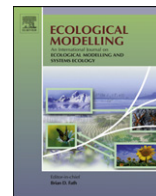




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Using multistate mark-recapture methods to model adult salmonid migration in an industrialized river

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ABSTRACT

A multistate mark-recapture (MSMR) model of the adult salmonid migration through the lower Columbia River and into the Snake River was developed, designed for radiotelemetry detections at dams and tributary mouths. The model focuses on upstream-directed travel, with states determined from observed fish movement patterns indicating directed upstream travel, downstream travel (*fallback*), and use of non-natal tributaries. The model was used to analyze telemetry data from 846 migrating adult spring-summer Chinook salmon (*Oncorhynchus tshawytscha*) tagged in 1996 at Bonneville Dam on the Columbia River. We used the model to test competing hypotheses regarding delayed effects of fallback at dams and visits to tributaries, and to define and estimate migration summary measures. Tagged fish had an average probability of 0.755 ($\widehat{SE} = 0.018$) of ending migration at a tributary or upstream of Lower Granite Dam on the Snake River, and a probability of 0.245 ($\widehat{SE} = 0.018$) of unaccountable loss (i.e., mortality or mainstem spawning) between the release site downstream of Bonneville Dam and Lower Granite Dam. The highest probability of unaccountable loss (0.092; $\widehat{SE} = 0.012$) was in the reach between Bonneville Dam and The Dalles Dam. Study fish used the tributaries primarily as exits from the hydrosystem, and visits to non-natal tributaries had no significant effect on subsequent movement upriver ($P = 0.4245$). However, fallback behavior had a small effect on subsequent tributary entry and exit ($P = 0.0530$), with fish using tributaries as resting areas after reascending Bonneville Dam after fallback. The spatial MSMR model developed here can be adapted to address additional questions about the interaction of migrating organisms with their environment, or for the study of migrations in other river systems.

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1. Introduction

Migratory species play a crucial role in ecological communities, connecting distant ecosystems through transfers of organic matter. From salmon returning to their natal streams to spawn, to songbirds traveling between breeding and wintering grounds, such species bring significant energetic contributions to numerous ecosystems. For example, salmon accrue much of their biomass during the ocean life stage but spawn in freshwater. Their decaying carcasses transfer rich marine-derived nutrients to their inland spawning habitat, thereby increasing productivity of the freshwater ecosystem. Although the migratory life stage is necessary for completing the life cycle, populations often incur high mortality during migration. As society works to protect migratory species from the effects of habitat loss, pollution, overharvest, and climate change, detailed information is needed regarding the migratory life stage: What regions and habitats are utilized and how? Where is survival most threatened during migration, and what are the domi-

nant mortality risks? How do human actions and habitat alteration help or hinder migration?

Pacific salmonids (*Oncorhynchus* spp.) from the Columbia and Snake river basins in the Pacific Northwest region of the United States pass up to nine large hydroelectric dams on both their juvenile migration to the ocean and their adult migration to inland spawning grounds (Fig. 1). With 12 of these populations protected under the Endangered Species Act of 1973 (U.S. Code, Title 16, Chapter 25, sections 1531–1544), much research attention has focused on the migratory life stage through the hydrosystem. Biologists have hypothesized that spawning success is affected by experiences during the adult upriver migration, such as non-natal tributary use and fallback over a dam (descending the dam after ascending it). Dam fallback and other downstream travel during the adult migration have been observed among numerous populations (Dauble and Mueller, 2000). Reischel and Bjornn (2003) and Boggs et al. (2004) hypothesized that fallback hinders migration success by depleting a fish's energy reserves or causing injury or direct mortality. Several researchers have studied non-natal tributary use by migrating adult salmonids. Quinn (1993) reported varying levels of straying to non-natal tributaries among wild and hatchery-produced salmonids, with high straying rates possibly

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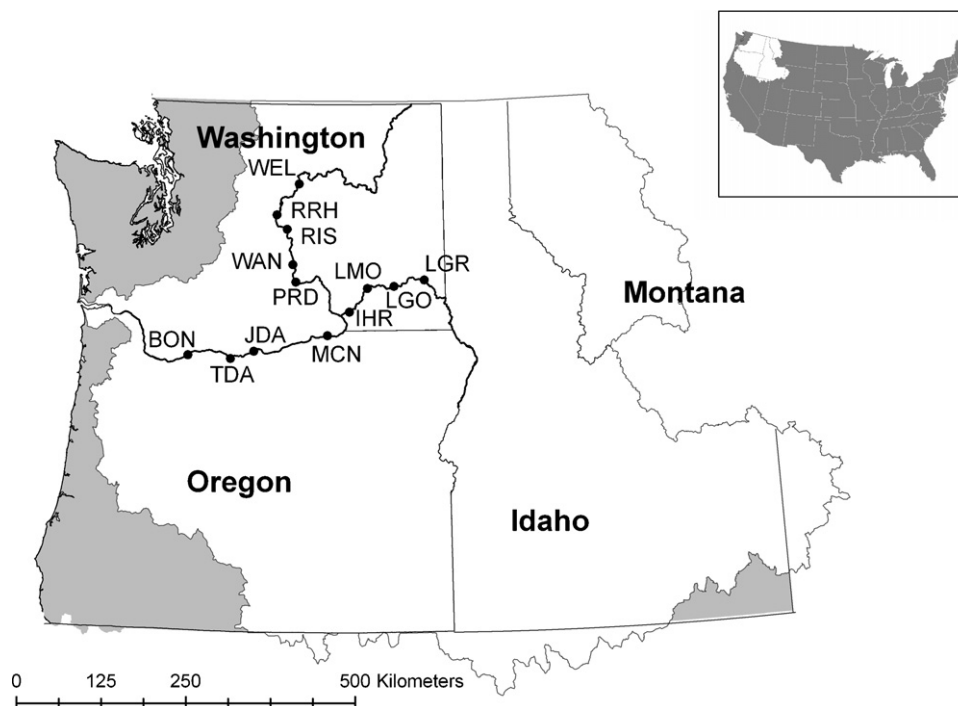


Fig. 1. Map of Columbia River and Snake River basins, with hydroelectric dams noted that were passed by salmon in 1996 release group. BON = Bonneville Dam, TDA = The Dalles, JDA = John Day, MCN = McNary, IHR = Ice Harbor, LMO = Lower Monumental, LGO = Little Goose, LGR = Lower Granite, PRD = Priest Rapids, WAN = Wanapum, RIS = Rock Island, RRH = Rocky Reach, WEL = Wells. The release site was located 9.5 km downstream of BON.

lowering long-term population survival. High et al. (2006) proposed that migrating adult steelhead (*O. mykiss*) temporarily use non-natal tributary rivers as thermal refugia, which may improve migration survival but is also associated with longer travel time. In addition to these issues, the current biological opinion on the federal hydropower system identifies survival during the adult migratory life stage as an important performance measure for fishery management and recovery of the populations (NMFS, 2008). Complex tagging studies have been implemented in order to monitor the salmonid migration.

