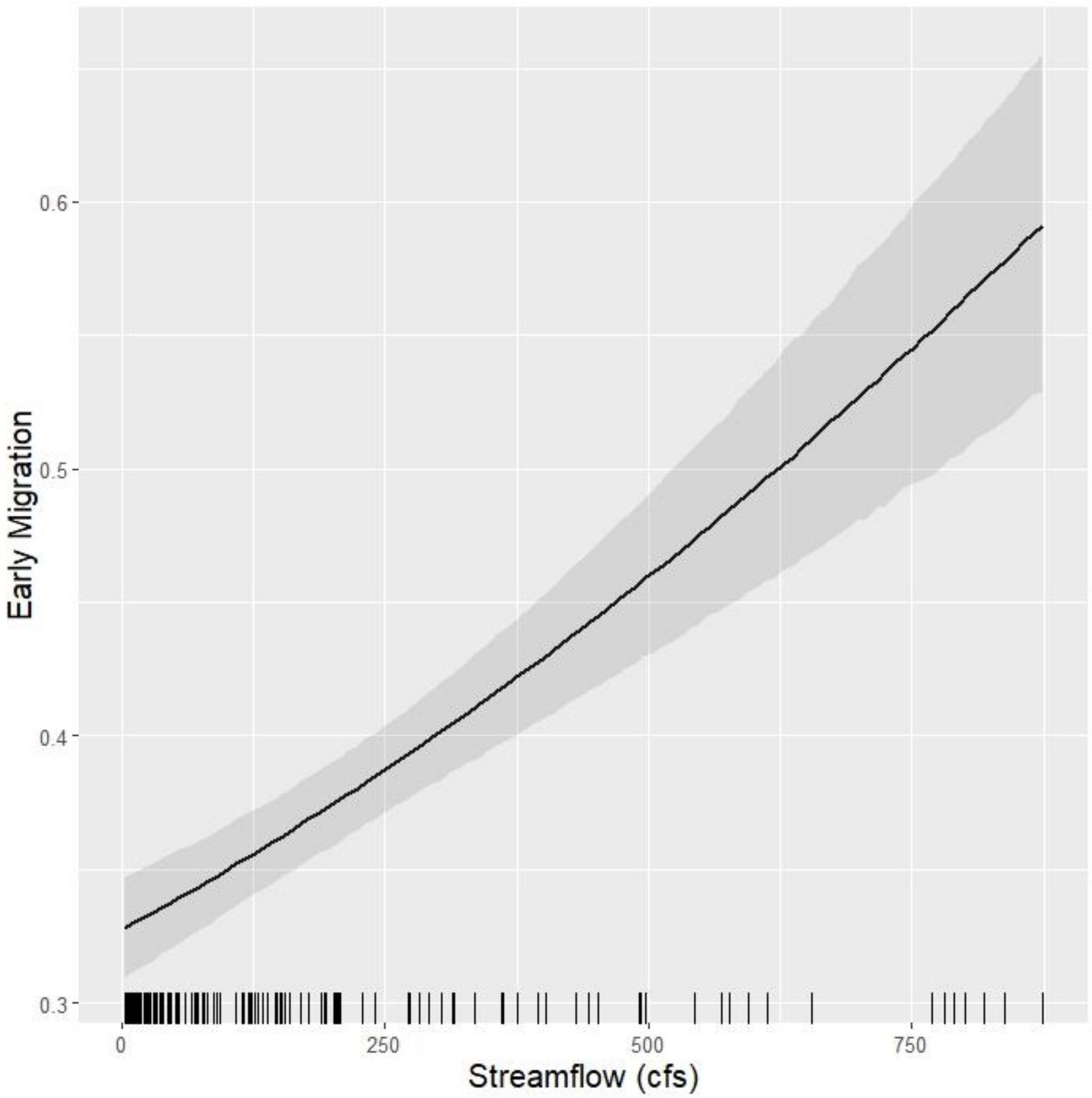

Figure 11. Early migration rates (95% confidence interval is shaded in grey) of juvenile Coho Salmon from the upstream state to the downstream state during the winter months as a function of streamflow. A rug plot along the x-axis displays the observed average weekly streamflow recorded on the Little River gauge.

DISCUSSION

I conducted this study to provide robust estimates of survival rates for spring migrants as well as early emigration rates for juvenile Coho Salmon, and to examine factors that affect movement and survival in Freshwater Creek. An extensive set of simulation trials were performed to test the feasibility of this multi-state model and evaluate the effects of varying the time step lengths with continuous data. Upon completion of the simulations, the multi-state model was used for a four-year dataset to estimate winter survival and early emigration rates and examine covariate effects on model parameters. My results provide evidence that substantial numbers of juveniles are emigrating downstream in the fall and winter, indicating that maintaining high quality estuarine rearing habitat could promote resiliency within the population. This implies that previous estimates of low overwinter survival of Coho salmon within Freshwater Creek could be due to high emigration rates to alternative rearing locations. I expand on these conclusions and management implications throughout this discussion.

Model Simulations

My simulation trials provide insight into the use of aggregating continuous detection data in mark-recapture models. Recent research has shown the importance of using simulations to explore the use of continuous data in both closed (Borchers et al. 2014) and open (Barbour et al. 2013) mark-recapture models. I found that decreasing the time interval reduced the amount of imposed error, which contrasts with results from Borchers et al. (2014). One explanation for this difference could be that Borchers et al. (2014) used a spatially explicit capture recapture model, where shortening the time interval length would reduce the amount of time for mixing between marked and unmarked individuals, and thus newly captured individuals would be more likely to be recaptured.

It is interesting to note that in my simulations the 95% confidence interval for the imposed error did not overlap the generating model value for the movement parameter with the longest time interval of 24 days (figure 5). Barbour et al. (2013) made a similar observation with the apparent survival parameter estimates obtained from a CJS model. They found that apparent survival estimates had consistently positive values for imposed error when aggregating continuous detection data. Overall, I found that decreasing the time-step length reduced the amount of imposed error for both survival and movement.

My simulations were made to imitate processes in Freshwater Creek, and subsequently test the performance of my multi-state model. The generating model used a daily time step to simulate encounter histories and then aggregated the data into various time intervals. Similar to the findings of Barbour et al. (2013), I found that I had consistent positive values for imposed error for my survival estimates. This imposed error is a result of violation of the assumption that sampling occasions are instantaneous. Sampling occasions are not instantaneous when continuous time data is aggregated into discrete units. It is important to note that when aggregating continuous data into discrete time bins, the multi-state model will estimate survival up until the beginning of the last occasion. If it is known exactly what the model is estimating, then there shouldn’t be any source of unexpected error. However, for winter movement, there appears to be some unexpected error that remains unaccounted for. I speculate that for the multi-state model, this unexpected error is because an individual’s transition probability is conditional on survival.

Benefits of Multi-state Model

My methods differ significantly from previous research estimating overwinter survival and movement. One key difference is that this study uses a multi-state model, which simultaneously estimates survival and movement. With proper designation of model states, multi-state models can account for permanent emigration from the study area. Horton et al. (2011) observed that CJS model estimates were consistently biased low when compared to a multi-state model because the CJS model does not account for permanent emigration from the study area. My multi-state model accounted for emigration from upper Freshwater Creek, as all fish migrating downstream are subject to detection in lower Freshwater Creek. Broadly, use of the multi-state model reduces bias, as it accounts for survival and movement in the same model structure.

