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High-stakes steeplechase: a behavior-based model to predict individual travel times through diverse migration segments

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Abstract. Many migratory species traverse highly heterogeneous landscapes, often including habitats that have been altered by human activities. Modeling migration dynamics is challenging because individual variability in behavior at multiple spatial and temporal scales can produce complex, multi-modal distributions in migration travel times. Moreover, behavioral responses to conditions encountered en route can affect habitat-specific migration rates which then influence bioenergetic costs and mortality risk over the entire migration. To quantify impacts of conditions within migration corridors, refined analyses of behavior are needed. In this study, we developed a behavior-based simulation model that predicts individual adult salmon migration duration over 24 distinct river reaches totaling 922 km, including eight hydropower dams. The study population, threatened Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*), had observed migration durations ranging from 23 to 108 d. In a novel application of N-dimensional mixture models, which can account for subpopulations that behave differently, we simulated "fast" vs. "slow" travel through migration reaches. The proportion of migrants in each category was determined by diel, seasonal, and proximate river conditions, which captured the temporally shifting bimodal patterns in the data. We fit reach-specific models with data from 2188 tagged salmon migrating in 2000–2013 and validated the cumulative model with additional data through 2015. By accounting for multiple behaviors in this way, the model successfully recreated the breadth and variability in total travel times to within 3% of observed durations throughout the 5th–95th quantiles. En route mortality appeared to account for the loss of the slowest fish that encountered record-breaking high temperatures in 2015. For Chinook salmon, this combined reach and cumulative travel-time model provides an opportunity to link high-resolution behavioral data to individual fitness and population-level impacts on viability. More generally, the N-dimensional modeling approach offers a framework for assessing the cumulative impacts of alternative behaviors at small spatial and temporal scales. Improved accounting of changes in migration rate in response to local conditions will aid recovery efforts for species of concern traversing complex migration corridors.

Key words: Chinook salmon; climate; Columbia River; hydrosystem; migration; N-dimensional mixture model; *Oncorhynchus tshawytscha*.

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INTRODUCTION

Complex migratory behavior has confounded conservation efforts for many highly mobile species. Migratory taxa that have declined or disappeared include mammals, birds, and fish (Both et al. 2006, Wilcove and Wikelski 2008), with long-distance migrants showing more severe declines than related non-migratory species (Sanderson et al. 2006). Energetic cost and mortality risk during migration can be naturally high and particularly vulnerable to amplification due to anthropogenic impacts or a changing environment (Both et al. 2006, Rand et al. 2006, Berthold et al. 2013). In reproductive migrations, excessive energetic depletion or failure to complete the migration can constitute total loss of lifetime fitness, particularly for semelparous species.

Detailed understanding of links between migratory costs and population declines has proven elusive for even the best-studied species (Wilcove and Wikelski 2008). Information gaps exist because both individual behaviors and environmental conditions are complex and challenging to quantify over long migrations. Migrants often encounter multiple habitats and express diverse behaviors both within and between different habitat types. Migrating animals may travel at different rates (Noad and Cato 2007) or make multiple stops of varying duration as they confront tradeoffs between migration speed and energetic demands or mortality risks (Alerstam et al. 2003, Lindström et al. 2016). Individual responses to conditions encountered en route can produce complex patterns in cumulative travel times that are difficult to characterize with standard statistical distributions.

Nonetheless, characterizing behavioral and temporal complexity is important because time spent in particular habitats can have a disproportionate effect on fitness via energy budgets and immediate or delayed mortality risks (Weimerskirch et al. 2015). Typically, longer duration increases energetic costs or exposure to mortality agents or creates a mismatch between arrival timing and conditions at breeding sites (Both et al. 2006). Conversely, slowed migration and stopovers can allow individuals to shelter from unfavorable conditions or improve their physiological status. Accurate estimates of migration fitness costs require development of models that explicitly link variation in behavior, timing, and migration duration to environmental conditions.

A common approach to modeling the energetic cost of migration assumes that animals travel at a constant speed (the average of observed rates) within a migration. Alternative rest-to-travel ratios might be compared to determine optimal strategies (Braithwaite et al. 2015), or energetic requirements under changing environmental conditions (Roff 1991, Southwood and Avens 2010, Villegas-Amtmann et al. 2015). However, rapid advances in tag technology and accumulation of telemetry data show highly variable migration rates within and among individuals in many species (Webster et al. 2002, Jellyman 2009, Crossin et al. 2014, Hussey et al. 2015). Mechanistic models of migration rate in response to environmental conditions are needed to explore complex migration conditions and tradeoffs (Costa et al. 2012). Here, we take a novel approach to the incorporation of intra- and inter-individual changes in behavior during migration, which is to allow mixture models to describe different patterns in migration rate.

Mixture models allow a sample population to be described by the sum of multiple statistical distributions or moments (McLachlan and Peel 2000, Skalski and Gilliam 2003). Because mixture models are not limited to a single statistical distribution for different groups, they provide an intuitive way to incorporate individual or group choices into models of population migrations. Such models are particularly useful for characterizing movement patterns as individuals alternate among behaviors, such as resting/feeding vs. active migration, breeding vs. non-breeding behavior, or migration diversions in response to anthropogenic disturbances (Skalski and Gilliam 2000, 2003). State-space models have also been used to detect these distinctions, or hidden states (Jonsen et al. 2006, Breed et al. 2009, Mills Flemming et al. 2010). Our approach is similar except that we do not differentiate observation error from process error, which simplifies the model, making it easier to fit. We justifiably assume observation error is low because of the fine scale at which radiotelemetry data were collected. Our model also takes the additional step of linking behavioral states and the characteristics of those states to dynamic environmental conditions. Mechanistic models such as these that relate movement duration to habitat use are needed to test hypotheses regarding energetic or other fitness-related costs under alternative future scenarios.

Salmon case study

Pacific salmon (*Oncorhynchus* spp.) offer an illuminating example where adequate data exist to improve our modeling toolbox for studying migratory behavior. Of 52 identified salmon and steelhead *Oncorhynchus mykiss* evolutionarily significant units on the contiguous U.S. west coast, 29 are listed as endangered, threatened, or species of concern (NMFS 2016), prompting extensive research and monitoring. Hindrances to migration, including hydropower projects, are considered limiting factors for Columbia and Snake River Chinook salmon, in addition to habitat loss, harvest, and hatcheries (NOAA Fisheries 2008, 2014). Direct adult salmon mortality during upstream passage of dams in this river system is uncommon, but cumulative impacts of slowed passage at one or more dams and downstream fallback over dams may culminate in delayed mortality or reduced fecundity (Keefer et al. 2005, Caudill et al. 2007). The indirect effects of the Federal Columbia River Power System (FCRPS, hereafter hydrosystem) on population mean fitness have not been quantified and are therefore not considered in Biological Opinions mandated for federal hydrosystem operations under the Endangered Species Act (NOAA Fisheries 2008, 2014).

Variation in individual experience, behavior, and encountered conditions can result in considerable differences in adult salmon migration rates, even among fish from a single cohort (Keefer et al. 2004*b*, Caudill et al. 2007). Moreover, cumulative variation along the migration route can result in total travel times that are strongly skewed or multi-modal. Such variation in individual experience and overall travel time could have large effects on energy use and fitness. For example, longer travel times in early summer can increase cumulative exposure to elevated water temperatures. Further, behaviors at different stages of migration are not necessarily independent. Individuals might vary systematically in their behavior, or environmental factors might drive correlations in behavior across migration stages. A complete model of fish travel time from river entry to spawning grounds that allows for variation in start dates, migration rates through individual river sections, and environmental variation is needed to accurately account for potentially compounding energetic costs and tradeoffs at the individual level. Similar variation in migration timing and encountered habitats is common among migratory species (Costa et al. 2012, Hussey et al. 2015).

Migration slowdowns can increase fish mortality through either energetic exhaustion (Castro-Santos and Letcher 2010, Burnett et al. 2014), elevated exposure to other threats such as harvest (Keefer et al. 2009), or reduced resilience to other stressors. Multiple stressors can cause mortality when a single factor might not (e.g., fish stressed by handling are more likely to die at moderately high temperatures; Gale et al. 2013). Notably, upstream migration corridors are often heterogeneous. Regulated river systems such as the Columbia and Snake include long, low-gradient reservoir reaches punctuated by high-gradient dam tailraces and fishways, as well as less regulated or unregulated reaches as fish approach spawning tributaries. Thus, migration duration and cost vary widely among individuals within and among these environments and a model accounting for duration in each habitat is needed to calculate fitness costs related to energetic costs or arrival timing on spawning grounds.

The travel-time model described in this paper can be used in future applications to quantify potential indirect effects of adult salmon travel time within and upstream of the hydrosystem, which is a critical need for migrants that are protected under the Endangered Species Act. For example, slower travel might lead to lower survival by increasing exposure to extrinsic mortality factors or through energetic costs that lower resilience to other stressors. Importantly, it is difficult to directly test mortality-related hypotheses when using observational passage-time data, because travel times of fish that die en route are not observed for the reach in which mortality occurs. In our case study, the model characterizes expected travel times without the confounding effects of variable mortality rates.

Model overview

Our primary study objective was to develop a general modeling framework using N-dimensional mixture models to capture a wide range of migratory animal behaviors, such as those observed in Chinook salmon. Our second objective was to demonstrate the good fit of a cumulative migration model that includes mixture models in our case study. Our third objective was to summarize patterns that emerged from the reach-specific and cumulative migration models that could inform future study of indirect fitness effects on Columbia River salmon, particularly in relation to potential energetic costs and exposure to known stressors.

We developed a simulation model based on salmon behavior that estimates individual travel time as a function of environmental conditions through 24 separate river reaches. The number of reaches reflects the management units under consideration in the FCRPS Biological Opinion (i.e., dam tailraces, fishways, and reservoirs, and the section upstream of the hydrosystem are differentiated). Different levels of time and exertion are required to traverse each of the different reach types. Within specific reaches, we used two-dimensional mixture models (McLachlan and Peel 2000) to account for bimodal patterns apparent in salmon behavior at diel and seasonal scales. River reaches were combined into a cumulative migration model, wherein the rate at which an individual model fish moved through each consecutive reach could be a function of time of day, migration date, individual variability, and/or abiotic river conditions.