A useful approach to interpreting highly structured tagging data is the multistate mark-recapture (MSMR) model, a type of capture-mark-recapture (CMR) model. Traditional CMR models assume homogeneous survival and detection (capture) probabilities among the tagged individuals. MSMR models relax that assumption by stratifying the tagged individuals based on their *state*, which may be defined in a variety of ways, such as spatial location or physiological status. MSMR models have been used to estimate exchange among populations or life stages within a population (Nichols et al., 1992, 1993), estimate annual survival in the presence of temporary emigration (Kendall and Nichols, 2002), and explore hypotheses in evolutionary ecology (Nichols and Kendall, 1995). Hestbeck et al. (1991) and Brownie et al. (1993) developed MSMR models to assess the “memory effect” of past experience on current migration behavior. The natural parameter in an MSMR model is the transition probability, which combines both survival and movement among sites or states. MSMR models are often expressed as matrix models, with square matrices representing transition probabilities among states at a given model “step,” which is usually temporal.

Most MSMR models focus on survival or abundance through time. Modeling migration has a spatial focus: transitions occur between spatially disparate sampling sites, and states may be dynamically defined based on past experiences, such as taking a particular migration route. Transition matrices represent joint movement and survival probabilities among states for a particular spatial step, rather than a temporal step. Gener-

ally, one transition matrix is required for each possible spatial step.

MSMR models can be used to test hypotheses concerning migration processes and fish fate. For example, if fallback depletes a fish's energy stores (Reischel and Bjornn, 2003), then survival in subsequent reaches may be lowered. Additionally, if fish use non-natal tributaries as thermal refugia during hot weather (High et al., 2006), then fish that visited a tributary may have a higher probability of successfully passing through the next reach. A competing hypothesis is that fish enter non-natal tributaries primarily as they search for their natal streams (Keefer et al., 2008). In this case, fish that return from tributaries to the mainstem may be expected to continue searching within the following reach, evidenced by additional tributary visits or fallback in that reach. Finally, because fish that recently exited tributaries may be distributed across the river channel differently from other fish, they may have unique detection probabilities at the next dam. Each of these hypotheses can be parameterized in an MSMR model of the adult salmonid migration and tested by comparing the fit of competing models.

In this paper, we present a general approach to modeling complex animal movements during migration. We develop the approach for the upstream migration of adult Chinook salmon (*O. tshawytscha*) in the Columbia and Snake rivers, and demonstrate the model using radiotelemetry detection data from 1996. We model and assess alternative hypotheses regarding migration behavior, and estimate summary measures of the migration. The approach developed here may be readily extended to other locations and species that use well-defined migration routes.

2. Methods: adult chinook salmon study

2.1. Study site and release-recapture methods

In 1996, 846 adult spring-summer Chinook salmon of unknown natal origin were collected at Bonneville Dam on the Columbia River (river kilometer 234) (Fig. 1) and outfitted with radio transmitters

from early April through late June (Keefer et al., 2004). The tagged salmon were released about 9.5 km downstream of Bonneville and monitored as they swam upriver. Aerial and underwater radio antenna arrays were positioned at four dams on the lower Columbia River (Bonneville, The Dalles, John Day, and McNary), at three dams on the lower Snake River (Ice Harbor, Lower Monumental, and Lower Granite), and at Priest Rapids Dam on the mid-Columbia River (Fig. 1). At most dams, detections were available from both the entrance (*base-of-dam* or *tailrace*) and exit (*top-of-dam* or *forebay*) of the adult fishways. Forebay antennas were arranged to detect tagged fish only as they exited the fishway. Additional aerial antennas were located near the mouths of major tributaries. Modeling focused on the lower Columbia and Snake rivers, with the mid-Columbia treated as a large tributary.

Detections at dams (*D*) were named $D_k B$ and $D_k T$ for the base-of-dam (*B*) site and top-of-dam (*T*) site, respectively, with $k = 1$ representing Bonneville Dam and $k = 7$ representing Lower Granite Dam. Tributary (*T*) detections between dams k and $k + 1$ were pooled and collectively named T_k . Tributaries downstream of Bonneville Dam were named T_0 . All detections in the mid-Columbia, including detections at Priest Rapids Dam, were included in T_4 .

2.2. Model development

The adult migration model focused on upstream movement and survival through the hydrosystem while also incorporating downstream travel. The model was parameterized as a spatial, multistate, multinomial release-recapture model. The basic spatial unit was the *reach*, i.e., the stretch of river between the tailraces of adjacent monitored dams (Fig. 2). The states in the multistate model represented different types of migration behavior and facilitated analysis of delayed effects of non-directed behavior such as downstream travel. The fundamental model parameters were the transition probabilities ϕ_{ij}^{xy} for transitions from state x at detection site i to state y at site j . The detection processes were modeled at the dams, with detection probability p_i^x for fish in state x at site i . Most tributary receivers used a single array, and so it was not possible to model the tributary detection processes. Tributary use was modeled as either permanent exit from the hydrosystem or temporary tributary visits followed by return to the mainstem river. Downstream

travel, referred to generally as *fallback*, was modeled indirectly as described below.

To quantify the effect of recent migratory behavior on transition probabilities, individuals were assigned states based on observed patterns of detection events indicating directed migration through a reach, tributary visits, or downstream travel (fallback). Distinct transition probabilities between two sites for fish in different states would then indicate a delayed effect of previous migration behavior. All fish were in the directed state (d) at the time of initial release. Fish entered the tributary state (t) upon returning to the mainstem river after visiting a tributary. Fish entered the fallback state (F) after descending a dam or swimming downriver between detection sites, and then either returning to upstream movement or entering a tributary.