Another difference in my approach is that by dividing the continuous antenna detections into many discrete time intervals, I was able to separately estimate survival and movement as a function of both time (week) and space (upper and lower Freshwater Creek). Preceding studies on juvenile Coho survival censored winter detections, and aggregated spring detection data at the trap to estimate winter survival. My multi-state model use data from both winter and spring, and aggregates detection data into weekly bins rather than seasonal units of time. Therefore, if a fish is detected in more than one week at a site, the detections are noted in different occasions in the encounter history for all unique weekly detections. Overall, this approach uses more of the available data, which could decrease the amount of imposed error, and increase precision in parameter estimates.

It should also be noted that classification of spring smolt migrants and early migrants also varied between my study and results from previous studies in Freshwater Creek. Previously, to have been considered a spring smolt migrant, fish would have had to survive throughout the winter and migrate to the downstream migrant trap (Rebenack et al. 2015; Ward and Anderson 2016). My project utilized an antenna further upstream near the Howard Heights bridge to classify early migrants and spring smolt migrants. I took this approach to improve detection in my lower Freshwater Creek during the winter, as individual detections were sparse at the antenna below the downstream migrant trap.

Apart from model structure, one final difference when comparing my project to previous studies, is that I used PIT tag/antenna data for fish that were on average larger. All fish in my model were tagged exclusively with HDX tags, where previous studies used a mix of HDX and full-duplex (FDX) tags (Rebenack et al. 2015; Ward and Anderson 2016). FDX tags are smaller, which allows for tagging smaller fish. However, FDX tags cannot be detected at any of the stationary channel-spanning antennas on Freshwater Creek. FDX tags could only be detected with handheld antennas used at the time of tagging in the fall, or recapture in the spring at the trap. HDX tags could be detected at all stationary antenna sites as well as the trap. Any inference made from my results is limited to fish that are greater than or equal to 65 mm in length, which was the size allowable for PIT tagging during the course of the study.

Freshwater Creek Results and Management Implications

My estimate for overwinter survival of spring smolt migrants is substantially higher than previous estimates throughout the Pacific Northwest, but these estimates are not directly comparable due to the formulation of the different models used. I estimated that survival for spring smolt migrants ranged from ranged from 0.87 (95% CI 0.78-0.92) to 0.90 (95% CI 0.81-0.94), whereas previous estimates in Freshwater Creek have ranged from 3-49% (Rebenack et al. 2015; Ward and Anderson 2016). Likewise, estimates of overwinter survival in other coastal streams in California (45%), Oregon (4-13%) , Washington (5-15%) and British Columbia (67-72%) were also lower than my estimate (Tschaplinski and Hartman 1983; Ebersole et al. 2006; Brakensiek and Hankin 2007; Roni et al. 2012). However, my estimates account for early emigrants, whereas previous studies did not. If I transform my estimates to apparent survival by taking the product of overwinter survival and overwinter fidelity to the upstream state (i.e., 1 - early emigration probability), my estimates of apparent overwinter survival range from 0.55-0.58, which are still higher than previous results from Freshwater Creek. Perhaps other differences in methodology, as described in the above section, could explain these contrasting results for overwinter survival estimates.

In addition to spring migrant survival, overwinter survival for early emigrants was also estimated as a parameter in the multi-state model. Specifically, these estimates are for juvenile Coho Salmon that moved into and reared in lower Freshwater Creek during the fall and winter. Estimates for early migrant overwinter survival ranged from 0.59 (95% CI 0.54-0.64) to 0.65 (95% CI 0.60-0.69), and was substantially lower than that of juveniles that reared upstream. However, my early migrant survival estimates are analogous to apparent survival in CJS models, as it is likely that at any given week, substantial numbers of fish could permanently migrate to an unobservable state (e.g., Humboldt Bay, Pacific Ocean).

Based on results from my model, smaller fish were predicted to have lower winter survival rates in the upstream rearing state when compared to larger conspecifics. There could be multiple explanations for this relationship. For example, a size-dependent dominance hierarchy could reduce fitness for smaller individuals competing for resources such as food, cover, and flow refugia (Chapman 1962). Alternatively, predators in Freshwater Creek may be limited by gape size, and prey more frequently on smaller fish, as has been demonstrated with other salmonids (Parker 1971; Hargreaves and LeBrasseur 1986). Studies suggesting that fish size has a positive effect on winter survival rates (Quinn and Peterson 1996; Ebersole et al. 2006), did not account for a size-dependent relationship with early migration. Use of the multi-state model was advantageous in evaluating the relationship between fish size and survival of spring migrants, as it accounted for early migrants within the model.

Estimates for early migration rates indicate that a large percentage of juveniles migrate downstream in the fall and winter in Freshwater Creek. Over four years, estimates for early migration in this study ranged from 0.34 (95% CI 0.32-0.36) to 0.40 (95% CI 0.38-0.43), which was slightly larger than previous estimates within Freshwater Creek (2-35%) (Rebenack et al. 2015; Ward and Anderson 2016), were comparable to Oregon estimates (25-40%) (Miller and Sadro 2003; Jones et al. 2014), and were lower than Washington estimates (44-84%) (Roni et al. 2012). These results suggest that early migration into the estuary or ocean is common life history strategy for Coho salmon and these non-natal rearing habitats are potentially extremely valuable to population production and sustainability.

Based on results from my model, smaller fish were predicted to have higher rates of early migration when compared to larger conspecifics. Roni et al. (2012) also observed a similar size dependent relationship for early migrants. It may be that with limited habitat, a dominance hierarchy influences the downstream displacement of smaller fish, as was demonstrated by Chapman (1962). However, historically low abundances of adults returning in recent years could suggest that density-independent drivers could be affecting early emigration. Perhaps juvenile Coho Salmon emigrate early to the estuary to have access to new rearing opportunities that may provide better food resources. Moreover, multiple migration patterns may exist to promote resiliency within a population. Perhaps these smaller individuals are utilizing estuarine food resources to achieve a larger size before ocean entry. Coho Salmon that rear in the estuary may have higher growth rates than fish that remain upstream (Koski 2009), and larger individuals generally have higher marine survival (Holtby et al. 1990; Bennett et al. 2015). Perhaps more importantly, recent studies in Oregon and Washington have shown that early migrants can make substantial contributions to adult returns (Jones et al. 2014; Bennett et al. 2015). Further research in Freshwater Creek, with increased tagging rates of both early- and spring- migrants, is necessary to more accurately determine if there are any differences in marine survival rates between individuals that express these two different life histories.

Stream flow appeared to have a positive effect on rates of early emigration. However, this relationship was not as strong as was suspected, as the 95% confidence interval for the beta parameter overlapped 0. I speculate that the reason for this is because that in addition to stream flow affecting movement rates, timing of increased runoff is also important. Perhaps there is a major redistribution of fish with the first round of winter freshets, followed by minimal movement, as was observed by Roni et al. (2012). In a general sense, fish could move when stream flow increases, but that rate of movement decreases through time. Stream flow has previously been shown to affect movement rates of juvenile Coho Salmon (Hartman et al. 1982; Tschaplinski and Hartman 1983; Giannico and Healey 1998), but the exact mechanism has yet to be examined. It may be that these fish are being forced downstream during higher flows, or they are moving of their own volition to exploit estuarine resources. If juvenile Coho Salmon are moving involuntarily in response to higher streamflow, variation in precipitation and runoff patterns due to drought, climate change, or the Pacific Decadal Oscillation could affect early emigration rates. Alternatively, fish may be moving voluntarily as connectivity increases with higher streamflow. Perhaps early migration is an expression of an alternate life history strategy that could promote resiliency within the population. Research has shown that diversity within adult salmonids provides stability within metapopulations (Schindler et al. 2010; Carlson and Satterthwaite 2011). It could be that diversity within juvenile portion of the life-cycle, specifically differences in migration timing, may have a portfolio effect on the population level.