METHODS

In the following sections, we describe (1) the study population; (2) the specific river reaches in their migration; (3) the data sources and criteria for including data in model fitting, validation, and application; and (4) the design and validation of the various models used. Our general analytical approach was to first fit reach-specific migration-time models to individually tagged fish detected at the beginning and end of each reach from 2000 through 2013. We then combined these individual reach models to build a cumulative migration model. We validated the cumulative model by comparing total salmon travel times through the 462-km hydrosystem and the full 922-km migration to the spawning grounds (Table 1). Finally, we applied the cumulative model to data from two years that were outside our training dataset (2014–2015), to demonstrate how deviations from model predictions related to salmon survival.

Study system

Chinook salmon *Oncorhynchus tshawytscha* and sockeye salmon *Oncorhynchus nerka* pursue some of the longest, most arduous migrations of any anadromous fish. In some populations, over 40% of total available energy is typically spent on the freshwater migration as salmon traverse over 1000 km and ascend to elevations >1000 m above sea level to reach spawning habitat (Crossin et al. 2004, Bowerman et al. 2017). The Snake River spring/summer Chinook salmon in our case study spawn and rear in low-order, high-elevation tributaries (Fig. 1). Many juvenile Snake River salmon are tagged with passive integrated transponder (PIT) tags in natal streams before they migrate to the Gulf of Alaska. After 1–4 yr of ocean residency, adults return to their natal stream for a single lifetime spawning event. Weirs that block return to certain spawning grounds provide an opportunity to identify which fish complete the migration and when they arrive. We selected the South Fork Salmon River (SFSR) population in central Idaho for our case study because fish returning to the spawning grounds pass through a weir, which is located 1550 m above sea level and 1200 km from the mouth of the Columbia

Table 1. Model steps and data used in each step.

Step	Data type	Years	Inclusion criteria
Fit model to individual reaches			
Hydrosystem section	RT	2000–2013	Detected at entry and exit of each reach
Snake/Salmon section	PIT	2002–2013	Detected at both Lower Granite Dam and South Fork Salmon River weir
Validate cumulative model			
Full migration	PIT	2002–2015	Detected at both Bonneville fishway and South Fork Salmon River weir

Note: RT, radio tag; PIT, passive integrated transponder tag.

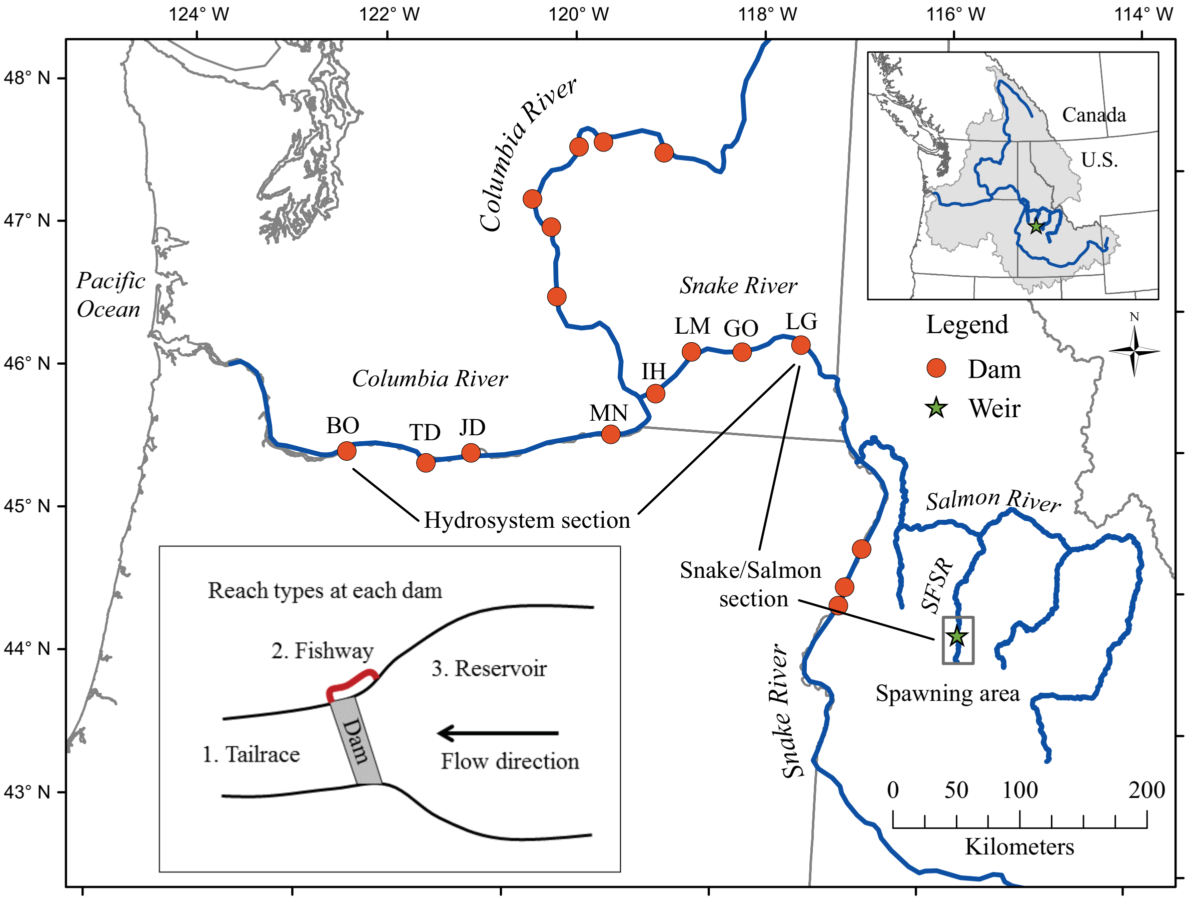

Fig. 1. Map showing study area within the Columbia River Basin (gray shading; inset), including the hydrosystem section from Bonneville Dam to Lower Granite Dam, and the Snake/Salmon section from Lower Granite Dam the South Fork Salmon River (SFSR) weir (star) within the spawning area (box). Dams are labeled as BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; IH, Ice Harbor; LM, Lower Monumental; GO, Little Goose; LG, Lower Granite. A schematic of the reaches modeled at each dam within the hydrosystem section is also shown.

River. All adults collected at the weir are measured and checked for tags, so a complete migration history can be generated.

The freshwater migration entails passage of four hydroelectric dams on the Columbia River and four dams on the Snake River, followed by passage through portions of the Snake, Salmon, and South Fork Salmon rivers. The hydrosystem study section extends from Bonneville Dam (235 km from the Columbia River mouth) to Lower Granite Dam (462 km, 180 m elevation gain). Above Lower Granite Dam, the Snake/Salmon section includes Lower Granite reservoir (~60 km), an unimpounded section of the lower Snake River (~70 km), and portions of the free-flowing Salmon and South Fork Salmon rivers (Snake/Salmon total: 460 km; 1370 m elevation gain). The study population typically initiates migration at Bonneville Dam from ~5 May to 22 June, arrives at the weir ~27 June to 28 August, and spawns ~23 August to 15 September.

In 11 yr, adult salmon were collected at Bonneville Dam and implanted with radiotelemetry transmitters, which provided detailed information about their movements through the hydrosystem. Salmon can exhibit qualitatively different stopover behaviors at dams and near spawning grounds, where individuals remain relatively stationary in a habitat for hours to weeks. Adult salmonids exhibit diel variation in passage behavior (Keefer et al. 2013) and temporary stopping or staging behavior to avoid warm water or other adverse conditions before continuing upstream to complete migration (Goniea et al. 2006, High et al. 2006). Many spring- and summer-run adult Chinook salmon also enter natal tributaries 1–2 months prior to spawning (Quinn et al. 2016, Bowerman et al. 2017). They spend this holding period near or downstream of spawning sites within tributaries, where proximate conditions (especially water temperature; Torgersen et al. 1999) affect energetic costs.

*Hydrosystem section.—*The first half of the migration, from Bonneville Dam to Lower Granite Dam, was partitioned into three reach types at each dam: tailrace, adult fishway, and reservoir (Fig. 1, inset). Dam tailraces are among the most turbulent and energetically expensive reaches of the migration (Brown et al. 2006). Passage requires ascending through high-velocity water, as well as finding and entering a fishway. Each dam had 1–2 aerial radio antennas positioned 1–4 km downstream to monitor salmon entry into the tailrace, and antennas at fishway entrances to monitor tailrace exit (Keefer et al. 2004*a*).

Once inside a fishway, navigation is more straightforward. Fishways provide structural guidance, and flow and hydraulics are more predictable and largely independent of river discharge. However, variability in water temperature gradients, fish density, and hydraulic conditions at fishway entrances can be challenging for some salmon, and consequently, some individuals make multiple attempts prior to successful passage (Caudill et al. 2013).

Chinook salmon migrate fastest through reservoirs (often 50–70 km/d; Keefer et al. 2004*a*). Energetically, reservoirs are the least expensive per km (Brown et al. 2006), but constitute a majority of the physical distance through the hydrosystem section. We defined reservoir time as beginning with fish detection at the fish ladder exit at one dam and ending with first detection in the tailrace of the next dam upstream.

When calculating the time a fish spent in each reach, we summed all time spent between designated beginning and ending points, regardless of the number of entries and exits. The one exception was for fish documented reascending a dam after a fallback (i.e., they passed downstream via a dam spillway, turbine, or other route; Boggs et al. 2004). For fallback fish, we conservatively excluded second or subsequent ascents at that dam. Thus, actual cumulative times for fish that fell back were expected to be longer than modeled times.

*Snake/Salmon section.—*The second half of the migration, from Lower Granite Dam fish ladder exit to the SFSR weir, was comparatively complex, consisting of many different gradients, discharge volumes, and water velocities. It was modeled as a single reach because Lower Granite Dam was the farthest upstream location where PIT tags were reliably detected before the SFSR weir. Lower Granite reservoir is also unique among reservoirs in this study area because it is thermally stratified due to cool-water releases from Dworshak Dam on the Clearwater River (Keefer and Caudill 2015). After leaving Lower Granite reservoir, summer-migrating salmon confront not only a major reduction in Snake River volume and increased velocity, but also much warmer temperatures above the Clearwater River–Snake River confluence. Migration rates decline as fish pass from Lower Granite reservoir (60–70 km/d; Keefer et al. 2004*a*) to the confluence of the Snake and Salmon rivers and finally into the free-flowing, steep gradient of the Salmon River (10–20 km/d; Keefer et al. 2004*b*). At the SFSR weir, all fish were collected and arrival time at the weir was recorded. Prespawn holding and spawning occur both above and below the weir, but only fish that were detected at the weir were included in the travel-time models.