All states were modeled as temporary (non-absorbing) conditions. This is equivalent to modeling temporary delayed effects of non-directed behavior. The directed state persisted until the fish exhibited non-directed behavior. The fallback and tributary states persisted until the fish either exhibited new non-directed behavior (resulting in a transition to a new non-directed state), or else exited the reach following the fallback or tributary visit (and thus reverted to the directed state), whichever came first. Because fish in the fallback state could fall back again, two types of fallback state were required to distinguish fish who had recently fallen back (state F) from those who were merely experiencing continued delayed effects of past fallback (state f). Thus, the four states were directed (d), tributary (t), new fallback (F), and old fallback (f). Only the state representing the most recent fallback or tributary visit was modeled.

We incorporated fallback by modeling the ultimate fate in each reach, represented by the final detection event at a dam or tributary. Thus, instead of explicitly modeling downstream travel, we absorbed the underlying probabilities associated with fallback into a single upstream transition probability (ϕ_{ij}^{xF}) to the new fallback state (F). The parameter ϕ_{ij}^{xF} was used to parameterize a detection history if it could be inferred that the fish fell back and then returned to upstream travel between passing site i and reaching site j . Such inference was based on repeated detections at $D_k T$ sites, or upstream detections followed by downstream detections. This modeling approach focused attention on the eventual migration success of the fish, and placed transition probabilities to the fallback state on the same spatial scale as the directed and tributary states. This in turn permitted us to directly test hypotheses about the consequences of fallback relative to the alternative states.

The nature of the observable data meant that not all state transitions were possible for all site transitions. For example, fish were detected at the top of a dam ($D_k T$) only as they exited the fishway from downstream, so no fish could be directly observed entering a new fallback state at $D_k T$. The model structure can be easily visualized using transition matrices (G_{ij}) containing the probabilities of moving between states during the spatial step from site i to j . Each transition matrix is a 4-by-4 matrix representing transitions among the states (d, t, F, f), with rows representing the state the fish is coming from; each row sums to no more than 1.

The matrix $G_{D_k B, D_k T}$ represents state transition probabilities during the ascent of dam k :

$$G_{D_k B, D_k T} = \begin{pmatrix} \phi_{D_k B, D_k T}^{dd} & 0 & 0 & 0 \\ 0 & \phi_{D_k B, D_k T}^{tt} & 0 & 0 \\ 0 & 0 & 0 & \phi_{D_k B, D_k T}^{Ff} \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Fish did not change state during dam ascent, except to transfer from the new fallback state (F) to the old fallback state (f). The row

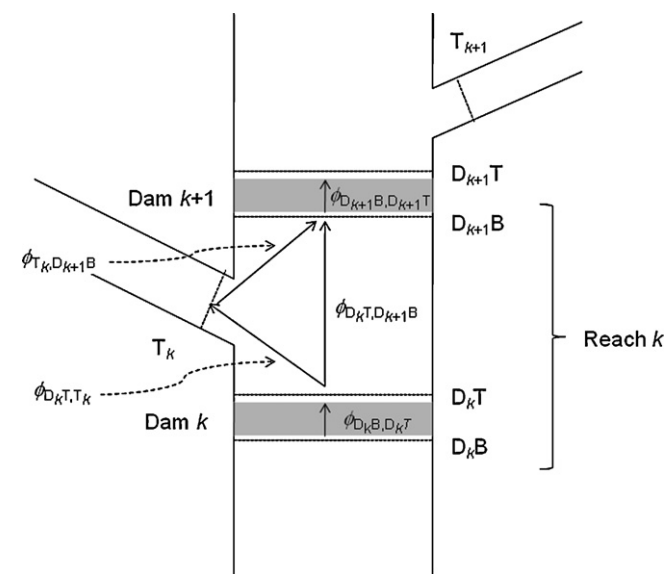


Fig. 2. Schematic diagram of reach k , with dams k and $k + 1$ (shaded rectangles) and tributaries k and $k + 1$ noted. Dotted lines denote antenna receiver arrays, located at the base ($D_k B, D_{k+1} B$) and top ($D_k T, D_{k+1} T$) of the dams and near the tributary mouths (T_k, T_{k+1}). Fundamental transition parameters ϕ_{ij} are indicated (states not shown).

of zeros indicates that no fish arrived at the base of a dam in the old fallback state (f).

The matrix $\mathbf{G}_{D_k T, D_{k+1} B}$ represents state transitions during movements from the top of dam k to the base of the next dam:

$$\mathbf{G}_{D_k T, D_{k+1} B} = \begin{pmatrix} \phi_{D_k T, D_{k+1} B}^{dd} & 0 & \phi_{D_k T, D_{k+1} B}^{dF} & 0 \\ \phi_{D_k T, D_{k+1} B}^{td} & 0 & \phi_{D_k T, D_{k+1} B}^{tF} & 0 \\ 0 & 0 & 0 & 0 \\ \phi_{D_k T, D_{k+1} B}^{fd} & 0 & \phi_{D_k T, D_{k+1} B}^{fF} & 0 \end{pmatrix}$$

Fish could be in any state at $D_k T$ except the new fallback state (F), and either changed to state F or reverted to the directed state during travel to $D_{k+1} B$.

The matrix $\mathbf{G}_{D_k T, T_k}$, for fish moving from the top of dam k to the tributary in that reach, is

$$\mathbf{G}_{D_k T, T_k} = \begin{pmatrix} \phi_{D_k T, T_k}^{dd} & 0 & \phi_{D_k T, T_k}^{dF} & 0 \\ 0 & \phi_{D_k T, T_k}^{tt} & \phi_{D_k T, T_k}^{tF} & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_{D_k T, T_k}^{ff} & \phi_{D_k T, T_k}^{ff} \end{pmatrix}$$

In general, fish changed states between the top of a dam and the next tributary only if they fell back on the way to the tributary. Fish did not enter the tributary state until they were observed exiting the tributary and continuing upriver.