Potential Biases and Future Research

Although my research has accounted for some of the bias inherent in previous methodology, some potential biases remain. This project did not account for any PIT tag loss or mortality as a result of tagging, but any tag loss or tag induced mortality would bias survival low. I assumed that the effects of mortality related to tagging were minimal. Rebenack (2015) found zero PIT tag induced mortality in her study, and methods for tagging remained unchanged for my project in Freshwater Creek. Tag loss was estimated to be 5% in Prairie Creek, California (Bell et al. 2001). However my project utilized fish that were larger by 10 mm in fork length, and other research suggests fork length has a positive effect on tag retention rates (Tiffan et al. 2015). Another source of potential bias is the presence of fish that do not migrate downstream during the course of the study. Some juvenile Coho salmon do stay in Freshwater Creek for up to two years. Bell (2007) found that 28% of fish displayed the 2-year residency life history in for one of the years in his study, and that the 2-year residency has a negative relationship with fish size. It is possible any potential bias caused by 2-year residency was somewhat reduced by the size of fish that I was tagging, as the individuals used in my project were larger than those used by Bell (2007) and Rebenack (2015).

It was advantageous to work in Freshwater Creek, as it has many antenna sites. However, none of the PIT tag readers can detect fish that are tagged with FDX tags. Use of FDX tags would allow for tagging and therefore detection of smaller fish, but antennas that can detect both HDX and FDX tags are costly, and many monitoring and research projects are limited by funding. It would also be interesting to use my study design in other coastal streams in northern California to compare results among different basins. However, other basins typically do not have as many antenna sites as Freshwater Creek. The use of time varying occasions on a weekly time step makes for a very low return rate in the encounter history, so it would seem that having more antennas in the study area would be beneficial. It is likely that my project would have not been possible without the large quantity of PIT tag antennas maintained throughout Freshwater Creek.

Although my modeling approach provides new insight into the dynamics of winter survival and movement of juvenile Coho Salmon, there is potential for future research. I did not account for individual heterogeneity in detection probability. An individual fish must move and swim past an antenna to be detected. Some fish will move during some weeks, and others will not. I used group covariates for the year and tagging reach to account for some sources of variation in detection probability, but there is likely heterogeneity on the individual level that I was unable to account for with my model in Program Mark. A Bayesian approach using a random effect for individual heterogeneity in detection could be used to potentially improve model performance.

Conclusions

Previously low estimates for apparent overwinter survival using CJS models (Rebenack et al. 2015; Ward and Anderson 2016) suggested that survival of juvenile Coho Salmon during the winter could limit smolt production of spring migrants in Freshwater Creek, but these estimates were inherently biased low because they did not include emigration from study area. This potential source of bias was suspected by Brakensiek and Hankin (2007), and demonstrated by Rebenack et al. (2015) and this study. My results provide evidence that a large percentage of these apparent mortalities in Freshwater Creek are early emigrants. High rates of early migration downstream could indicate a lack of suitable winter rearing habitat, or a life history strategy that provides juveniles with opportunities for increased growth in an estuarine environment. Future research examining relationships between density of juveniles and early migration rates could provide some insight into potential drivers in downstream movement. Preferred winter habitat for juvenile Coho Salmon rearing upstream consists of pools having low water velocity including backwaters, alcoves, and beaver ponds (Nickelson et al. 1992; Bell et al. 2001). My results provide evidence that survival rates are high for fish that rear upstream throughout the winter. Thus, restoration aimed at increasing the amount of winter rearing habitat may increase retention in natal rearing environments. However, given that a large percentage of juveniles are moving downstream in the fall and winter, restoration in the estuary would likely benefit the early migrants. Freshwater Creek and many other estuaries in the Pacific Northwest have been highly altered. Streams have been diked and channelized, resulting in a reduction in habitat loss and degradation. Restoration aimed at providing fish passage through modification of tide gates, as well as creation of new off-channel features are often utilized immediately (Wallace et al. 2015). Historically, research and restoration for Coho Salmon has been focused on improving habitat higher in the watershed. However, given that large percentages of juveniles utilize downstream rearing environments, further research and monitoring would likely be important in guiding restoration efforts that promote resiliency and potential recovery of Coho Salmon.

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APPENDIX A

Appendix A: Model parameters and associated models for survival (*S*), movement (ψ), and detection (*p*). All possible combinations of each parameter model were run.

Model Parameter and Model	Description
S~	
Season*Strata	Survival is estimated independently for each season and strata
Season*Strata*Year	Survival is estimated independently for each season, strata and year
Season*Strata*Year+Reach	Survival is estimated independently for each season, strata and year, with an additive effect of reach
ψ (A to B)~	
Season	Movement is estimated independently for each season
Season*Year+Reach	Movement is estimated independently for each season and Year, with an additive effect of reach
p~	
Season*Year+Reach	Detection is estimated independently for each season and year, with an additive effect of reach
Season*Strata*Year	Detection is estimated independently for each season, strata and year
Season*Strata*Year+Reach	Detection is estimated independently for each season, strata and year, with an additive effect of reach