Model structure

*Tailrace and fishway reaches.—*One aspect of salmon behavior that has not been fully explored in previous models is a curious bimodal pattern of diel behavioral change in tailraces and fishways (Fig. 2). Previous analyses identified slowed movement at night, especially in complex reaches (Keefer et al. 2013, Zabel et al. 2014). However, the simple day vs. night dichotomy applied in past models did not capture the continuous variation of the temporally shifting bimodal pattern we observed, especially in dam tailraces.

To model the bimodal pattern, we considered the passage-time distribution of the whole population to be a combination of two separate

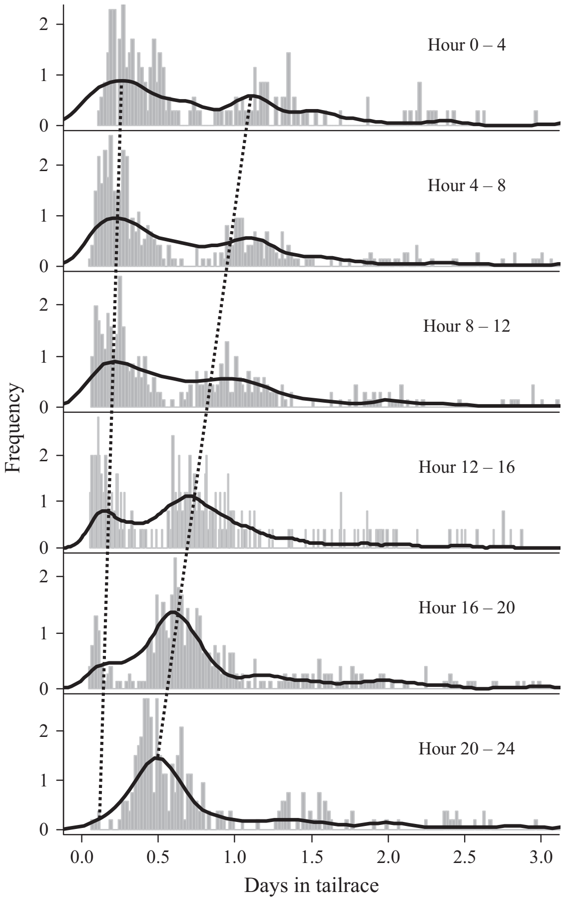

Fig. 2. Histograms showing the frequency distribution of Chinook salmon observed passage times in 4-h increments through the combined tailraces of the four Columbia River dams (Bonneville, The Dalles, John Day, and McNary). Panels show patterns for Chinook salmon that enter the reach at different times of day, indicated by panel titles. The solid line is a smoothed line of the density distribution from the model simulation. The dotted lines show the shift in mean travel time for the fast and slow modes over a 24-h period.

probability distributions using a two-dimensional finite mixture model (McLachlan and Peel 2000). The proportion of fish in the first mode fluctuated as a function of the time of day. At each hour of the day, each fish had a probability p of belonging to the first distribution (G_f) and a probability $1 - p$ of belonging to the second distribution (G_s). This model structure has the added benefit of improving characterization of the extreme right-skew in tailrace and fishway passage times.

The probability of travel time t for an individual fish i through reach ξ was:

$$F(t_{i,\xi}|\theta_{f,\xi}, \theta_{s,\xi}) = p_{i,\xi} G_{f,\xi}(t_{i,\xi}|\theta_{f,\xi}) + (1 - p_{i,\xi}) G_{s,\xi}(t_{i,\xi}|\theta_{s,\xi}) \quad (1)$$

where travel times were conditioned on the parameters in θ, which differed for the fast f and slow s mode within each reach ξ. We modeled the diel pattern of proportions of fish in the fast vs. the slow mode as a sine function with amplitude ς, phase φ, and shift α. We constrained p between 0 and 1 using a logit transformation:

$$\text{Logit}(p_{i,\xi}) = \varsigma_\xi \sin(2\pi(H_i - \phi_\xi)) + \alpha_\xi \quad (2)$$

where time of day H was a fraction of the day (i.e., h/24). The two distributions G_f and G_s in the dam passage models (i.e., all tailraces and fishways) were both lognormal probability distributions with mean μ and standard deviation σ, and $\theta_{f,\xi} = [\mu_{f,\xi}, \ \sigma_{f,\rho}]$ and $\theta_{s,\xi} = [\mu_{s,\xi}, \ \sigma_{s,\rho}]$, where ρ represented the river (Columbia or Snake) and type of reach (tailrace or fishway). We constrained μ_f to be less than μ_s for identifiability reasons, and to assign the fast and slow modes, respectively.

The model was fit separately for tailraces in the Columbia River, tailraces in the Snake River, fishways in the Columbia River, and fishways in the Snake River. We grouped dams in this way because we assumed the effects of covariates were shared among dams within each river, but were potentially different between the much larger and seasonally cooler Columbia River vs. the smaller and warmer Snake River. Although we modeled the mean of each distribution as a function of covariates, the standard deviation was held constant within each reach/river combination ρ.

We allowed the means of both distributions to vary with reach, time of day H, water temperature T, and flow F determined at the hour the individual fish arrived at the reach. For each distribution, we fit additive models that included all possible combinations of the covariates up to a maximum of three covariates per model. We included quadratic terms for time of day and temperature, resulting in the following full model:

$$\mu_{i,m,\xi} = \beta_{m,\xi} + \beta_{m,\rho,H} H_i + \beta_{m,\rho,H^2} H_i^2 + \beta_{m,\rho,T} T_i + \beta_{m,\rho,T^2} T_i^2 + \beta_{m,\rho,F} F_i \quad (3)$$

where $\mu_{m,i,\xi}$ is the mean expected travel time for fish i in distribution m in reach ξ. The estimated coefficients $\beta_{m,\xi}$, $\beta_{m,\rho,H}$, β_{m,ρ,H^2}, $\beta_{m,\rho,T}$, β_{m,ρ,T^2}, and $\beta_{m,\rho,F}$ define the intercept for each dam and slopes for hour (H), hour^2 (H^2), temperature (T), temperature^2 (T^2), and flow (F).

We minimized the negative log likelihood function based on Eq. 1 using the maximum likelihood estimator mle2 (package bbmle), implemented with the Nelder and Mead (1965) optimizer. Within each reach/river combination, we selected the most parsimonious model as the one with the lowest Akaike's information criterion (AIC) value compared with all other possible model subsets (Akaike 1973, Burnham and Anderson 2002). We analyzed travel time in minutes, although we converted summary statistics to hours for a more intuitive interpretation. All analyses were conducted using R (R Core Team 2013).

*Reservoir reaches.—*Visual examination of salmon travel times through reservoirs showed no indication of bimodality. Assuming the variable reservoir lengths (36–120 km) would not result in variable swim speeds, we standardized migration time by unit distance (h/km), such that travel time through a specific reservoir is the product of unit travel time and reservoir length (Zabel 2002). Unlike dam passage, where there is no theoretical justification for choosing a specific distribution, movement through reservoirs can be described as a general dispersal process with drift observed at an absorbing boundary at the upstream dam (Zabel 2002). We therefore modeled migration time with an inverse Gaussian distribution, which was consistent with the theoretical underpinnings of dispersal (Okubo 1980). The mean and shape parameters were modeled as linear functions of covariates with a log-link function to ensure positive travel times. The probability density function of the inverse Gaussian distribution is

$$f(t|\mu,\lambda) = \left[\frac{l}{2\pi t^3}\right]^{\frac{1}{2}} \exp\left[\frac{-\lambda(t-\mu)^2}{2\mu^2 t}\right] \tag{4}$$

for travel time $t > 0$, where $\mu > 0$ is the mean and $\lambda > 0$ is the shape parameter. Following Zabel (2002), the expected mean and shape of the distribution were allowed to vary with fish length, L_i, water temperature, T_i, and flow, F_i, at the time the individual salmon i entered reservoir r:

$$\begin{aligned} \mu_{i,r} &= \beta_r + \beta_L L_i + \beta_T T_i + \beta_F F_i \\ \lambda_{i,r} &= S_r + S_L L_i + S_T T_i + S_F F_i \end{aligned} \tag{5}$$

where β_r and S_r were the intercepts for each reservoir, and the effects of covariates (β_L, β_T, β_F, S_r, S_L, S_T, and S_F) were constant across all reservoirs. We minimized the negative log likelihood function based on Eq. 4 using the maximum likelihood estimator mle2 (package bbmle), implemented with the Nelder and Mead (1965) optimizer. We selected the model with the lowest AIC score among all possible subsets of covariates.

*Snake/Salmon reach.—*Travel times through the final leg of the migration from Lower Granite Dam to the SFSR weir pointed to two distinct behavior patterns (Fig. 3). As holding habitat is available both above and below the weir, we interpreted the observed bimodal arrival pattern

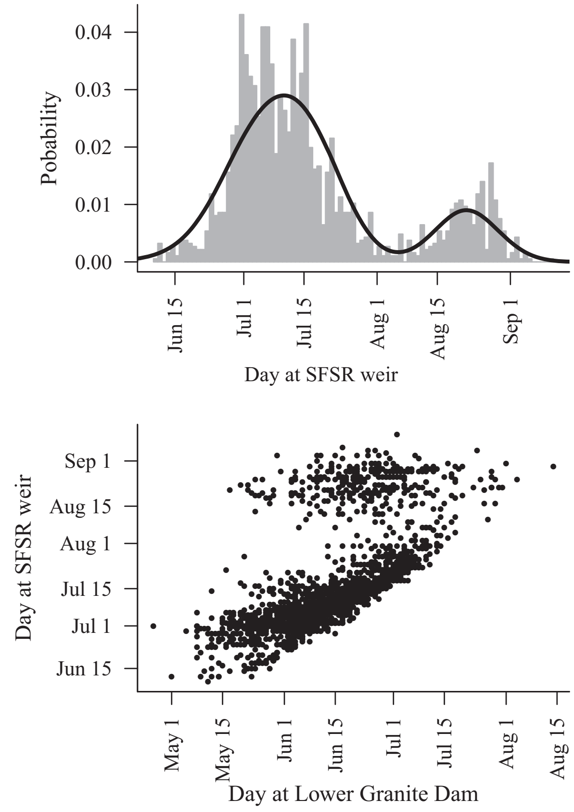

Fig. 3. Arrival day at the South Fork Salmon River (SFSR) weir (left) for 2002–2013 as observed in PIT-tagged adult Chinook salmon (histogram) and modeled (line). Arrival day at the weir relative to the day salmon were detected at Lower Granite Dam (right).

at the weir as an indication that some fish held above the weir, while others held below it until it was near time to spawn.