The matrix $\mathbf{G}_{T_k, D_{k+1} B}$ represents state transitions during movement from tributary T_k to the base of the next dam:

$$\mathbf{G}_{T_k, D_{k+1} B} = \begin{pmatrix} 0 & \phi_{T_k, D_{k+1} B}^{dt} & \phi_{T_k, D_{k+1} B}^{dF} & 0 \\ 0 & \phi_{T_k, D_{k+1} B}^{tt} & \phi_{T_k, D_{k+1} B}^{tF} & 0 \\ 0 & \phi_{T_k, D_{k+1} B}^{ft} & \phi_{T_k, D_{k+1} B}^{fF} & 0 \\ 0 & \phi_{T_k, D_{k+1} B}^{ft} & \phi_{T_k, D_{k+1} B}^{fF} & 0 \end{pmatrix}$$

Fish could be in any state at tributary T_k . Because visiting a tributary and then continuing on to the next dam is non-directed behavior, $\mathbf{G}_{T_k, D_{k+1} B}$ includes no transitions into the directed state.

Transition matrices are useful for visualizing model structure and interpreting results but do not account for imperfect detection probabilities (e.g., see Brownie et al., 1993). A non-matrix approach to parameterizing a given detection history uses scalar multiplication. As an example of parameterizing fallback, consider the chronological detection history fragment “R D₁ T D₁ B D₁ T D₂ T...” A fish with this detection history was released downstream of dam 1, moved upstream and ascended dam 1 without detection at the fishway entrance, and was detected at the fishway exit at the top of the dam (i.e., “R D₁ T”). The fish subsequently descended the dam (fell back) and re-entered the fishway at the base of the dam (i.e., segment “D₁ T D₁ B”), and then reascended the dam with detection at the fishway exit. Finally, the fish moved upstream and ascended dam 2 with detection only at the fishway exit. The fallback transition is modeled from the release point (R) to the post-fallback detection at D₁ B (state F), and the old fallback state (f) persists until the end of the following reach. Thus, this fragment has probability $\phi_{R, D_1 B}^{dF} p_{D_1 B}^F \phi_{D_1 B, D_1 T}^{fF} p_{D_1 T}^f \phi_{D_1 T, D_2 B}^{fd} (1 - p_{D_2 B}^d) \phi_{D_2 B, D_2 T}^{dd} p_{D_2 T}^d \dots$. Other detection histories are parameterized using the same rules.

The likelihood model is multinomial under the assumptions of homogeneous state-specific transition (ϕ_{ij}^{xy}) and detection (p_i^x) probabilities and independent fate of individual fish. A mixed-stock release group may violate the first assumption. In this case, point estimates of transition probabilities will be unbiased estimates of the average transition probabilities across the release group,

although standard errors based on the hessian matrix may be too large (Feller, 1950, pp. 230–231).

An exception to the assumption of common detection probabilities was that fallback fish were assumed to be detected at the first dam they reascended after fallback. Detection probabilities were near 1 at most locations, thereby satisfying this assumption. The use of single receiver arrays in the tributary mouths required the assumption of perfect detection probabilities at the tributary arrays. For the 1996 data set, most tributary receivers were in operation at least 90% of the possible operation hours. Only the receiver in the Walla Walla River (1 of 3 receivers comprising site T₄) had significant outages, and it was in operation 54.6% of the time (Bjornn et al., 2000). Overall, site T₄ had receiver coverage approximately 90% of the time (Bjornn et al., 2000).

2.3. Model applications

2.3.1. Derived parameters

A major use of MSMR models is estimation of measures summarizing a system or, in this case, a migration. For a migratory model, these measures include fate and migration behavior and incorporate multiple reaches and states. Such measures can be used to identify areas of high loss or migration stress. These measures are easily defined using the transition matrices and evaluated using the MLEs of the model parameters; standard errors are based on the delta method (Seber, 2002, pp. 7–9).

Unaccountable loss at a site is the probability of failing to successfully reach the next dam site or tributary system. It includes natural mortality as well as harvest, mainstem spawning or other migration cessation, and unknown turnoff to tributaries. Minimizing unaccountable loss in the mainstem river is an important management objective. Unaccountable loss at dam site i , \mathbf{U}_i , is defined as follows (where $\mathbf{e} = (1 \ 1 \ 1 \ 1)'$):

$$\mathbf{U}_i = \begin{cases} \mathbf{e} - \mathbf{G}_{D_k B, D_k T} \mathbf{e}, & i = D_k B; \\ \mathbf{e} - (\mathbf{G}_{D_k T, T_k} + \mathbf{G}_{D_k T, D_{k+1} B}) \mathbf{e}, & i = D_k T. \end{cases}$$

The measure \mathbf{U}_i is a vector representing the state-specific conditional probabilities of unaccountable loss at site i . Unaccountable loss can be extended to the reach level by $\mathbf{U}_k = \mathbf{U}_{D_k B} + \mathbf{G}_{D_k B, D_k T} \mathbf{U}_{D_k T}$ for reach k . The variance-covariance matrix of \mathbf{U}_i , $\mathbf{V}(\hat{\mathbf{U}}_i)$, is estimated by $\mathbf{V}(\hat{\mathbf{U}}_i) = \hat{\mathbf{J}}_i \hat{\mathbf{H}}^{-1} \hat{\mathbf{J}}_i'$, where \mathbf{H} is the hessian of the likelihood function and \mathbf{J}_i is the jacobian for \mathbf{U}_i . The hessian is estimated in the numerical routine used to maximize the likelihood, and the jacobian can be defined analytically or using a symbolic derivative routine (e.g., in Mathematica or Matlab).

Analogous to $\mathbf{U}_{D_k B}$ and $\mathbf{U}_{D_k T}$, the measure \mathbf{U}_{T_k} is the probability of remaining in tributary T_k after entering it, and is defined by $\mathbf{U}_{T_k} = \mathbf{e} - \mathbf{G}_{T_k, D_{k+1} B} \mathbf{e}$. Interpretation of \mathbf{U}_{T_k} depends on the composition of the release group and whether it consists of known-source fish. In our case study using unknown-source fish, we could not differentiate straying from successful return to a natal tributary. High values of \mathbf{U}_{T_k} would be expected for stocks whose natal streams are in the T_k stream network. For fish whose natal streams are known to be upstream of T_k , \mathbf{U}_{T_k} would be interpreted as straying to non-natal streams.