APPENDIX B

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model.

```
install.packages("RMark")
install.packages("dplyr")
library(RMark)
library(dplyr)


#Assign number of simulations to run and create matrix to store results for parameters of interest
nsims<-1000
results<-matrix(nrow=nsims, ncol=6)
colnames(results) <- c("S8day", "Psi8day", "S15day", "Psi15day", "S24day", "Psi24day")



nA=1600                              #Number Marked in State A
nB=400                               #Number Marked in State B
nC=0                                 #Number Marked in State C
occasions=241                        #Number of Occasions
seasons <- (occasions-1)/2           #Number of intervals per season

#Seasonal Survival in states A, B, and C
SA_Winter <- 0.3
SA_Spring <- 0.6
SB_Winter <- 0.3
SB_Spring <- 0.6
SC_Winter <- 0.3
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
SC_Spring <- 0.3


#Seasonal detection in states A, B, and C
pA_Winter <- 0.2
pA_Spring <- 0.3
pB_Winter <- 0.2
pB_Spring <- 0.5
pC_Winter <- 0
pC_Spring <- 0

#Seasonal movement in states A, B, and C
psiAB_Winter <- 0.2
psiAB_Spring <- 0.5
psiBC_Winter <- 0.2
psiBC_Spring <- 0.5
psiCB_Winter <- 0
psiCB_Spring <- 0

#Daily Survival
SA1 <- SA_Winter^(1/seasons)
SA2 <- SA_Spring^(1/seasons)
SB1 <- SB_Winter^(1/seasons)
SB2 <- SB_Spring^(1/seasons)
SC1 <- SC_Winter^(1/seasons)
SC2 <- SC_Spring^(1/seasons)

#Daily Detection
pA1 <- 1-((1-pA_Winter)^(1/seasons))
pA2 <- 1-((1-pA_Spring)^(1/seasons))
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
pB1 <- 1-((1-pB_Winter)^(1/seasons))
pB2 <- 1-((1-pB_Spring)^(1/seasons))
pC1 <- pC_Winter/seasons
pC2 <- pC_Spring/seasons

#Daily Movement (No movement from A to B or from C to B in this simulation)
psiAB1 <- 1-((1-psiAB_Winter)^(1/seasons))
psiAB2 <- 1-((1-psiAB_Spring)^(1/seasons))
psiBC1 <- 1-((1-psiBC_Winter)^(1/seasons))
psiBC2 <- 1-((1-psiBC_Spring)^(1/seasons))
psiCB1 <- psiCB_Winter/seasons
psiCB2 <- psiCB_Spring/seasons

#This step provides parameter values in each state for each interval/occasion
#Parameter values are constant within a season
surv.vectA = c(rep(SA1,seasons), rep(SA2,seasons))
surv.vectB = c(rep(SB1,seasons), rep(SB2,seasons))
surv.vectC = c(rep(SC1,seasons), rep(SC2,seasons))


detect.vectA = c(rep(pA1,seasons), rep(pA2,seasons))
detect.vectB = c(rep(pB1,seasons), rep(pB2,seasons))
detect.vectC = c(rep(pC1,seasons), rep(pC2,seasons))


psi.vectAB <- c(rep(psiAB1,seasons), rep(psiAB2,seasons))
psi.vectBC <- c(rep(psiBC1,seasons), rep(psiBC2,seasons))
psi.vectCB <- c(rep(psiBC1,seasons), rep(psiCB2,seasons))
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
for (s in 1:nsims)
{
#Creates State Matrix (This represents the 'true' or latent state of the individual)
  stateMat <- data.frame(matrix(nrow=nA+nB+nC, ncol=(occasions)))
  names(stateMat) = c(1:occasions)

  #Populate first occasion with marked animals
  stateMat[,1] = c(rep(1, nA), rep(2, nB), rep(3, nC))


  #Create Encounter History Matrix (This represents the observed state of the individual)
  EH = data.frame(matrix(nrow=nA+nB+nC, ncol=(occasions)))
  names(EH) = c(1:occasions)
  EH[,1] = c(rep(1, nA), rep(2, nB), rep(3, nC)) #Populate first occasion with marked animals

  ##################################################
  #Simulates encounter history on a daily time step
  ##################################################
  for (row in 1:nrow(EH))
  {
    for (col in 2:ncol(EH))
    {

      if(stateMat[row,col-1]==1) #If animal was in state A in occ-1...
      {
        survA = runif(1)

        if(survA <= surv.vectA[col-1]) #If animal survived in state A...
        {
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
transAB <- runif(1)
if(transAB >= psi.vectAB[col-1]) #If animal stayed in state A after surviving...
{
  stateMat[row,col]=1 #Assigns 1 in State Matrix for animal that is in state A

  detectA = runif(1)
  if(detectA <= detect.vectA[col-1]) #If animal was detected in state A...
  {
    EH[row, col]=1 #Assigns 1 in Encounter History for animal detected in state A
  }else #...animal not detected in state A

  {
    EH[row, col]=0 #Assigns 0 in Encounter History for animal that was not detected
  }

}else#...animal survived in state A and moved to state B

{
  stateMat[row,col]=2 #Assigns 2 in State Matrix for animal that is in state B
  detectB = runif(1)
  if(detectB <= detect.vectB[col-1]) #If animal was detected in State B...
  {
    EH[row,col]=2 #Assigns 2 in Encounter History for animal detected in state B
  }else #...animal not detected in state B

  {
    EH[row, col]=0 #Assigns 0 in Encounter History for animal that was not detected
  }
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
  }
 }else#...animal did not survive in state A and was not encountered

 {
  stateMat[row,col:ncol(stateMat)]=0 #Assigns 0 in State Matrix for dead animal
  EH[row, col:ncol(EH)] = 0 #Assigns 0 in Encounter History for animal that was not detected
  break
 }

}else#...animal was not in state A on occ-1


 if(stateMat[row,col-1]==2) #If animal was in state B in occ-1...
 {
  survB = runif(1)
  if(survB <= surv.vectB[col-1]) #If animal survived in state B...
  {
   transBC <- runif(1)
   if(transBC >= psi.vectBC[col-1]) #If animal stayed in state B after surviving...
   {
    stateMat[row,col]=2 #Assigns 2 in State Matrix for animal that is in state B
    detectB = runif(1)

    if(detectB <= detect.vectB[col-1]) #If animal was detected in state B...
    {
     EH[row, col]=2 #Assigns 2 in Encounter History for animal detected in state B
    } else #...animal not detected in State B

    {
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
        EH[row, col]=0 #Assigns 0 in Encounter History for animal that was not detected
      }
    }else #...Animal survived in state B and moved to state C

    {
      stateMat[row,col]=3 #Assigns 3 in State Matrix for animal that is in state C
      detectC = runif(1)

      if(detectC <= detect.vectC[col-1]) #If animal was detected in State C...
      {
        EH[row,col]=3 #Assigns 3 in Encounter History for animal detected in state C
      }else #...Animal not detected in State C

      {
        EH[row, col]=0 #Assigns 0 in Encounter History for animal that was not detected
      }
    }

  }else #Animal did not survive and was not detected


  {
    stateMat[row,col:ncol(stateMat)]=0 #Assigns 0 in State Matrix for dead animal
    EH[row, col:ncol(stateMat)] = 0 #Assigns 0 in Encounter History if dead or undetected
    break

  }

}else#...Animal was not in State A or B in occ-1
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
if(stateMat[row,col-1]==3) #If animal was in State C in occ-1...
{
  survC = runif(1)
  if(survC <= surv.vectC[col-1]) #If animal survived in state C...
  {
    transCB <- runif(1)
    if(transCB >= psi.vectCB[col-1]) #If animal stayed in state C after surviving
    {
      stateMat[row,col]=3 #Assigns 3 in State Matrix for animal that is in state C
      detectC = runif(1)

      if(detectC <= detect.vectC[col-1]) #If animal was detected in State C...
      {
        EH[row, col]=3 #Assigns 3 in Encounter History for animal detected in state C
      }else #...animal was not detected in State C

      {
        EH[row, col]=0 #Assigns 0 in Encounter History for animal that was not detected
      }

    }else#...animal survived in State C and moved to State B


    {
      stateMat[row,col]=2 #Assigns 2 in State Matrix for animal that is in state B
      detectB = runif(1)

      if(detectB <= detect.vectB[col-1]) #If animal was detected in State B...
      {
        EH[row,col]=2 #Assigns 2 in Encounter History for animal detected in state B
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
                }else #...animal was not detected in State B

                {