We again used a two-dimensional mixture model to capture this variation in behavior, but in this reach the fast and slow modes were characterized by different probability density functions. Fish that passed the weir before holding (the fast mode) were modeled using the inverse Gaussian distribution (Eq. 4), following the same logic that we applied for reservoirs. Because only one reach was modeled in this section, there was no need to standardize by unit distance. The mean of the inverse Gaussian distribution was allowed to vary by date at Lower Granite Dam, fish length, water temperature, and flow. The model was fit with a log link to ensure a positive travel time. To limit the total number of parameters in the model, we did not consider covariates for the shape parameter λ.

If a fish held below the weir (the slow mode), its travel time was constrained between 0 and a maximum assumed to be determined by spawning date. Although both arrival timing at Lower Granite Dam and spawn timing vary slightly from year to year, we assumed the maximum holding time (and hence maximum travel time for the slow mode) was fixed over the study period. Because the inverse Gaussian distribution does not have a maximum, we instead used a logistic probability distribution for the slow mode in this reach. We multiplied observed travel times by 0.01 to scale them to a range between 0 and 1. We then modeled scaled travel times using the logistic distribution, in which the location parameter was determined by the date at Lower Granite Dam.

The probability that a fish would hold below the weir (p) was constrained between 0 and 1 using a logit link. The probability p was allowed to vary with fish length, day of year, temperature, and flow at Lower Granite Dam. Day J was standardized by subtracting the minimum observed arrival day at the weir (26 April).

We minimized the negative log likelihood function for Eq. 1 where G_f was the probability density function for the inverse Gaussian (Eq. 4; fast fish) and G_s was the logistic function (slow fish) using the maximum likelihood estimator mle2 (package bbmle), implemented with the Nelder and Mead (1965) optimizer. We compared models in each mode with different subsets of covariates and selected the most parsimonious model based on AIC values.

*Cumulative migration model.—*After selecting the most parsimonious model for each river reach, we combined all reach-specific models into a full-migration simulation model from Bonneville Dam to the SFSR weir. We initialized the cumulative model with start dates and times observed at Bonneville Dam between 2002 and 2015 for PIT-tagged salmon from the South Fork Salmon River. We then simulated individual salmon passage through each reach sequentially, drawing reach-specific travel times randomly from the fitted distributions, using continuously updated environmental conditions. Cumulative migration time C_i was the sum of time spent in each reach (t_i) for an individual salmon i:

$$\begin{aligned} C_i = \sum_{1}^{8} t_{i,\text{tailrace}} + \sum_{1}^{8} t_{i,\text{fishway}} \\ + \sum_{1}^{7} t_{i,\text{reservoir}} + t_{i,\text{Snake/Salmon}} \end{aligned} \tag{6}$$

Data

*Data used in model fitting.—*Reach-specific travel times were calculated from adult Chinook salmon returning to spawn, some of which were implanted with radio transmitters at the Adult Fish Facility at Bonneville Dam. Full methods describing salmon collection, radio-tagging, monitoring, and data processing are described elsewhere (Boggs et al. 2004, Keefer et al. 2004*a*). We analyzed data from 554 radio-tagged salmon that could be associated with the SFSR population (n = 108 PIT-tagged as juveniles and radio-tagged as adults; n = 309 radio-tagged adults that returned to the SFSR), or the larger Snake River spring/summer Chinook salmon population group (n = 137 PIT-tagged as juveniles upstream from Lower Granite Dam and radio-tagged as adults).

Each Snake and Columbia River dam in the hydrosystem section was equipped with radio antennas in 11 yr from 2000 to 2013 (Table 2). Detection data from multiple antennas at each dam were used to delineate salmon passage timing through the tailrace, fishway, and reservoir. To avoid unreasonable times resulting from missed detections, fish with reach passage times <2 min in a tailrace or 55 min in a fishway were

Table 2. The number of records used in the analyses.

	Reach model fitting				Bonneville to SFSR weir	
Year	Tailrace	Fishway	Reservoir	Snake/Salmon	Cumulative model testing	Survival analysis
2000	328	344	275	0	0	0
2001	932	875	760	0	0	0
2002	458	451	393	236	214	0
2003	369	453	317	189	188	0
2004	300	300	258	151	148	525
2005	119	192	119	105	97	286
2006	110	118	82	75	74	188
2007	44	60	63	86	85	231
2008	0	0	0	166	166	488
2009	38	52	81	162	161	408
2010	34	58	66	205	231	627
2011	0	0	0	92	108	397
2012	0	0	0	91	99	333
2013	154	182	136	86	87	225
2014	0	0	0	0	99	373
2015	0	0	0	0	137	591
Total	2886 (543)	3085 (545)	2550 (546)	1644	1894	4672

Notes: The reach model fitting columns show the sum of records in each reach type per year. For reaches within the hydrosystem (eight dam tailraces, eight fishways, seven reservoirs), data are from radio-tagged fish and multiple records for individual fish occur at different dams. The row showing total numbers includes the number of unique fish in parentheses. All records used for fitting the Snake/Salmon reach, cumulative model testing, and survival analyses reflect PIT-tagged fish. SFSR = South Fork Salmon River.

excluded from the model fit for that reach. These criteria stemmed from natural breaks in the data and author experience watching fish behavior in these locations.

In contrast, PIT-tag monitoring systems were located only inside the adult fishways at a subset of dams. PIT-detection capability increased from 2002 to 2015. To maximize the strengths of each type of data (the fine spatio-temporal scale of radiotelemetry [RT] data and large numbers of PIT-tagged fish), we used RT data to fit models of reach-specific travel time within the hydrosystem, and PIT-detection data for model fitting and validation at larger spatial scales. Due to insufficient numbers of RT fish that completed the entire migration, we used PIT-tag data first to fit the model in the Snake/Salmon River section, and second, to validate cumulative travel times for the entire hydrosystem section as well as over the full migration (Table 1).

For travel times modeled in the Snake/Salmon section, we used data from the PTAGIS database (PTAGIS 2015) for 1644 Chinook salmon that had been PIT-tagged as juveniles in the SFSR (i.e., known-origin SFSR fish) and detected as adults at both Lower Granite Dam and the SFSR weir. Using salmon PIT-tagged as juveniles eliminated any bias from adult handling effects and collection dates and locations that might affect travel times.

*Data used in model validation.—*The cumulative model (Bonneville Dam to SFSR weir) was tested against 1894 PIT-tagged salmon that returned as adults in 2002–2015. Selection criteria for inclusion of individuals for testing and validating included detection at both Bonneville and Lower Granite dams for the hydrosystem section and at both Bonneville Dam and the SFSR weir for the full migration. Many (1611) of the 1644 fish used in the Snake/Salmon model fitting process were also used in the test of the full migration from Bonneville Dam to the weir. However, the PIT-tagged salmon that returned in 2014 and 2015 were not included in any part of model parameterization.

On 7 August 2014, a large sediment-laden flood event shut down SFSR weir operations for several days and may have killed adult salmon below the weir. We excluded returns after the flood event from both the observation and modeled datasets.

*Data used in model application to survival.—*One critical element of travel time data is that reach duration can only be measured for fish that survive through that particular reach. If the probability of survival varies systematically with travel time, then unsuccessful migration patterns will not be included in the model. This is a potential limitation of most travel-time models, because they can only be fit to survivors, and model validation depends on an assumption of consistent survival. However, interactions between travel time and survival are also an important reason a null model of travel time is useful.

Our reach models were primarily fit to fish that survived the entire migration. To test whether travel times differed for fish that completed a migration reach vs. those that did not required a separate dataset. Therefore, we evaluated the relationship between travel time and survival using data from all Chinook salmon that had been PIT-tagged as juveniles in the SFSR, and hence were expected to return to spawn in the SFSR. We used data from the subset of these fish that were detected as adults at Bonneville Dam in 2004–2015 (n = 4672), because we knew these individuals had initiated migration to spawning grounds. This dataset had previously been used to estimate adult survival through the hydrosystem (Crozier et al. 2016).

Environmental data.—We associated the total time a salmon spent in each reach with environmental conditions at the time it first entered that reach. Environmental conditions do change between reach entries and exits, especially over longer passage times (Zabel et al. 2014). However, the environmental variables considered here (water temperature and discharge, or flow) are strongly temporally and spatially autocorrelated, such that initial conditions were representative of future conditions within the reach. Temperature and flow can also be correlated with each other, causing statistical problems of collinearity. During the migration window for the SFSR population, however, flow tends to be relatively stable while temperatures increase, such that the daily values used in our analysis were not strongly correlated (r = −0.5 from 18 May to 4 June, which is the interquartile arrival date for SFSR Chinook salmon at Bonneville Dam). We therefore included both raw temperature and flow in our models.

At each of the eight Snake and Columbia River dams, hourly environmental data were collected by the U.S. Army Corps of Engineers and compiled by the University of Washington Columbia River Research program (Columbia Basin Research 2016). We used environmental data from the scroll case of each dam wherever possible. We removed outliers over 35°C or under 5°C, which were assumed to be recording errors. If data were missing for fewer than three sequential hours, we linearly interpolated between observations. For longer stretches of missing data, we used data from the dam forebay, the nearest water quality monitoring station, or by regression estimation with data from a neighboring dam.

We used hourly data in the reach models and the cumulative model. We used annual metrics of environmental conditions for the survival analysis. Annual metrics consisted of mean temperature and flow at Bonneville Dam from May through June. Environmental data were standardized (mean = 0, standard deviation = 1) so that coefficient magnitude reflects relative impact across covariates, and to assist model fitting.

Model validation

To assess cumulative model fit, we compared simulated migration times with observed times of PIT-tagged fish. One challenge in making this comparison was that detections of PIT tags occurred inside adult fishways and thus did not coincide exactly with reach definitions used in the model, which were based on RT detection sites. To initialize the model for this comparison, we subtracted 1 d from PIT-detection time at Bonneville Dam to account for the median time it took a Chinook salmon to pass through the Bonneville tailrace and enter the fishway, based on RT data; we set the start hour arbitrarily to 6:00 am.