2.3.2. Alternative hypotheses

The modeling framework described above can be used to test hypotheses relating to fallback and tributary memory effects. For example, a fallback memory effect exists if the fallback and directed states have different transition probabilities (i.e., if ϕ_{ij}^{fy} or $\phi_{ij}^{ff} \neq \phi_{ij}^{dy}$ for state y). Hypotheses that are essentially one-sided (e.g., $\phi_{ij}^{dd} / \phi_{ij}^{fd} < 1$) can be tested using z-tests for individual sites.

Table 1
Summary of models representing alternative hypotheses regarding memory effects of fallback and tributary visits. Model $M_{f(\phi)t(\phi,p)}$ estimated ϕ_{ij}^{dy} and ϕ_{ij}^{dy} ($y = d, t, F$), ϕ_{ij}^{dd} , ϕ_{ij}^{tt} , ϕ_{ij}^{ff} , ϕ_{ij}^{ff} , ϕ_{ij}^{tt} , p_i^d , and p_i^t separately, with $p_i^t = p_i^f = p_i^d$.

Model	Fallback effect on transitions	Tributary effect on transitions	Tributary effect on detections	Changes relative to Model $M_{f(\phi)t(\phi,p)}$	No. of parameters estimated	Log-likelihood
$M_{f(\phi)t(\phi,p)}$	X	X	X	–	96	–386.117
$M_{f(\phi)t(p)}$	X		X	$\phi_{ij}^{dy} = \phi_{ij}^{dy}$ for $y = d, t, F$	75	–396.724
$M_{f(\phi)t(\phi)}$		X	X	$\phi_{ij}^{dd} = \phi_{ij}^{dd} = \phi_{ij}^{ff} = \phi_{ij}^{dd}$, $\phi_{ij}^{tt} = \phi_{ij}^{tt} = \phi_{ij}^{ff} = \phi_{ij}^{tt}$	81	–398.498
$M_{f(\cdot)t(p)}$			X	$\phi_{ij}^{dd} = \phi_{ij}^{dd} = \phi_{ij}^{ff} = \phi_{ij}^{ff} = \phi_{ij}^{dd}$, $\phi_{ij}^{tt} = \phi_{ij}^{tt} = \phi_{ij}^{ff} = \phi_{ij}^{ff}$, $\phi_{ij}^{ff} = \phi_{ij}^{ff} = \phi_{ij}^{tt} = \phi_{ij}^{tt}$, $\phi_{ij}^{ff} = \phi_{ij}^{ff}$	60	–408.603
$M_{f(\phi)t(\phi)}$	X	X		$p_i^t = p_i^d$	90	–389.105
$M_{f(\phi)t(\cdot)}$	X			$\phi_{ij}^{dy} = \phi_{ij}^{dy}$ for $y = d, t, F$, and $p_i^t = p_i^d$	69	–399.891
$M_{f(\cdot)t(\phi)}$		X		$\phi_{ij}^{dd} = \phi_{ij}^{dd} = \phi_{ij}^{ff} = \phi_{ij}^{dd}$, $\phi_{ij}^{tt} = \phi_{ij}^{tt} = \phi_{ij}^{ff} = \phi_{ij}^{tt}$, $p_i^t = p_i^d$	75	–401.495
$M_{f(\cdot)t(\cdot)}$				$\phi_{ij}^{dd} = \phi_{ij}^{dd} = \phi_{ij}^{ff} = \phi_{ij}^{ff} = \phi_{ij}^{dd}$, $\phi_{ij}^{tt} = \phi_{ij}^{tt} = \phi_{ij}^{ff} = \phi_{ij}^{ff}$, $\phi_{ij}^{ff} = \phi_{ij}^{ff} = \phi_{ij}^{tt} = \phi_{ij}^{tt}$, $\phi_{ij}^{ff} = \phi_{ij}^{ff}$, $p_i^t = p_i^d$	54	–411.762

More general two-sided hypotheses (e.g., $\phi_{ij}^{fd} \neq \phi_{ij}^{dd}$) can be tested for multiple sites concurrently using a likelihood ratio test (LRT; Sokal and Rohlf, 1995) or other likelihood-based method (e.g., AIC; Burnham and Anderson, 2002) to compare models with different state-specific parameterizations.

Eight models were parameterized for the 1996 Chinook salmon study, including or excluding transition memory effects of fallback, tributary use, or both, and detection memory effects of tributary use (Table 1). The most general model, labeled $M_{f(\phi)t(\phi,p)}$, included a memory effect of fallback on transition parameters, as well as a memory effect of tributary visits on both transition and detection parameters. The simplest model, $M_{f(\cdot)t(\cdot)}$, included no memory effects on any parameter (i.e., $\phi_{ij}^{xy} = \phi_{ij}^{dy}$ and $p_i^x = p_i^d$ for all sites i and j and states x and y). The other six models included all intermediate combinations of fallback and tributary memory effects (Table 1). Nested models (e.g., $M_{f(\phi)t(\phi)}$ and $M_{f(\phi)t(\phi,p)}$) were compared using LRTs. Model selection was based on first fitting the most general model and then using a generalized backward selection process using LRTs to identify the most parsimonious model.

2.4. Numerical methods

We fit the alternative migration models in Program USER 4.1, available at the University of Washington (www.cbr.washington.edu/paramest/user). The 1996 Chinook salmon data set required certain modifications to the general MSMR model: the deployment of radio antenna arrays in the 1996 study excluded sites D_2B , D_3B , D_6T , and T_6 , and sparse data prevented estimation of certain memory effect parameters. For example, no fish detected in the mid-Columbia River was subsequently detected in the Snake River, so no memory effect of a visit to T_4 was considered. Furthermore, because of the rarity of multiple fallback events (<2% of release group), we modeled only the first fallback transition for each fish.

3. Results

A total of 846 radio-tagged adult spring-summer Chinook salmon tagged and released in 1996 were analyzed. Of these fish, 513 were last detected between Bonneville Dam and the mid-Columbia River (T_4), 150 in the mid-Columbia, 12 in the Snake River downstream of Lower Granite Dam, and 63 upstream of Lower

Granite. A total of 583 fish were last detected at a tributary site, 242 were last detected at a dam site, and 161 were observed to move downriver (fall back) and then return to upriver travel or enter a tributary. Most fish fell back for the first time at Bonneville Dam, and no fish fell back for the first time upstream of Ice Harbor Dam.