                  EH[row, col]=0 #Assigns 0 in Encounter History for animal that was not detected
                }
              }

            }else # Animal did not survive and was not detected

            {
              stateMat[row,col:ncol(stateMat)]=0 #Assigns 0 in State Matrix for dead animal
              EH[row, col:ncol(stateMat)] = 0 #Assigns 0 in Encounter History if dead or undetected
              break

            }

          }else #...animal was not in State A, B, or C in occ-1 (It was dead)


          {
            stateMat[row,col]=0 #Assigns 0 in Encounter History if dead or undetected
          }
    }
  }

EH <- replace(EH, EH==1,"A")
EH <- replace(EH, EH==2,"B")

####################################
#Aggregates data into 8 day time step
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
####################################

intLength <- 8
index <- seq(2, dim(EH)[2], by=intLength)
newDat <- data.frame(matrix(nrow=dim(EH)[1], ncol=length(index)))

for(i in index[-length(index)])
{
  if(i==index[1])
  {
    newDat[,1] <- EH[,1]
    newcol = 2

  }else
    {
    newcol = newcol+1
    }

  startcol <- i
  endcol <- i+intLength-1

  temp <- apply(EH[,startcol:endcol], 1, paste, collapse = '')
  newDat[,newcol] <- 0

  #individuals detected in both state A and B are assigned to state B
  newDat[grep('A', temp), newcol] <- "A"
  newDat[grep('B', temp), newcol] <- "B"
}

#Format data for use in RMark
mark.final<-data.frame(apply(newDat, 1, paste, collapse=""))
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
colnames(mark.final) <- "ch"
mark.final$ch<-as.character(mark.final$ch)
#Process data
mstrata.process=process.data(mark.final,model="Multistrata")

#Create design data (Fixing movement from B to A to zero)
mstrata.ddl=make.design.data(mstrata.process,parameters=
                               list(Psi=list(subtract.stratum=c("A","B"))))
mstrata.ddl$Psi$fix=with(mstrata.ddl, ifelse(mstrata.ddl$Psi$stratum=="B" &
                                            mstrata.ddl$Psi$tostratum=="A", 0, NA))

#Create column in design data for season(Winter = 1, Spring = 0)

mstrata.ddl$S$Winter=1
mstrata.ddl$S$Winter[mstrata.ddl$S$occ>(max(mstrata.ddl$S$occ)/seasons)]=0
mstrata.ddl$S$Winter=factor(mstrata.ddl$S$Winter)

mstrata.ddl$p$Winter=1
mstrata.ddl$p$Winter[mstrata.ddl$p$occ>(max(mstrata.ddl$p$occ)/seasons)]=0
mstrata.ddl$p$Winter=factor(mstrata.ddl$p$Winter)

mstrata.ddl$Psi$Winter=1
mstrata.ddl$Psi$Winter[mstrata.ddl$Psi$occ>(max(mstrata.ddl$p$occ)/seasons)]=0
mstrata.ddl$Psi$Winter=factor(mstrata.ddl$Psi$Winter)

#Create parameter-specific models
p.WinterPlusStratum=list(formula=~-1+Winter:stratum)
S.WinterPlusStratum=list(formula=~-1+Winter:stratum)
Psi.WinterPlusStratum=list(formula=~-1+Winter:stratum:tostratum)
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
#Run model
model <-mark(mstrata.process, mstrata.ddl, model.parameters=list(S=S.WinterPlusStratum,
             p=p.WinterPlusStratum,Psi=Psi.WinterPlusStratum), adjust = FALSE)

model.results <- suppressWarnings(summary(model, se=T))
results[s,1]<- model.results$reals$S[1,3] #extracts survival est
results[s,2] <- model.results$reals$Psi[1,3] #extracts Psi

#After storing results, this will remove any mark files from the working directory
rm(model)
cleanup(ask = FALSE)

#####################################
#Aggregates data into 15 day time step
#####################################

intLength <- 15
index <- seq(2, dim(EH)[2], by=intLength)
newDat <- data.frame(matrix(nrow=dim(EH)[1], ncol=length(index)))

for(i in index[-length(index)])
{
  if(i==index[1])
  {
    newDat[,1] <- EH[,1]
    newcol = 2

  }else
  {
    newcol = newcol+1
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
  }

  startcol <- i
  endcol <- i+intLength-1

  temp <- apply(EH[,startcol:endcol], 1, paste, collapse = '')
  newDat[,newcol] <- 0

  #individuals detected in both state A and B are assigned to state B
  newDat[grep('A', temp), newcol] <- "A"
  newDat[grep('B', temp), newcol] <- "B"
}


#Format data for use in RMark
mark.final<-data.frame(apply(newDat, 1, paste, collapse=""))
colnames(mark.final) <- "ch"
mark.final$ch<-as.character(mark.final$ch)

#Process data
mstrata.process=process.data(mark.final,model="Multistrata")

#Create design data (Fixing movement from B to A to zero)
mstrata.ddl=make.design.data(mstrata.process,parameters=
                               list(Psi=list(subtract.stratum=c("A","B"))))
mstrata.ddl$Psi$fix=with(mstrata.ddl, ifelse(mstrata.ddl$Psi$stratum=="B" &
                                             mstrata.ddl$Psi$tostratum=="A", 0, NA))

#Create column in design data for season(Winter = 1, Spring = 0)
mstrata.ddl$S$Winter=1
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
mstrata.ddl$S$Winter[mstrata.ddl$S$occ>(max(mstrata.ddl$S$occ)/seasons)]=0
mstrata.ddl$S$Winter=factor(mstrata.ddl$S$Winter)
mstrata.ddl$p$Winter=1
mstrata.ddl$p$Winter[mstrata.ddl$p$occ>(max(mstrata.ddl$p$occ)/seasons)]=0
mstrata.ddl$p$Winter=factor(mstrata.ddl$p$Winter)

mstrata.ddl$Psi$Winter=1
mstrata.ddl$Psi$Winter[mstrata.ddl$Psi$occ>(max(mstrata.ddl$p$occ)/seasons)]=0
mstrata.ddl$Psi$Winter=factor(mstrata.ddl$Psi$Winter)

#Create parameter-specific models
p.WinterPlusStratum=list(formula=~-1+Winter:stratum)
S.WinterPlusStratum=list(formula=~-1+Winter:stratum)
Psi.WinterPlusStratum=list(formula=~-1+Winter:stratum:tostratum)

#Run model
model2 <-mark(mstrata.process, mstrata.ddl, model.parameters=list(S=S.WinterPlusStratum,
              p=p.WinterPlusStratum,Psi=Psi.WinterPlusStratum), adjust = FALSE)

model2.results <-suppressWarnings(summary(model2, se=T))
results[s,3]<- model2.results$reals$S[1,3] #extracts survival est
results[s,4] <- model2.results$reals$Psi[1,3] #extracts Psi

#After storing results, this will remove any mark files from the working directory
rm(model2)
cleanup(ask = FALSE)


#####################################
#Aggregates data into 24 day time step
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```r
#####################################

intLength <- 24
index <- seq(2, dim(EH)[2], by=intLength)
newDat <- data.frame(matrix(nrow=dim(EH)[1], ncol=length(index)))

for(i in index[-length(index)])
{
  if(i==index[1])
  {
    newDat[,1] <- EH[,1]
    newcol = 2

  }else
  {
    newcol = newcol+1
  }

  startcol <- i
  endcol <- i+intLength-1

  temp <- apply(EH[,startcol:endcol], 1, paste, collapse = '')
  newDat[,newcol] <- 0

  #individuals detected in both state A and B are assigned to state B
  newDat[grep('A', temp), newcol] <- "A"
  newDat[grep('B', temp), newcol] <- "B"
}
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
#Format data for use in RMark
mark.final<-data.frame(apply(newDat, 1, paste, collapse=""))
colnames(mark.final) <- "ch"
mark.final$ch<-as.character(mark.final$ch)


#Process data
mstrata.process=process.data(mark.final,model="Multistrata")

#Create design data (Fixing movement from B to A to zero)
mstrata.ddl=make.design.data(mstrata.process,parameters=
                               list(Psi=list(subtract.stratum=c("A","B"))))
mstrata.ddl$Psi$fix=with(mstrata.ddl, ifelse(mstrata.ddl$Psi$stratum=="B" &
                                             mstrata.ddl$Psi$tostratum=="A", 0, NA))

#Create column in design data for season(Winter = 1, Spring = 0)
mstrata.ddl$S$Winter=1
mstrata.ddl$S$Winter[mstrata.ddl$S$occ>(max(mstrata.ddl$S$occ)/seasons)]=0
mstrata.ddl$S$Winter=factor(mstrata.ddl$S$Winter)

mstrata.ddl$p$Winter=1
mstrata.ddl$p$Winter[mstrata.ddl$p$occ>(max(mstrata.ddl$p$occ)/seasons)]=0
mstrata.ddl$p$Winter=factor(mstrata.ddl$p$Winter)

mstrata.ddl$Psi$Winter=1
mstrata.ddl$Psi$Winter[mstrata.ddl$Psi$occ>(max(mstrata.ddl$p$occ)/seasons)]=0
mstrata.ddl$Psi$Winter=factor(mstrata.ddl$Psi$Winter)

#Create parameter-specific models
p.WinterPlusStratum=list(formula=~-1+Winter:stratum)
```