We compared the distribution of simulated to observed arrival dates and travel times from Bonneville Dam to the SFSR weir. We conducted these comparisons first using data from the period used in model fitting (2002–2013) and secondly using data collected in later years (2014 and 2015; see *Model applications: potential indirect effects of travel time*).

Because our interest lay explicitly in our ability to model the full distribution of observed migration times at both reach and cumulative migration scales, we assessed model fit by quantile-to-quantile comparison. We compared the observed data to model predictions in increments of 5, from the 5th to the 95th quantiles for all reaches individually, and for the cumulative model.

Model applications: potential indirect effects of travel time

To explore potential future applications of the model, we assessed model fit when challenged with data from outside the training period. We initialized the model with start times from PIT-tagged salmon detected at Bonneville Dam in 2014 and 2015 and compared modeled and observed travel times through the hydrosystem and to the spawning grounds.

The strongest indirect effects of longer travel time should be detectable as increased mortality within the migration itself. We tested whether slower travel time through one reach was a predictor of mortality in the next reach by regressing salmon travel times through the hydrosystem against the probability of reaching the SFSR weir using generalized linear models. We included annual indices of temperature and flow, as well as conditions on the day of passage for an individual fish at Lower Granite Dam in the model. Environmental conditions could have imposed independent (but coincidental) effects on survival and travel time.

We estimated mortality based on the proportion of PIT-tagged adult Chinook salmon from the SFSR population that were detected at Bonneville Dam but never detected at the SFSR weir. We assumed that detection efficiency at the weir was high and constant over time because all fish are handled during a period of relatively low and stable flows, and the weir acted as a complete barrier to upstream movement. Thus, management actions were consistent among years and we assumed temporal variation could be attributed to covariates.

Some fish that were not detected at the weir may have still spawned successfully downstream from the weir. Therefore, the estimates of apparent survival were treated as an index of relative survival among years, assuming a constant proportion of adults from the SFSR population spawned above the weir across years. We evaluated this assumption using detections at two additional PIT antennas installed in 2008 and 2009 below all spawning areas in the SFSR. Detections at these sites in subsequent years indicated a relatively constant proportion of spawners above and below the weir across time, even in years with lower apparent survival (i.e., there was no sign of spatial re-distribution in spawning activity in 2015, a low survival year, compared with other years with average apparent survival).

In 2015, temperatures throughout the migration route approached lethal levels (>22°C) much earlier in the season than usual. Therefore, late or slow migrants were more likely to encounter these stressful conditions than early or fast migrants. If early or fast migrants were more likely to survive, we anticipated that the observed travel time distribution would be faster than model predictions in years with higher mortality.

To explore whether reduced survival of slower fish might have resulted from exposure to stressful temperature, we tested the extent to which slower fish were exposed to higher temperatures by comparing the temperatures encountered by modeled fish at Lower Granite Dam as a function of their travel time from Bonneville Dam to Lower Granite Dam. We used linear regression to test this hypothesis and compared the AIC scores of models that included travel time alone, year alone, and a travel time × year interaction.

RESULTS

Reach model fit

*Tailrace and fishway models.—*Using observed start times at each reach, simulated passage times were very similar to observed passage times. In tailraces, observed passage times ranged from <1 h to 17 d. The difference between observed and modeled times across all quantiles was <1.1 h through the 85th quantile. The 90th and 95th quantiles differed by 2.4 h and 3.2 h, respectively, which were 6% and 8% of the observed times. For fishways, observed salmon passage times ranged from 1.8 h to 16.9 h (5th–95th quantiles). For all fishway comparisons, the difference between modeled and observed quantiles was <0.4 h (5% of observed time at the 95th quantile). Thus, all model quantiles were within 8% of observed quantiles (Fig. 4).

Based on model selection, there was strong support for using the mixture model to include both modes for Snake and Columbia River tailrace and fishway models. Time of day and temperature were important explanatory variables that affected the mean of both modes for nearly all of the top-ranking models, whereas flow was not included in any of the most parsimonious models (Appendix S1: Table S1). In the tailrace

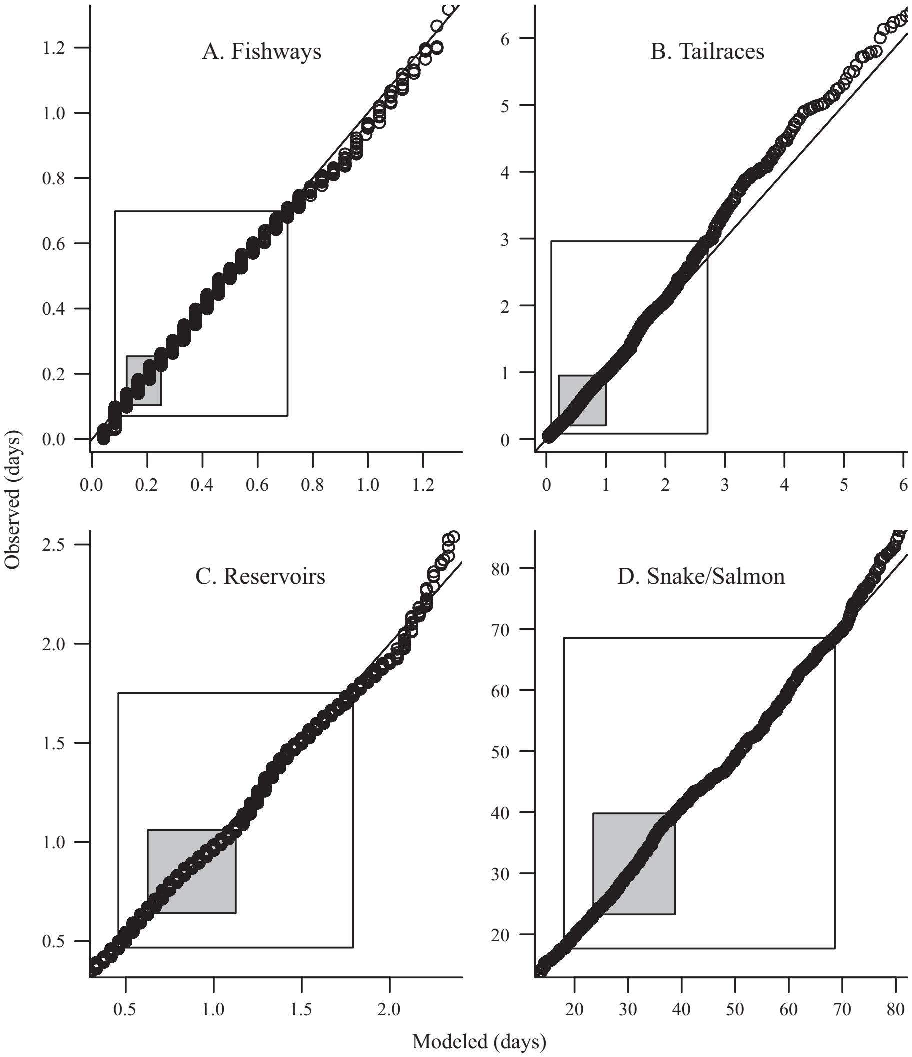

Fig. 4. Quantile plots of model-predicted Chinook salmon travel times compared with observed times. Separate panels show fits within each reach from 2000 to 2013 in fishways, tailraces, and reservoirs, and from Lower Granite Dam ladder exit to the South Fork Salmon River (SFSR) weir. Large boxes show 5th–95th quantile range for both modeled (box width) and observed (box height) travel time; small boxes show interquartile ranges. The 1:1 line is also shown. Axes are set to the 99th quantile of their respective datasets.

models, temperature consistently had a negative correlation with passage time, such that salmon moved faster in warmer water (Appendix S1: Table S2). In the fishways, however, temperature had the opposite effect on travel time: Fish tended to take longer in warmer water.

There was also strong support for keeping dam-specific intercepts in both tailrace and fishway models, as there was considerable variation in salmon passage time among dams. Tailrace intercepts varied from a lognormal mean of 8.3 h at Lower Granite Dam to 17.2 h at John Day Dam for the first mode (Appendix S1: Table S2). For the second mode, lognormal mean tailrace passage time varied from 29.7 h at The Dalles Dam to 52.2 h at Ice Harbor Dam. Lower Granite Dam had the slowest salmon passage time through fishways in both fast and slow mode (4.3 h and 7.7 h, respectively). Salmon passed fishways fastest at The Dalles Dam for mode 1 (2.7 h) and Ice Harbor Dam for mode 2 (3.2 h).

The reach-specific mixture models reproduced the observation of a continually shifting bimodal distribution of travel times. In all four top Columbia and Snake River tailrace and fishway models, the proportion of salmon in the fast mode peaked in the morning and hit a nadir in the late afternoon (Fig. 5). In fishways and tailraces, mean travel time in the fast mode was <1 d. Thus, the two modes in the mixture model largely captured the higher probability of an individual fish exiting the reach within one day (first mode) vs. the lower probability of an overnight or longer residence period (second mode). The majority of fish that entered a reach in the first half of the day passed the reach before dusk, while fish that entered a reach later in the day typically did not exit until the following morning. Thus, the probability of spending the night increased with arrival time closer to dusk. However, fish entered and exited tailraces and fishways at all times of the day and night. Therefore, even when the majority of fish at a given time of day were in the fast group, substantial proportions (e.g., 20–50%) were still in the slow mode. Similarly, the proportion of fish in the slow mode never exceeded 0.8 (Fig. 5).

The bimodal pattern was weaker in the fishways than in tailraces. The fishway modes essentially overlapped because mean times were very similar in both modes. Consequently, proportions in the respective modes did not correspond to visually bimodal behavior in the model.

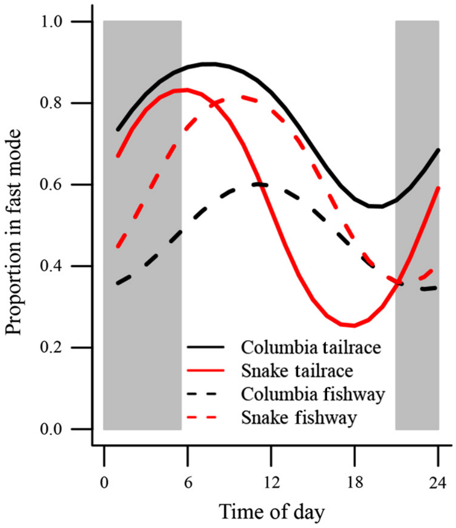

Fig. 5. The proportion of Chinook salmon drawn from the fast distribution (p) as a function of time of day at reach entry in the different reach types. Shaded areas represent approximate nighttime hours.