A likelihood ratio test comparing models $M_{f(\phi)t(\phi,p)}$ and $M_{f(\phi)t(\phi)}$ found no evidence that tributary visits affected detection probabilities at the dams ($P = 0.4259$; Table 1). Also, no evidence of a tributary effect on subsequent transition probabilities was found ($M_{f(\phi)t(\phi)}$ vs. $M_{f(\phi)t(\cdot)}$, $P = 0.4245$). However, fallback was found to have a significant effect on subsequent transitions ($M_{f(\phi)t(\phi)}$ vs. $M_{f(\cdot)t(\phi)}$, $P = 0.0530$) at the 10% significance level. Therefore, model $M_{f(\phi)t(\cdot)}$ was used for subsequent parameter estimation and characterization of migration success of the release group. It should be noted, however, that this model was not independently validated and that the results reported here have direct inference only to the individuals in the release group.

Tagged fish had an average probability of 0.438 ($\hat{SE} = 0.018$) of ending the study in the tributaries downstream of McNary Dam, and a probability of 0.178 (0.013) of ending in the mid-Columbia upstream of McNary Dam (Fig. 3). The average probability of ending the study in the Snake River upstream of Lower Granite Dam was estimated to be 0.139 (0.012). This left a probability of 0.245 (0.018) of unaccountable loss between the release site downstream of Bonneville Dam and Lower Granite Dam on the Snake River (Fig. 3). This unaccountable loss included natural mortality, harvest, tag loss, and spawning in the mainstem river, considered to be rare for spring and summer Chinook salmon (Healy, 1991). Of the total amount of unaccountable loss in the system, 85.1% occurred in the Columbia River between the release site and the McNary forebay. Both hatchery and wild fish were subject to fishing pressure in this region and harvest may account for much of the loss.

A more localized picture of unaccountable loss is given by the conditional reach-specific loss estimates (Fig. 4). These estimate the probability of migration cessation in a given reach of the mainstem river conditional on arriving at the downstream boundary of the reach. Conditional reach-specific loss estimates ranged from 0.013 ($\hat{SE} = 0.032$) between Ice Harbor and Lower Monumental dams on the Snake River to 0.092 (0.012) between the Bonneville and The Dalles forebays on the Columbia River (Fig. 4).

Tributaries were used primarily for permanent exit from the mainstem river. The estimated probability of remaining in a tributary after entering it ranged from 0.636 ($\hat{SE} = 0.145$) for tributaries

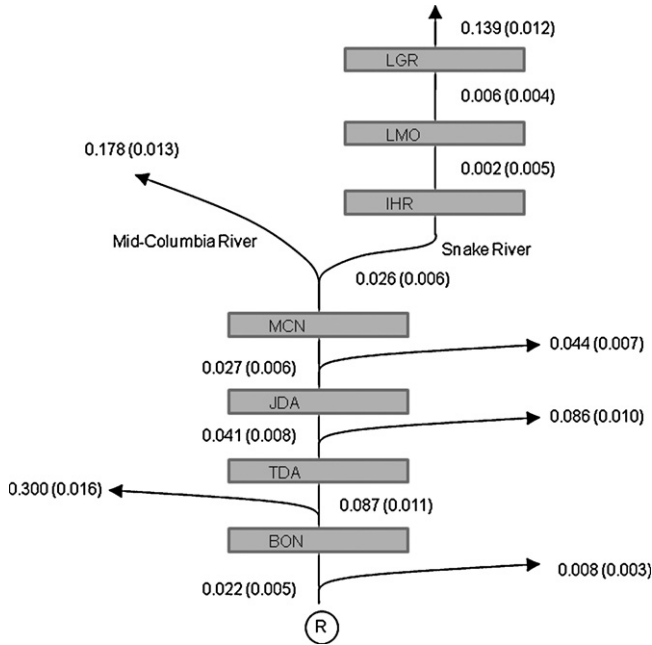


Fig. 3. Estimates (and standard errors) of probability of final fate for the 1996 adult spring-summer Chinook salmon study.

downstream of Bonneville to 1.000 (0.000) for the mid-Columbia River (treated as tributary T_4). The low probability of remaining in tributaries downstream of Bonneville is reasonable, considering that all study fish were initially collected at Bonneville and thus had already passed the downstream tributaries. The high probability of remaining in the mid-Columbia was also expected because the mid-Columbia receivers were all located a considerable distance upstream of the confluence with the Snake River, suggesting the

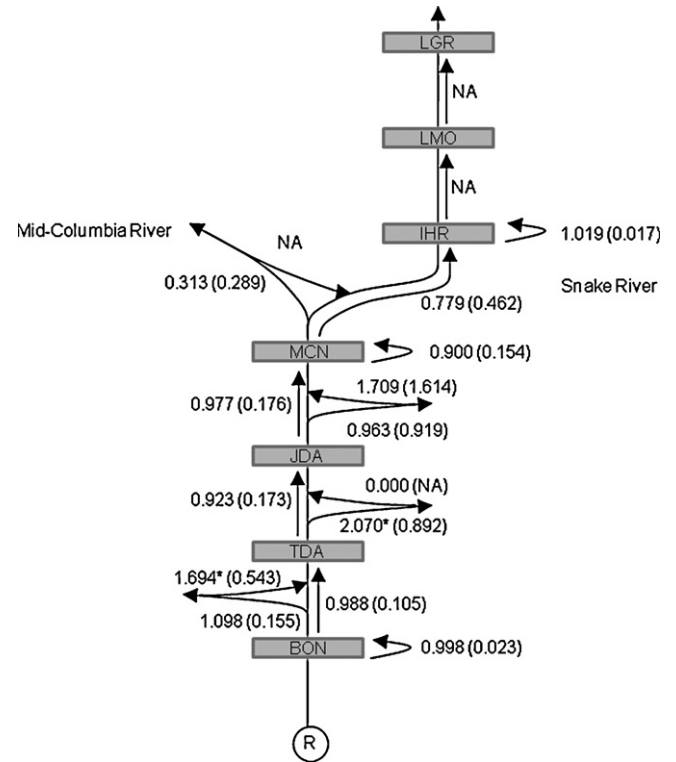


Fig. 5. Estimates (and standard errors) of the multiplicative fallback effect for each transition: $\hat{\phi}_{ij}^{ff}/\hat{\phi}_{ij}^{dd}$, $\hat{\phi}_{ij}^{fd}/\hat{\phi}_{ij}^{dd}$, $\hat{\phi}_{ij}^{fe}/\hat{\phi}_{ij}^{dt}$, and $\hat{\phi}_{ij}^{fd}/\hat{\phi}_{ij}^{dd}$ as appropriate for sites i and j (i.e., the ratio of the transition probabilities from the fallback and directed states). Fallback effects that are statistically significant at the 10% significance level are marked by *. NA: not available.

fish detected that far upstream were committed to that migration route.