Appendix B: R code for simulating an encounter histories of aggregated detection data evaluation in a multi-state mark-recapture model (continued).

```
S.WinterPlusStratum=list(formula=~-1+Winter:stratum)
Psi.WinterPlusStratum=list(formula=~-1+Winter:stratum:tostratum)

#Run model
model3 <-mark(mstrata.process, mstrata.ddl, model.parameters=list(S=S.WinterPlusStratum,
              p=p.WinterPlusStratum,Psi=Psi.WinterPlusStratum), adjust = FALSE)

model3.results <-suppressWarnings(summary(model3, se=T))
results[s,5]<- model3.results$reals$S[1,3] #extracts survival est
results[s,6] <- model3.results$reals$Psi[1,3] #extracts Psi

#After storing results, this will remove any mark files from the working directory
rm(model3)
cleanup(ask = FALSE)

}

#Creates a csv file for the simulation results
write.csv(results, "G:/My Drive/Sim Results/N2000_S0.3_Psi0.1.csv")
```

APPENDIX C

Appendix C: Weekly survival probabilities for state and season.

State	Season	Estimate	95% CI Lower	95% CI Upper
Upstream	Winter	0.996565	0.9806255	0.999399
Upstream	Spring	0.99618	0.5787837	0.9999798
Downstream	Winter	0.979132	0.9624786	0.9884819
Downstream	Spring	0.845668	0.8193503	0.8687652

APPENDIX D

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River.

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2013	1	0.0186392	0.0143961	0.0241022	10.92
2013	2	0.0185994	0.0143446	0.0240855	8.43
2013	3	0.0185976	0.0143422	0.0240848	8.32
2013	4	0.0185947	0.0143385	0.0240836	8.14
2013	5	0.0186099	0.0143582	0.0240899	9.09
2013	6	0.0186486	0.0144083	0.0241062	11.50
2013	7	0.0188448	0.0146614	0.0241927	23.69
2013	8	0.0186422	0.0144000	0.0241035	11.11
2013	9	0.0189544	0.0148016	0.0242438	30.44
2013	10	0.0187110	0.0144891	0.0241331	15.40
2013	11	0.0186420	0.0143998	0.0241034	11.10
2013	12	0.0186093	0.0143573	0.0240896	9.05
2013	13	0.0185873	0.0143288	0.0240805	7.68
2013	14	0.0189656	0.0148159	0.0242491	31.13
2013	15	0.0187453	0.0145334	0.0241481	17.53

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2013	16	0.0186211	0.0143727	0.0240946	9.79
2013	17	0.0189545	0.0148017	0.0242438	30.45
2013	18	0.0206420	0.0167994	0.0253408	129.83
2013	19	0.0302127	0.0204476	0.0444300	576.14
2013	20	0.0218101	0.0179106	0.0265355	194.06
2013	21	0.0204891	0.0166349	0.0252135	121.16
2013	22	0.0000084	0.0000035	0.0000200	496.96
2013	23	0.0036733	0.0026241	0.0051397	239.87
2013	24	0.1434735	0.1260445	0.1628635	78.69
2013	25	0.0003909	0.0002302	0.0006637	334.64
2013	26	0.0270525	0.0225258	0.0324587	154.54
2013	27	0.1836166	0.1609144	0.2087251	66.25
2013	28	0.2768944	0.2412790	0.3155804	43.77
2013	29	0.2387373	0.2084365	0.2719297	52.21
2013	30	0.3142394	0.2734990	0.3580574	36.19
2013	31	0.1695755	0.1487540	0.1926519	70.33
2013	32	0.3080193	0.2681234	0.3510044	37.41

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2013	33	0.3594213	0.3127056	0.4089633	27.64
2013	34	0.3972657	0.3458282	0.4510784	20.84
2013	35	0.4189399	0.3649459	0.4749480	17.05
2013	36	0.4371690	0.3811209	0.4948688	13.90
2013	37	0.4485212	0.3912422	0.5071993	11.96
2013	38	0.4138762	0.3604688	0.4693889	17.93
2014	1	0.0185457	0.0142747	0.0240633	5.07
2014	2	0.0188144	0.0146223	0.0241789	21.81
2014	3	0.0205327	0.0166822	0.0252491	123.64
2014	4	0.0196268	0.0156394	0.0246053	71.04
2014	5	0.0188602	0.0146811	0.0241997	24.64
2014	6	0.0197518	0.0157900	0.0246827	78.44
2014	7	0.0239385	0.0192417	0.0297469	302.90
2014	8	0.0205934	0.0167476	0.0252997	127.08
2014	9	0.0218053	0.0179067	0.0265298	193.81
2014	10	0.0237178	0.0191407	0.0293566	292.07
2014	11	0.0377155	0.0206691	0.0678467	838.36

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2014	12	0.0233509	0.0189559	0.0287349	273.83
2014	13	0.0199432	0.0160168	0.0248079	89.68
2014	14	0.0193573	0.0153088	0.0244498	54.93
2014	15	0.0220603	0.0181127	0.0268448	207.38
2014	16	0.0200180	0.0161041	0.0248591	94.04
2014	17	0.0207087	0.0168699	0.0253984	133.59
2014	18	0.0251617	0.0196865	0.0321098	361.26
2014	19	0.0208049	0.0169702	0.0254837	139.00
2014	20	0.0196030	0.0156105	0.0245910	69.63
2014	21	0.0193186	0.0152607	0.0244288	52.61
2014	22	0.3094455	0.2693556	0.3526225	37.13
2014	23	0.2960258	0.2577697	0.3373788	39.82
2014	24	0.0300814	0.0252144	0.0358532	149.92
2014	25	0.0564776	0.0488876	0.0651652	122.15
2014	26	0.1483973	0.1303404	0.1684711	77.02
2014	27	0.1494396	0.1312490	0.1696589	76.68
2014	28	0.2651701	0.2311838	0.3021890	46.28