In the Columbia River dam tailraces, there was a hint of a third mode of fish that took more than 2 d to pass (Fig. 2), a behavior that was approximated in the model with a long tail. This phenomenon accounted for the slight bias in upper quantiles in the tailrace model (Fig. 4B).

Reservoir models.—Differences between modeled and observed quantiles were <1.6 h through the 95th quantile (6% of observed travel time; Fig. 4C) through reservoirs. The most parsimonious reservoir model included covariates in both the mean and shape term, as well as dam-specific offsets in both (Appendix S1: Tables S3 and S4). In this model, temperature and flow were selected to modify mean rate, but the shape term was only modified by flow. This model produced shorter travel times in warmer water and at lower flows. The interquartile range of salmon travel times through reservoirs was 63–82 km/d, with a median of 73 km/d.

Snake/Salmon model.—The modeled mixture distribution captured the observed bimodal pattern of travel times from Lower Granite Dam to the SFSR weir (Fig. 3). The 5th–95th quantiles ranged from 18 to 69 d for both modeled and observed data from 2002 to 2013 (Fig. 4D). At all quantiles, modeled travel times were within 1.5 d of observed times, which was always within 5% of observed times. The full range of travel times observed (10–95 d) was slightly longer than the full range modeled (6–88 d), but the majority of fish behaviors were captured in the model. In the 5th–95th quantiles, both observed and modeled arrival dates at the weir were 29 June–27 August (median date was 16 July).

The most parsimonious Snake/Salmon model included only temperature and date at Lower Granite Dam. Both temperature and date had negative coefficients (Appendix S1: Table S5), such that travel was faster with warmer water and later in the season. These same two covariates were also selected in models to determine the probability that a fish would hold below the SFSR weir. Holding was more likely later in the season, but this was modified by temperature. Under warmer conditions, fish were more likely to swim directly to the weir.

Cumulative model validation

Cumulative travel through the full migration, Bonneville Dam to SFSR weir, took 23–108 d (observed) and 22–108 d (modeled). For 2002–2013, model estimates were within 2.7 d of times observed through the 95th quantile (3%; Fig. 6A). The cumulative model thus performed as well as the independent reach models. Modeled reach-specific passage times were within 4 h of observed through the 95th quantile for all reach types within the hydrosystem and were within 1.2 d in the Snake/Salmon section.

Analysis of years outside the training dataset.— In 2014–2015 comparisons, cumulative model quantiles were within 2.2 d of observed through the 95th quantile (4% of 55 d observed at the 90th quantile), with a median of 39 d for modeled and 38 d for observed (Fig. 6B). In 2014, the model travel times from Bonneville Dam to Lower Granite Dam were within 0–1.8 d (13%) of those observed across quantiles (Fig. 7A). The observed fish travel times below the median tended to be faster than modeled, whereas observed and modeled times were very similar for fish moving at above the median rate (less than half a day, or 4%, difference). The median travel time in 2014 was observed to be 0.8 d faster than the 2002–2013 average, while the modeled median was 0.1 d faster than the long-term average. In the Snake/Salmon section, model predictions differed by 0–7% of observed times (max difference of 2.5 d, at an observed travel time of 34 d, Fig. 7B).

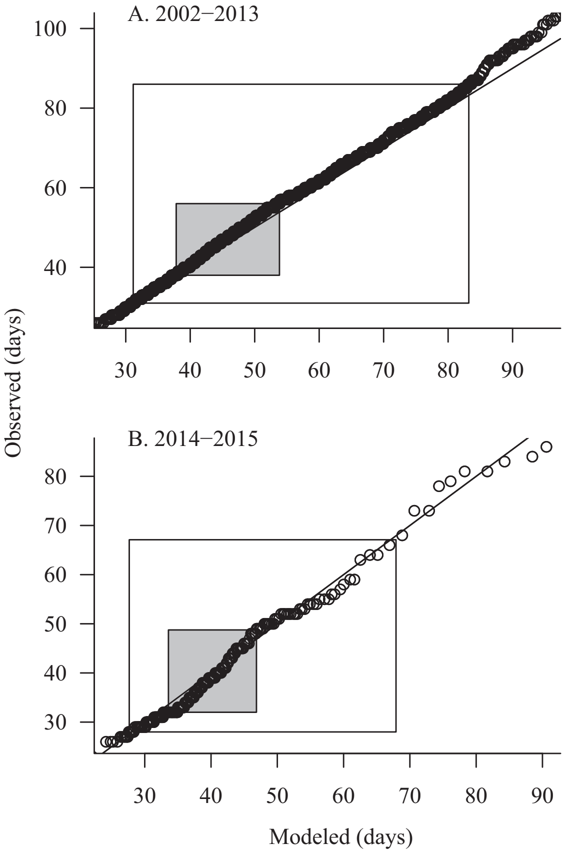

Fig. 6. Quantile plots of model-predicted compared with observed Chinook salmon travel times for the entire migration from Bonneville Dam to the South Fork Salmon River (SFSR) weir for 2002–2013 (left) and 2014–2015 (right). Large boxes show 5th–95th quantile range for both modeled (box width) and observed (box height) travel time; small boxes show interquartile ranges. The 1:1 line is also shown.

In 2015, the model-predicted travel times through the hydrosystem were 2 d faster than the 2000–2013 average due to environmental conditions—both low flows and high temperatures produce faster migration. However, observed times through the hydrosystem were 4 d faster than average. Across quantiles, observed salmon were consistently 1.1–1.8 d faster through the hydrosystem than modeled fish (Fig. 7C). For the upstream Snake/Salmon section in 2015, modeled times were within 0.5 d of observed times through the 70th quantile (which was always within 2% of observed times, Fig. 7D).

Model applications

Identifying high-impact reaches.—We summarized model results by characterizing time spent within each reach type (i.e., tailraces, fishways, reservoirs within the hydrosystem) and over the entire migration (Fig. 8). Modeled median times from Bonneville Dam to Lower Granite Dam were 14 d (14 d observed) and 30 d from Lower Granite Dam to the SFSR weir (29 d observed). For the entire migration from Bonneville Dam to the weir, median modeled time was 43 d (45 d observed). Thus, based on medians, 30% of total migration time was spent within the hydrosystem (excluding Lower Granite Reservoir).

In the hydrosystem, model results indicated that 65% of salmon spent <2 d in dam fishways, and this time constituted <15% of total hydrosystem passage time. Some fish spent almost a quarter of their hydrosystem time in fishways (up to

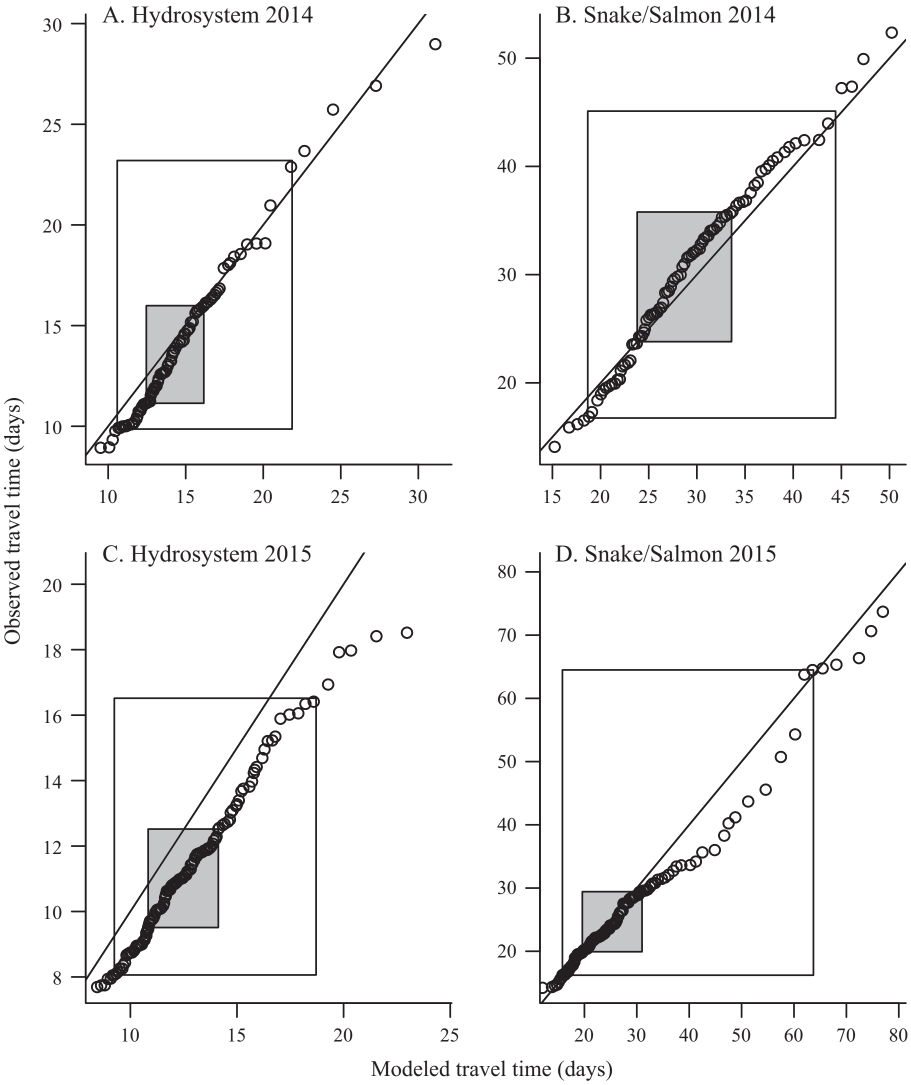

Fig. 7. Quantile plots of model-predicted compared with observed Chinook salmon travel times in 2014 (top panels) and 2015 (lower panels) within the hydrosystem (left panels) and Snake/Salmon section (right panels). Large boxes show 5th–95th quantile range for both modeled (box width) and observed (box height) travel time; small boxes show interquartile ranges. The 1:1 line is also shown.

3.25 d). The interquartile range was similar in fishways and reservoirs (21 and 28 h, respectively), but was much wider in tailraces (88 h). The slower half of fish (50th–95th quantiles) spent 6–13 d in tailraces. Tailrace time constituted 44–66% of the total hydrosystem time and 14–29% of full migration time (50th–95th quantiles).

