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

Rebecca A. Buchanan*, John R. Skalski

*Columbia Basin Research, School of Aquatic & Fishery Sciences, University of Washington, 1325 Fourth Avenue, Suite 1820, Seattle, WA 98101-2509, USA*

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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.



## 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 dominant 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

* Corresponding author. Tel.: +1 206 685 2793; fax: +1 206 616 7452.
*E-mail address:* rabuchan@u.washington.edu (R.A. Buchanan).

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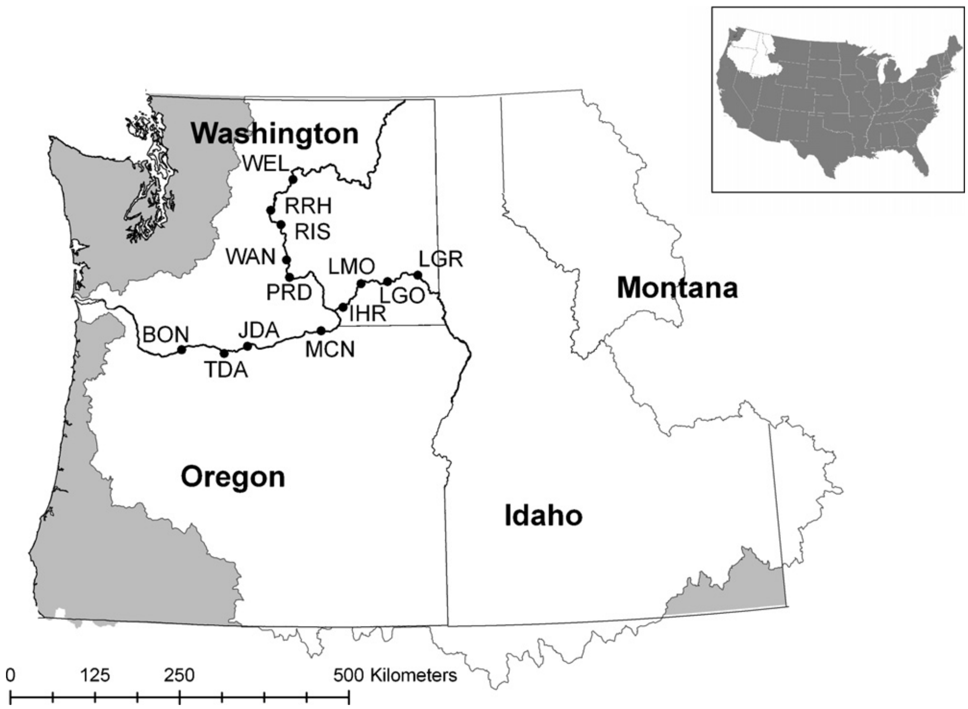


**Fig. 1.** Map of Columbia River and Snake River basins, with hydroelectric dams noted that were passed by salmon in 1996 release group. BON = Bonneville Dam, TDA = The Dalles, JDA = John Day, MCN = McNary, IHR = Ice Harbor, LMO = Lower Monumental, LGO = Little Goose, LGR = Lower Granite, PRD = Priest 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. Generally, 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