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2014	29	0.3340836	0.2906811	0.3804904	32.36
2014	30	0.3703984	0.3222826	0.4212329	25.64
2014	31	0.3931736	0.3422317	0.4465506	21.56
2014	32	0.4076382	0.3549625	0.4625257	19.02
2014	33	0.4155893	0.3619826	0.4712707	17.63
2014	34	0.4297039	0.3744857	0.4867285	15.19
2014	35	0.4436024	0.3868519	0.5018638	12.80
2014	36	0.4617670	0.4031017	0.5215106	9.70
2014	37	0.4697895	0.4103120	0.5301377	8.34
2014	38	0.4791011	0.4187080	0.5401113	6.76
2015	1	0.0185194	0.0142405	0.0240526	3.41
2015	2	0.0185466	0.0142760	0.0240637	5.13
2015	3	0.0185905	0.0143330	0.0240818	7.88
2015	4	0.0186896	0.0144615	0.0241238	14.07
2015	5	0.0186435	0.0144017	0.0241041	11.19
2015	6	0.0189977	0.0148567	0.0242645	33.10
2015	7	0.0189996	0.0148592	0.0242654	33.22

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2015	8	0.0186128	0.0143620	0.0240911	9.27
2015	9	0.0213612	0.0175157	0.0260285	169.78
2015	10	0.0359396	0.0206490	0.0618380	781.17
2015	11	0.0388731	0.0206768	0.0719070	874.26
2015	12	0.0307111	0.0204792	0.0458160	595.42
2015	13	0.0219644	0.0180368	0.0267240	202.29
2015	14	0.0220271	0.0180866	0.0268027	205.63
2015	15	0.0361863	0.0206525	0.0626565	789.27
2015	16	0.0269676	0.0200930	0.0361078	442.55
2015	17	0.0281500	0.0202606	0.0389892	492.95
2015	18	0.0210264	0.0171946	0.0256898	151.35
2015	19	0.0198035	0.0158517	0.0247157	81.48
2015	20	0.0217688	0.0178761	0.0264864	191.85
2015	21	0.0202593	0.0163802	0.0250336	108.01
2015	22	0.0002031	0.0001129	0.0003654	362.30
2015	23	0.0000005	0.0000002	0.0000016	613.50
2015	24	0.0001489	0.0000805	0.0002753	375.41

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2015	25	0.0092223	0.0071018	0.0119682	200.76
2015	26	0.1141247	0.1002943	0.1295876	89.78
2015	27	0.2080113	0.1819765	0.2366930	59.70
2015	28	0.1607547	0.1410964	0.1825697	73.03
2015	29	0.1183268	0.1039977	0.1343343	88.05
2015	30	0.1752154	0.1536425	0.1991049	68.66
2015	31	0.2726592	0.2376316	0.3107456	44.67
2015	32	0.3339041	0.2905255	0.3802880	32.40
2015	33	0.3443190	0.2995653	0.3920166	30.43
2015	34	0.3862870	0.3361877	0.4389157	22.78
2015	35	0.4130124	0.3597056	0.4684394	18.08
2015	36	0.4254102	0.3706765	0.4820354	15.93
2015	37	0.4373121	0.3812482	0.4950245	13.88
2015	38	0.4506923	0.3931822	0.5095506	11.59
2016	1	0.0185486	0.0142785	0.0240645	5.25
2016	2	0.0213747	0.0175282	0.0260429	170.52
2016	3	0.0207860	0.0169506	0.0254667	137.94

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2016	4	0.0219992	0.0180645	0.0267675	204.14
2016	5	0.0203887	0.0165247	0.0251332	115.43
2016	6	0.0207989	0.0169640	0.0254782	138.66
2016	7	0.0233202	0.0189395	0.0286845	272.29
2016	8	0.0260742	0.0199204	0.0340630	403.02
2016	9	0.0209159	0.0170839	0.0255853	145.21
2016	10	0.0370693	0.0206631	0.0656288	817.85
2016	11	0.0235332	0.0190504	0.0290395	282.93
2016	12	0.0215162	0.0176568	0.0261967	178.22
2016	13	0.0233421	0.0189512	0.0287204	273.39
2016	14	0.0323087	0.0205569	0.0504326	655.22
2016	15	0.0258860	0.0198776	0.0336482	394.52
2016	16	0.0271822	0.0201279	0.0366165	451.85
2016	17	0.0209618	0.0171301	0.0256282	147.76
2016	18	0.0355676	0.0206432	0.0606143	768.84
2016	19	0.0280979	0.0202544	0.0388585	490.77
2016	20	0.0365130	0.0206568	0.0637484	799.93

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2016	21	0.0241899	0.0193482	0.0302059	315.13
2016	22	0.0000015	0.0000005	0.0000042	569.78
2016	23	0.0047526	0.0034688	0.0065086	228.94
2016	24	0.0000028	0.0000010	0.0000073	543.90
2016	25	0.0000404	0.0000194	0.0000839	430.52
2016	26	0.0119737	0.0094095	0.0152259	189.61
2016	27	0.0085597	0.0065529	0.0111743	203.93
2016	28	0.0077469	0.0058837	0.0101942	208.18
2016	29	0.0006255	0.0003839	0.0010192	314.76
2016	30	0.0242692	0.0200662	0.0293263	159.24
2016	31	0.1070526	0.0940478	0.1216141	92.82
2016	32	0.0669164	0.0582684	0.0767433	114.52
2016	33	0.1662258	0.1458479	0.1888216	71.34
2016	34	0.2418833	0.2111437	0.2755350	51.48
2016	35	0.2745092	0.2392247	0.3128579	44.28
2016	36	0.3013322	0.2623489	0.3434114	38.75
2016	37	0.3648825	0.3174673	0.4150728	26.64

Appendix D: Weekly early emigration rates, and average weekly streamflow at Little River (continued).

Year	Week	Estimate	95% CI Lower	95% CI Lower	Average Streamflow (cfs)
2016	38	0.3957026	0.3444539	0.4493496	21.11

APPENDIX E

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged.

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Downstream	2013	Winter	978	0.017	0.013	0.022
Downstream	2013	Spring	978	0.074	0.059	0.091
Downstream	2014	Winter	978	0.025	0.019	0.033
Downstream	2014	Spring	978	0.055	0.043	0.071
Downstream	2015	Winter	978	0.007	0.004	0.011
Downstream	2015	Spring	978	0.042	0.031	0.057
Downstream	2016	Winter	978	0.014	0.010	0.020
Downstream	2016	Spring	978	0.040	0.030	0.054
Upstream	2013	Winter	979	0.004	0.003	0.005
Upstream	2013	Spring	979	0.022	0.016	0.030
Downstream	2013	Winter	979	0.028	0.021	0.037

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged (continued).

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Downstream	2013	Spring	979	0.117	0.095	0.144
Upstream	2014	Winter	979	0.004	0.003	0.005
Upstream	2014	Spring	979	0.017	0.012	0.026
Downstream	2014	Winter	979	0.041	0.030	0.055
Downstream	2014	Spring	979	0.089	0.072	0.109
Upstream	2015	Winter	979	0.003	0.002	0.005
Upstream	2015	Spring	979	0.008	0.004	0.015
Downstream	2015	Winter	979	0.011	0.007	0.019
Downstream	2015	Spring	979	0.068	0.051	0.090
Upstream	2016	Winter	979	0.002	0.001	0.004
Upstream	2016	Spring	979	0.009	0.006	0.013
Downstream	2016	Winter	979	0.023	0.016	0.033
Downstream	2016	Spring	979	0.065	0.050	0.084

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged (continued).