Total time in tailraces was strongly correlated with total time in the hydrosystem ($r = 0.95$, $P < 0.001$, based on linear regression; Fig. 8). Fishway and reservoir passage times were also statistically significant predictors of hydrosystem time ($P < 0.001$), but the correlation coefficients were much lower than for tailraces ($r = 0.13$ and $r = 0.27$, respectively). Similarly, times for all three reach types were statistically significant predictors of time from Lower Granite Dam to the SFSR weir, but the correlations were low ($r \leq 0.10$).

Impact of environmental conditions on travel time.— Changes in environmental conditions from year to year are expected to alter travel times. Among years from 2002 through 2015, median modeled

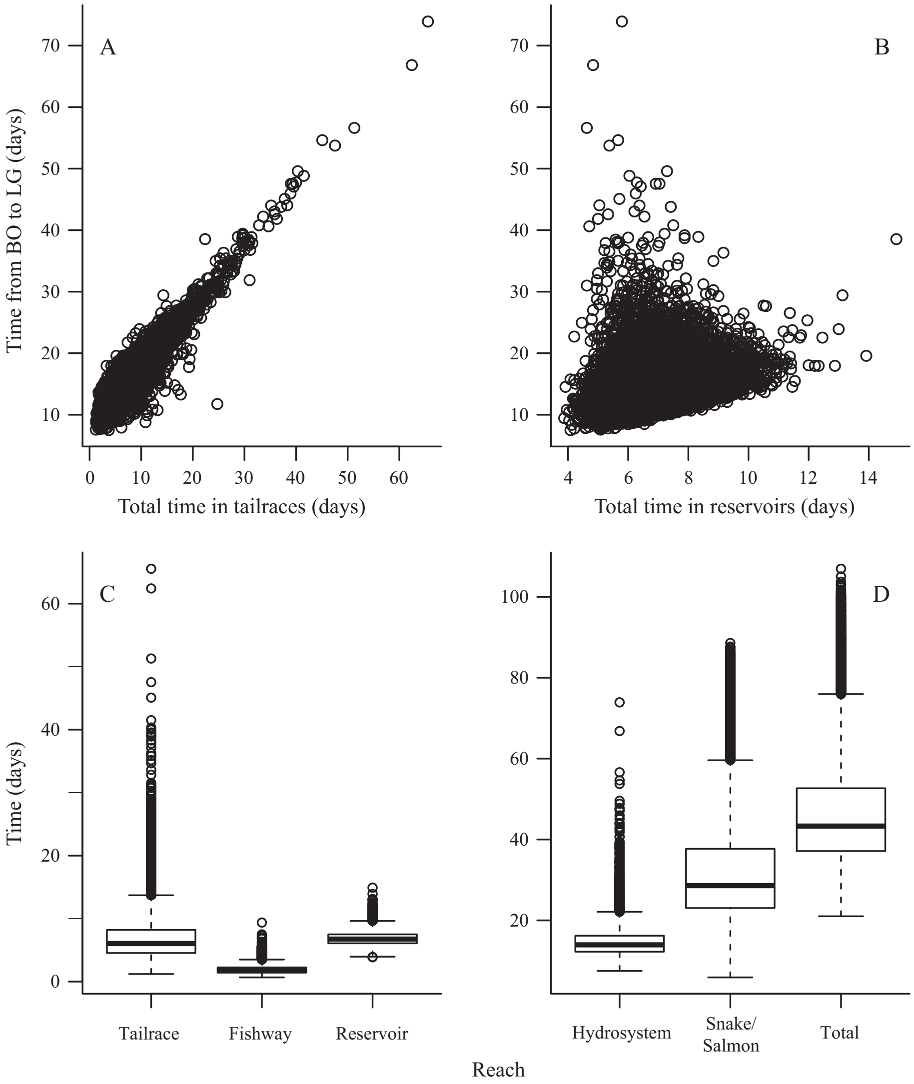

Fig. 8. Scatter plots of time Chinook salmon spent in tailraces (upper left) or reservoirs (upper right) compared with total hydrosystem time (Bonneville to Lower Granite Dam). Box and whisker plots show the time spent in different types of reaches within the hydrosystem (lower left), and for the hydrosystem as a whole compared with the Snake/Salmon reach and full migration (lower right). Whiskers show 1.5× the interquartile range.

migration times varied by 3 d through the hydrosystem (range of medians: 12–15 d) and by 10 d for the migration as a whole (36–46 d; Appendix S1: Fig. S1). The cumulative model produced a pattern of median annual migration times similar to that of the median times observed across years, in that years were correctly assigned as having faster or slower salmon than average. Median times were negatively related to annual temperature and positively related to annual flow for both the modeled and observed data. However, interannual variation was lower in the model than in the observation dataset (observed range of 11–20 d in median travel time in the hydrosystem, and 34–57 d in the Snake/Salmon section).

*Delayed mortality.—*If longer travel times have negative indirect effects on fish, one would expect that delayed mortality would be correlated with travel times. We found that survival through the Snake/Salmon reach was strongly associated with travel time through the hydrosystem, in addition to environmental variables. Therefore, slower fish that survived the hydrosystem were more likely to die during the remainder of the migration. Among salmon that survived the entire migration, travel times through the Snake/Salmon section were not correlated with travel times through the hydrosystem ($r = 0.002$, $P > 0.05$).

Travel time, annual flow, individual temperature, and day at Lower Granite Dam were in the top model based on AIC scores, with individual flow added in the next most important model (Appendix S1: Table S6). The top two models captured 98% of the cumulative model weight. Salmon that passed Lower Granite Dam later in the season and those with longer travel times from Bonneville Dam to Lower Granite Dam had lower survival.

Based on the survival analysis, we observed a general relationship between survival and travel time, and this relationship was stronger in some years than others (Fig. 9). Very few slow fish survived in 2015, a year in which a strong relationship between survival and travel time was apparent. In contrast, there was a weak relationship between travel time and survival in 2011, a cooler-than-average year.

Temperature exposure.—Temperature exposure was strongly correlated with travel time: Averaged across all years, the mean temperature salmon encountered at Lower Granite Dam increased by about 0.5°C for every week added to salmon travel time through the hydrosystem up to about 8 weeks (Fig. 9). Mean temperature increased from 14°C to almost 19°C as hydrosystem travel times increased from 2 to 12 weeks. However, there was also a strong year effect, such that temperatures experienced by slow migrants in cool years could be less than the temperatures experienced by fast migrants in warm years. In 2015, for example, the mean temperature at Lower Granite Dam increased from about 18–21°C throughout the migration period, whereas in 2011 the maximum temperature was only 17°C. The most parsimonious model used to evaluate temperature exposure included the year × travel time interaction, indicating that travel time increased temperature exposure in some years more than others. Thus, although temperature exposure generally increased with longer travel times, the biological significance of temperature as a stressor was likely much higher in some years.

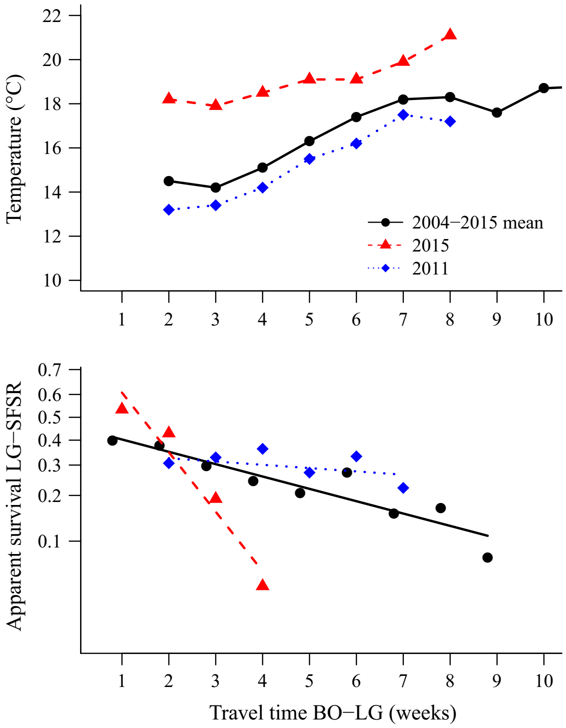

Fig. 9. Chinook salmon travel time from Bonneville Dam to Lower Granite Dam relative to the mean temperature at Lower Granite Dam (top) and the probability of reaching the South Fork Salmon River (SFSR) weir (apparent survival; bottom), with data aggregated into weekly cohorts. The final cohort includes multiple weeks if the weekly sample size dropped below 10 fish. The *y*-axis of the lower panel is on a logit scale to show linear regression lines resulting from a generalized linear model, although labels are back-transformed survival probabilities.

DISCUSSION

Long-distance migrants are especially difficult to protect because they can span multiple jurisdictional boundaries, habitat types, and climate zones. Even in species with relatively simple migrations, migratory behaviors can be complex. Individual variation in behaviors can affect survival depending upon decisions made en route in response to local conditions, and choices made in one habitat can have impacts on behavior and survival in subsequent habitats (Alerstam et al. 2003). Therefore, improved understanding of migratory behavior, especially regarding stops or changes in migration rate, will help managers identify specific factors that increase costs of migration and decrease survival. To this end, mixture models offer a promising approach for modeling switches in behavior, such as slowed or paused migration at obstacles or stopovers at various spatial and temporal scales.

The model framework presented here captures the diversity of movement rates observed in a very large database of migratory behavior. The results demonstrate that N-dimensional mixture models constitute a general framework for modeling variation in complex migratory behavior in which travel time distributions with multiple modes are observed. Additionally, the flexibility of an N-dimensional model allows for any number of behaviors to be incorporated. Telemetry-based animal movement datasets such as ours are becoming more common in other systems where environmental data likely exist (Hussey et al. 2015). Linking telemetry data to mechanistic models of movement is a growing need as large biotelemetry datasets accumulate (Costa et al. 2012, López-López 2016). While our model used a large sample size and a high level of spatial complexity, the mixture model structure used here could be applied to systems informed by smaller datasets or where less spatial resolution is available. Models with fewer segments would be sufficient to address management concerns for many other species. For instance, the bimodality in behavior (e.g., Fig. 3) would likely be detectable and relevant to the analysis of samples of tens to hundreds of individuals migrating through spatially complex habitats, particularly those for which high-resolution tracking data were available. It could even apply to movements sequenced over time within a small habitat (Skalski and Gilliam 2000, 2003).