The multistate recapture model provided a format for analyzing effects of past migration experience on current transition probabilities. The model selected ($M_{f(\phi)l(\cdot)}$) estimated unique transition probabilities for fish in the fallback states compared to the directed state. Thus, we estimated the multiplicative effect of recent fallback on transition probabilities via the ratios $\hat{\phi}_{ij}^{ff}/\hat{\phi}_{ij}^{dd}$, $\hat{\phi}_{ij}^{fd}/\hat{\phi}_{ij}^{dd}$, $\hat{\phi}_{ij}^{fe}/\hat{\phi}_{ij}^{dt}$, and $\hat{\phi}_{ij}^{fd}/\hat{\phi}_{ij}^{dd}$ for transitions between sites i and j . Estimates of these ratios less than 1 imply that fish that recently fell back were less likely to complete the transition than non-fallback fish. Only two of the fallback memory effects were significantly different from 1 ($P < 0.10$; Fig. 5). The transition between the mid-Columbia receivers and the base of Ice Harbor Dam was excluded because no fish returned from the mid-Columbia to the Snake River. Too few fish fell back upstream McNary Dam to estimate fallback memory effects farther upstream.

Fallback over Bonneville Dam resulted in a greater probability of returning to the mainstem river after visiting tributaries between Bonneville and The Dalles ($\hat{\phi}^{fe}/\hat{\phi}^{dt} = 1.694$, $\widehat{SE} = 0.543$; $P = 0.0501$; Fig. 5). This suggests that fallback fish used these tributaries as resting areas after reascending Bonneville. Fallback and reascension at The Dalles Dam resulted in a greater probability of entering the tributary between The Dalles and John Day ($\hat{\phi}^{fd}/\hat{\phi}^{dd} = 2.070$, $\widehat{SE} = 0.892$; $P = 0.0456$). Additionally, none of the fallback fish that entered that tributary subsequently returned to the mainstem river (Fig. 5). This suggests that the fish fell back over The Dalles Dam primarily as they searched for the tributary to their natal stream. Overall, no dam-to-dam transition was significantly affected by fallback.

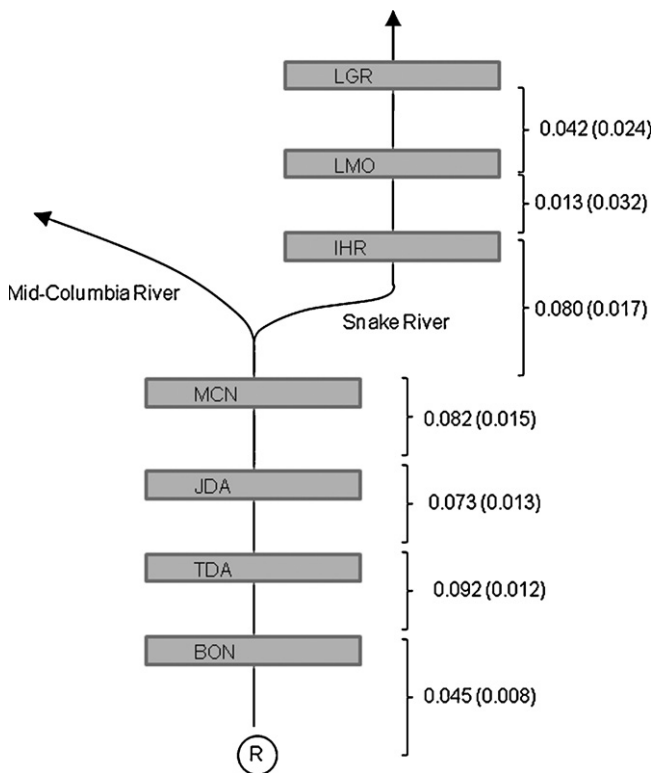


Fig. 4. Estimates (and standard errors) of mainstem reach-specific unaccountable loss, conditional on surviving to the downstream boundary of the reach.

The assumption of perfect knowledge of state transitions may fail if detection probabilities are less than 1. We estimated the possible bias in performance measures for the 1996 study caused by imperfect detection. Tributary detection probabilities were estimated as the proportion of time the receivers were functional (Bjornn et al., 2000), and dam detection probabilities were estimated by the MSMR models. Overall, imperfect knowledge of state transitions had little effect on estimates of most performance measures because most dam and tributary detection probabilities were high (>0.9). The only significant differences were caused by imperfect detection at the mid-Columbia receivers ($\hat{p}_{T_4} = 0.905$). The estimated probability of ending the study in the Snake River downstream of Ice Harbor Dam changed from 0.026 ($\hat{SE} = 0.006$; Fig. 3) to 0.004 when imperfect tributary detection was incorporated. Likewise, the estimate of unaccountable loss between the release site and Lower Granite Dam changed from 0.245 (0.018) to 0.233, and the estimated proportion of all unaccountable loss that occurred in the Columbia River downstream of the McNary Dam forebay changed from 85.1% to 94.3%. Using multiple receivers in each tributary and dual arrays at dams would improve detection rates, allow for estimation of tributary detection probabilities, and further reduce the risk of bias.

4. Discussion

4.1. Modeling animal migrations

Animal migrations have long been studied to gain insight into the population dynamics of migratory species. Organisms making annual migrations may be encountered either along their migration route or at their destination. Numerous capture-mark-recapture (CMR) models have taken advantage of this fact to study temporal (e.g., multi-year) population dynamics of a wide range of species; see Lebreton et al. (1992) for a useful overview of methods. A smaller collection of CMR migration models have been developed for fish migrations (e.g., Burnham et al., 1987; Skalski et al., 1998). Unlike these existing fish migration models, the model developed here incorporates multi-directional travel, defines states based on past migratory experiences, and uses alternative states to test hypotheses concerning migration behavior.