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Upstream	2013	Winter	980	0.003	0.002	0.005
Upstream	2013	Spring	980	0.021	0.015	0.029
Downstream	2013	Winter	980	0.026	0.019	0.035
Downstream	2013	Spring	980	0.111	0.088	0.139
Upstream	2014	Winter	980	0.004	0.002	0.005
Upstream	2014	Spring	980	0.016	0.011	0.025
Downstream	2014	Winter	980	0.039	0.028	0.053
Downstream	2014	Spring	980	0.084	0.066	0.106
Upstream	2015	Winter	980	0.003	0.002	0.005
Upstream	2015	Spring	980	0.008	0.004	0.014
Downstream	2015	Winter	980	0.011	0.006	0.018
Downstream	2015	Spring	980	0.064	0.048	0.086
Upstream	2016	Winter	980	0.002	0.001	0.003

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged (continued).

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Upstream	2016	Spring	980	0.008	0.006	0.012
Downstream	2016	Winter	980	0.022	0.015	0.032
Downstream	2016	Spring	980	0.061	0.047	0.080
Upstream	2013	Winter	981	0.006	0.004	0.008
Upstream	2013	Spring	981	0.034	0.025	0.046
Downstream	2013	Winter	981	0.042	0.031	0.057
Downstream	2013	Spring	981	0.170	0.136	0.211
Upstream	2014	Winter	981	0.006	0.004	0.008
Upstream	2014	Spring	981	0.027	0.018	0.040
Downstream	2014	Winter	981	0.062	0.045	0.086
Downstream	2014	Spring	981	0.131	0.104	0.163
Upstream	2015	Winter	981	0.005	0.003	0.008
Upstream	2015	Spring	981	0.013	0.007	0.023

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged (continued).

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Downstream	2015	Winter	981	0.018	0.010	0.029
Downstream	2015	Spring	981	0.102	0.075	0.136
Upstream	2016	Winter	981	0.003	0.002	0.006
Upstream	2016	Spring	981	0.014	0.009	0.020
Downstream	2016	Winter	981	0.035	0.024	0.052
Downstream	2016	Spring	981	0.097	0.073	0.128
Upstream	2013	Winter	1004	0.006	0.005	0.009
Upstream	2013	Spring	1004	0.038	0.028	0.050
Downstream	2013	Winter	1004	0.046	0.034	0.063
Downstream	2013	Spring	1004	0.185	0.149	0.227
Upstream	2014	Winter	1004	0.007	0.005	0.009
Upstream	2014	Spring	1004	0.029	0.020	0.044
Downstream	2014	Winter	1004	0.068	0.049	0.093

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged (continued).

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Downstream	2014	Spring	1004	0.143	0.114	0.177
Upstream	2015	Winter	1004	0.006	0.003	0.009
Upstream	2015	Spring	1004	0.014	0.008	0.025
Downstream	2015	Winter	1004	0.019	0.012	0.032
Downstream	2015	Spring	1004	0.111	0.083	0.147
Upstream	2016	Winter	1004	0.004	0.002	0.006
Upstream	2016	Spring	1004	0.015	0.010	0.022
Downstream	2016	Winter	1004	0.039	0.027	0.056
Downstream	2016	Spring	1004	0.106	0.081	0.139
Upstream	2013	Winter	1014	0.007	0.005	0.009
Upstream	2013	Spring	1014	0.040	0.029	0.054
Downstream	2013	Winter	1014	0.049	0.035	0.067
Downstream	2013	Spring	1014	0.194	0.154	0.241

Appendix E: Weekly detection probabilities for state, year tagged, season, and reach tagged (continued).

State	Year Tagged	Season	Reach Tagged	Estimate	95% CI Lower	95% CI Upper
Upstream	2014	Winter	1014	0.007	0.005	0.010
Upstream	2014	Spring	1014	0.031	0.021	0.047
Downstream	2014	Winter	1014	0.072	0.051	0.100
Downstream	2014	Spring	1014	0.150	0.117	0.190
Upstream	2015	Winter	1014	0.006	0.003	0.010
Upstream	2015	Spring	1014	0.015	0.008	0.027
Downstream	2015	Winter	1014	0.020	0.012	0.034
Downstream	2015	Spring	1014	0.117	0.087	0.157
Upstream	2016	Winter	1014	0.004	0.002	0.007
Upstream	2016	Spring	1014	0.016	0.011	0.024
Downstream	2016	Winter	1014	0.041	0.028	0.060
Downstream	2016	Spring	1014	0.112	0.084	0.147
Upstream	2013	Winter	978	0.000	0.000	0.000

APPENDIX F

Appendix F: Top model beta parameter estimates for survival (S), detection (p), and movement (ψ) probabilities.

Parameter Type	Beta Parameter	Estimate	Standard Error	95% CI Lower	95% CI Upper
S	Intercept	5.670	1.086	3.542	7.798
S	Spring	-0.107	3.998	-7.944	7.730
S	Downstream	-1.822	1.253	-4.277	0.633
S	Length	0.341	0.068	0.207	0.475
S	Spring*Downstream	-2.041	4.089	-10.055	5.973
p	Intercept	-6.118	0.238	-6.583	-5.652
p	Spring	1.826	0.237	1.361	2.290
p	2014	0.041	0.272	-0.491	0.574
p	2015	-0.122	0.363	-0.832	0.589
p	2016	-0.581	0.383	-1.332	0.170
p	Downstream	2.045	0.261	1.533	2.557

Appendix F: Beta parameter estimates for survival (S), detection (p), and movement (ψ) probabilities (continued).

Parameter Type	Beta Parameter	Estimate	Standard Error	95% CI Lower	95% CI Upper
p	Reach 979	0.512	0.158	0.203	0.821
p	Reach 980	0.449	0.173	0.109	0.788
p	Reach 981	0.948	0.178	0.600	1.296
p	Reach 1004	1.047	0.176	0.703	1.392
p	Reach 1014	1.107	0.187	0.740	1.474
p	Spring*2014	-0.291	0.391	-1.057	0.476
p	Spring*2015	-0.898	0.532	-1.940	0.144
p	Spring*2016	-0.355	0.469	-1.274	0.564
p	Spring*Downstream	-0.284	0.301	-0.874	0.306
p	2014*Downstream	0.367	0.354	-0.326	1.060
p	2015*Downstream	-0.781	0.500	-1.760	0.199
p	2016*Downstream	0.403	0.477	-0.533	1.338
p	Spring*2014*Downstream	-0.427	0.463	-1.335	0.481

Appendix F: Beta parameter estimates for survival (S), detection (p), and movement (ψ) probabilities (continued).

Parameter Type	Beta Parameter	Estimate	Standard Error	95% CI Lower	95% CI Upper
p	Spring*2015* Downstream	1.205	0.644	-0.057	2.467
p	Spring*2016* Downstream	-0.114	0.546	-1.184	0.956
ψ	Intercept	-3.829	0.126	-4.076	-3.581
ψ	Winter*Length	-0.265	0.104	-0.469	-0.061
ψ	Spring*Length	-0.125	0.092	-0.304	0.055
ψ	Winter*Flow	0.182	0.118	-0.049	0.413
ψ	Spring*Flow	-4.924	0.279	-5.471	-4.377