Chinook salmon case study

Minimizing anthropogenic stressors and anticipating impacts of climate change on population viability are management imperatives for threatened and vulnerable species (Groves et al. 2008, McClure et al. 2013, Link et al. 2015). We capitalized on a large 15-yr database of individual Chinook salmon movements to build a simulation model of migration travel time with several key features. First, the model accounts for a proportion of the population which slows down at dams and/or holds position near spawning grounds by aggregating fish into distinct distributions at each dam and near the final point of detection. In this case, the resulting mixture distribution is bimodal in the most complex reaches (i.e., some fish proceed directly through these reaches, whereas others pause for a period), which closely matches the observed population distribution of travel times. Although the model was fit to one population of Chinook salmon, hydraulic complexity among habitats is associated with diel variability in behavior across five species of migrating anadromous fishes in the lower Columbia River (Keefer et al. 2013). Migrating adults of these species swim at a relatively constant rate through reservoirs, regardless of time of day. However, when these and other visually orienting species (including salmon, steelhead, and American shad, *Alosa sapidissima*) encounter high velocity and turbulence at dams, their movements tend to be primarily diurnal (Keefer et al. 2013).

Second, the model explicitly estimates travel times through short reaches at dams, where energetic costs differ markedly, allowing appropriate cataloging of time spent in different types of migration environments (e.g., low-velocity reservoirs vs. turbulent dam tailraces). Third, travel times are conditioned by the environmental state and by reach, an attribute that facilitates hypothesis exploration across scenarios of altered conditions, such as potential climate changes and reach-specific management actions. The model predicts not only arrival timing on the spawning ground, but also the amount of time spent in each tailrace, fishway, and reservoir along the migration route.

Our cumulative model included multiple behavioral elements (diel behaviors, variation in prespawn holding strategy) and reproduced travel times for the vast majority of individual salmon across a subcontinental-scale migration and through a complex environment. The large amount of data against which we tested this model was unprecedented for anadromous fish and was particularly useful for demonstrating the flexibility of the model structure. Previous simulation models of anadromous fish migration, including sockeye salmon in the Fraser River (Rand et al. 2006) and American shad in the Connecticut River (Castro-Santos and Letcher 2010), largely consisted of extrapolations from small-scale studies of relatively few fish. In contrast, our model was fit using thousands of observations at specific reaches and tested against nearly two thousand individual Chinook salmon migration histories. The extensive data available for the Columbia River Basin thus increase our confidence in the management utility of the model for scenario exploration.

The model accurately reconstructed salmon migration durations and our test applications provided indirect evidence of reduced survival by slow migrants during adverse conditions. Future applications can explicitly add fitness-related functions to quantify the costs of especially slow migration in specific reaches and exposure to additional stressors. The ability to quantify indirect effects of travel time through the hydrosystem will improve estimates of the fitness cost related to these anthropogenic factors and will help prioritize conservation efforts under alternative climate and management scenarios.

*High-cost migration segments.—*Migration travel time through the hydrosystem was most strongly correlated with time salmon spent in the tailraces at dams. In general, adult migrants spend disproportionately longer time in dam tailraces relative to other reaches while searching for fishway openings, moving in and out of fishways, and waiting for suitable environmental cues, including daylight (e.g., Keefer et al. 2004*a*, 2013, Caudill et al. 2013). The next step toward quantifying the fitness impact of time spent in these turbulent locations is to integrate equations on energetics (e.g., Bowerman et al. 2017) with the travel-time model.

For any given migration, increased duration is generally associated with higher energetic costs and lower survival (Naughton et al. 2005, Caudill et al. 2007, 2013), both of which are affected by environmental conditions (Crossin et al. 2008, Keefer et al. 2008, Nadeau et al. 2010). Snake River spring- and summer-run Chinook salmon undergo a reproductive migration of 1000–1500 km with little or no food intake, so energy expenditure is expected to be closely tied to fitness. Energetic costs are the product of duration and metabolic rate for any given set of conditions, which are strongly influenced by temperature and flow in migrating fishes. Energetic costs are a primary explanation for negative cumulative effects of passing dams and stressful environmental conditions on population viability, through either effects on survival or reduced allocation to reproduction (National Research Council 1996, Rand et al. 2006). Salmon energetic rates in regulated rivers are typically highest in tailraces (e.g., Brown et al. 2006), so the considerable amount of time spent in tailraces (44–66% of total time in the first 460 km of the migration) likely has a disproportionate effect on the total energetic cost of the migration.

In contrast, prespawn holding in tributaries for spring-run Pacific salmon has a low daily energetic cost, but relatively long duration. Both the duration and metabolic cost of holding are influenced by temperature, illustrating the importance of accurately modeling the duration of each component of the migration to effectively calculate energetic costs. Individual-level decisions relative to the allocation of time spent in active migration vs. holding, and distribution of time within the hydrosystem, can result in quite different survival outcomes, which would not be fully appreciated by summaries of mean travel times in each reach. For example, two fish simulated by the model that had the same total travel times of 75 d differed dramatically in the amount of time they spent in tailraces (3 d compared with 62 d). These fish might both arrive at the spawning grounds at the same time, but energetic reserves for spawning would likely be very different as a result of differences in migration behavior and en route environmental experiences.

*Climate effects.—*Across all reaches, temperature had the largest influence on salmon travel time, which is an important consideration in the context of climate change. In most reaches, travel times decreased under higher water temperatures, although passage time through fishways increased (see Caudill et al. 2013 for mechanisms). However, we advise caution when applying our travel-time model without modification to temperatures beyond the range of what was used in the model, because of known non-linear relationships (Salinger and Anderson 2006) including temperature-driven blockages to migration (Hyatt et al. 2003, Strange 2010). Temperatures above 20°C are encountered much more frequently by late-summer- and fall-run Chinook salmon, sockeye salmon, and steelhead than by the spring-/summer-run analyzed here. Populations migrating during the warmest season are known to use thermal refugia more extensively than spring/summer Chinook salmon (Goniea et al. 2006, Keefer et al. 2009). However, the Columbia

River has been warming during summer over several decades (Crozier et al. 2011) and will likely exceed 20°C for much longer periods in the future due to climate change (Mantua et al. 2010), increasing exposure to stressful temperatures for many populations, including the case study population. As a result, behavior of this population could change in the future, but the current model structure could easily accommodate temporary or permanent migration barriers as another mixture mode triggered by environmental conditions if these data become available.

*Implications for salmon survival.—*An important aspect of migration and survival studies is that differential survival can bias observed travel times to a given destination, and hence estimates of model performance. Migration timing and duration is intimately linked to survival in many animal populations (Gienapp et al. 2007, Reed et al. 2011). Slower individual travel times were associated with a lower probability of survival in most years in our population (Fig. 9; Caudill et al. 2007). If the duration–survival relationship were constant over time, survival could be modeled as a simple function of travel time. However, we found that the relationship between travel time and survival was stronger in some years than others, probably because the costs of longer travel times are higher in some years.

In 2015, for example, higher mortality of slower-than-average fish likely drove observed travel times to be shorter on average than they would have been in the absence of en route mortality. The slow fish that did not return to the SFSR weir may have died from acute heat stress during migration, as temperatures approached or exceeded lethal limits (~25°C) in the Columbia, Snake, and Salmon rivers in early July (NOAA Fisheries 2016). Mortality can also be increased at sublethal temperatures (18–25°C) through temperature-mediated disease or exacerbated energetic costs leading to exhaustion (Crossin et al. 2008, Martins et al. 2012, Ray et al. 2012). Warmer temperatures may also have caused fish to seek thermal refugia that exposed them to some additional source of mortality, such as fishery harvest (Goniea et al. 2006, Keefer et al. 2009). Regardless of the cause of mortality, without an estimate of the travel time of unsuccessful fish, it is difficult to estimate the magnitude of the bias imposed by differential mortality.

Innate variation among individuals can also affect migration rate (Moser et al. 2014), and adding a random effect to capture this possibility might remove the slight skew in the model fit in certain reaches. However, the correlation between travel times of survivors in successive segments in our data was low. For example, the correlation between salmon passage time from Bonneville Dam to McNary Dam and from McNary Dam to Lower Granite Dam was $r = 0.13$ on average across years, and in some years as low as $r = 0.04$. Nonetheless, during years with a strong relationship between travel time and survival, such as in 2015, the correlation among times was higher ($r = 0.29$). Thus, correlation in travel times in this case appears to be a result of differential survival rather than an inherent fish effect. An important application of this model is the ability to systematically explore the factors that contribute to cumulative effects, including individual effects that may be much more influential in some species or situations.

CONCLUSION

Existing migration impediments and increasing threats such as climate change have been difficult to model due to a lack of both suitable data and analytical structures (Kunz et al. 2008). Rapidly advancing technology has made linking long-range tracking of individuals to data on environmental conditions possible for many more species, filling data gaps and providing insight into individual behaviors. However, applications of telemetry data suitable for estimates of population-level fitness and variability are still very rare (Crossin et al. 2014). The cumulative travel-time model developed here for Chinook salmon provides a crucial stepping-stone to bridge the gap between high-resolution, individual-based behavioral data, data on environmental conditions, and population-level impacts on viability. Future research incorporating individual covariates in specific reaches to explore the probability of being in the fast or slow groups, summing energetic balances across the entire migration, and integrating survival with the travel-time model will further enhance the applicability of this model to decision makers in the Columbia River Basin. The modeling approach developed here provides the essential framework that has been lacking for these investigations.

The mixture model approach presented here is flexible and can be easily modified to accommodate a variety of migratory conditions and discrete changes in freshwater, marine, and terrestrial systems. For example, meteorological conditions during flight can affect the decision to use stopover sites, and the conditions of those sites combine to affect the duration of migration and energetic status of migratory birds arriving on breeding grounds (Battley et al. 2005). Other alternative movement behaviors mediated by environmental conditions include resting or active migration in humpback whales *Megaptera novaeangliae* (Braithwaite et al. 2015), and avian soaring vs. flapping (Mandel et al. 2008). Current optimization approaches might fail to capture the real tradeoffs animals confront in an increasingly complex ecosphere (Kunz et al. 2008). We present this framework such that behavioral decisions conditioned on the environment can be incorporated into efforts to estimate the costs of migration in changing environments in support of future recovery planning and management decisions.

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