There are key differences between using CMR and MSMR methods to study migration dynamics and using CMR data from repeated annual migrations to study temporal population dynamics. In particular, the former focuses primarily on spatial dynamics within a limited time frame, whereas the latter focuses primarily on temporal dynamics within a limited spatial region. A major difference between spatial and temporal CMR models is that time is unidirectional and space is not. In a temporal CMR study, organisms may return to a previous state but always move forward in time. In a spatially focused CMR migration study, organisms may return to previously visited sites even if they are generally directed forward (e.g., upriver for the adult salmonid model). Success in migration may be determined either by the extent of forward movement or by ultimate fate. In the adult salmonid migration model we used ultimate fate to determine success. In particular, ascending a dam and then falling back over it did not count as a successful ascension. Perry et al. (2010) took a similar approach to modeling a juvenile salmonid migration through the complex, branching, tide-influenced environment of the Sacramento River delta.

The dichotomy between temporal and spatial modeling extends to the hypotheses that may be explored. CMR and MSMR models of temporal dynamics are often used to test hypotheses of common survival probabilities and other parameters over time (e.g., Kendall and Nichols, 2002). The spatial focus of a migration model means that processes occurring in different study “periods” occur in different spatial locations, which may have vastly different envi-

ronments. Common survival and migration probabilities in the different periods is not a natural hypothesis for a spatial migration model. Instead, the natural hypotheses focus on delayed effects of past migratory experiences (as in the model here), treatment effects as in the models of Burnham et al. (1987), or subpopulation- or stock-specific effects on migration.

One difficulty with modeling migration is accounting for heterogeneous migration probabilities. Even if all tagged organisms are released at approximately the same time and location, variations in travel time, migratory experience, and environmental conditions might mean that by the later stages, animals may exhibit heterogeneity in survival and/or detection. Additionally, they may have disparate destinations, as in the 1996 salmon study in which the release group contained an unknown mixture of Chinook salmon from different stocks. We accounted for likely differences in survival and detection probabilities by using a multistate model with states defined by fish behavior during migration, a type of post-stratification (e.g., see Schwarz et al., 1988). Alternative approaches to accounting for heterogeneity include defining states based on the origin of known-source fish or modeling transition probabilities in terms of local environmental covariates (e.g., Pollock et al., 1984).

An alternative modeling approach that explicitly accounts for imperfect knowledge of state transitions is the hidden Markov model (HMM; MacDonald and Zucchini, 1997). The HMM framework has been used to expand MSMR modeling, although typically for studies in which tagged animals are sampled at discrete time steps (Pradel, 2005; Conn and Cooch, 2009). For a migration study, the iterative steps would be spatial instead of temporal, and states would consist of both location (detection site) and fish “condition” (e.g., directed, tributary, fallback). With imperfect detection, the HMM states are partially hidden, and both state transition and observation probabilities must be estimated as in the case of the MSMR parameterization. However, because both the state and the iterative step in the HMM would be spatially defined in a migration model, an unobserved state may also be an unobserved iteration. For example, non-detection at a tributary receiver would not only miss a transition to the tributary state, but it would also miss a spatial step in the migration, analogous to missing a sampling point in a temporal model without knowing that it was missing. This will be true for any optional detection site, and prevents estimation of state observation probabilities for states defined by such sites. Thus, the HMM framework seems more suitable for migration models whose focus is a linear migration with no alternative migration paths or optional detection sites.

4.2. Model applications

The modeling framework adopted here can provide insight into how migrating organisms interact with their environment. For example, we found that the Chinook salmon in the 1996 case study used tributaries primarily as exits from the hydrosystem. The exception was for fish that fell back over Bonneville Dam, who appeared to use tributaries as resting areas after reascending the dam. The model also identified the reach between Bonneville and The Dalles dams as having the highest amount of unaccountable loss, suggesting that further examination is warranted of the natural and fishing mortality pressures in this reach. As with all CMR models, however, the results of a model based on a single data set have inference only to the individuals in that study, and should not be blindly applied to other groups or data sets without careful consideration of the modeling assumptions. Thus, because these results come from a single year of data, analysis of similar migration data from other years is required before conclusive statements can be made about the factors that consistently influence the upstream migration of spring-summer Chinook salmon from the Columbia River Basin.

The migration model developed here can be further adapted to a variety of applications. If the release group consisted of known-source fish (e.g., adults that were tagged during their downstream juvenile migration), the multistate model could be extended to include fish source as a permanent state, with river exit into non-origin tributaries interpreted as straying. This approach provides a framework for assessing straying rates among different populations or among fish with different rearing histories (i.e., hatchery vs. wild) or migration experiences (e.g., fallback vs. directed). The effect of barging juvenile salmonids downriver past the hydroelectric dams on subsequent adult straying rates could be assessed with a multistate migration model using active-tagged fish with known source and known juvenile outmigration history.

Different applications arise for migrations in other river systems. For example, the Sacramento–San Joaquin River delta consists of a complex river environment with multiple natural and manmade channels leading to the San Francisco Bay (Perry et al., 2010). Tides influence river flow far upriver. The multistate modeling framework can be used to assess migration success through different routes or on different migration schedules. States can be defined by tidal stage or the position of canal gates (open or closed) at the time of fish passage of a given waypoint, and used to assess the importance of these factors on migration success.

The salmonid data in this study have been previously analyzed using binomial response models and logistic or linear regression (e.g., Boggs et al., 2004; Keefer et al., 2004, 2005). Using separate conditional binomial models to examine escapement, fallback, and non-homing behavior limits integration of these processes over multiple reaches and distorts precision. By jointly incorporating survival, fallback, and tributary use, the comprehensive modeling framework presented here enables exploration of the interplay between these multiple aspects of adult salmonid migration. This framework is useful for both hypothesis testing (e.g., fallback affects subsequent upstream transitions) and estimation purposes (e.g., unaccountable loss within the hydrosystem). By using a comprehensive modeling framework that focuses on the individual fish as the unit of observation, more information can be extracted from costly telemetry studies for better understanding of anthropogenic effects on wild populations.

Acknowledgments

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