Hydrobiologia (2008) 609:289–300
DOI 10.1007/s10750-008-9407-z

Comprehensive passage (COMPASS) model: a model of downstream migration and survival of juvenile salmonids through a hydropower system

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Abstract Migratory fish populations are impacted worldwide by river impoundments. Efforts to restore populations will benefit from a clear understanding of survival and migration process over a wide-range of river conditions. We developed a model that estimates travel time and survival of migrating juvenile salmonids (*Oncorhynchus* spp.) through the impounded Snake and Columbia rivers in the northwestern United States. The model allows users to examine the effects of river management scenarios, such as manipulations of river flow and spill, on salmonid survival. It has four major components: dam passage and survival, reservoir survival, fish travel time, and hydrological processes. The probability that fish pass through specific routes at a dam and route-specific survival probabilities were based on hydroacoustic, radio telemetry, PIT tag, and acoustic tag data. We related reservoir mortality rate (per day and per km) to river flow, water temperature, and percentage of fish passing through spillways and then fit the relationships to PIT-tag survival data. We related fish migration rate to water velocity, percentage of fish passing through spillways, and date in the season. We applied the model to two threatened "Evolutionarily Significant Units" (as defined under the US Endangered Species Act): Snake River spring/summer Chinook salmon (*O. tshawytscha* Walbaum) and Snake River steelhead (*O. mykiss* Walbaum). A sensitivity analysis demonstrated that for both species survival through the hydropower system was responsive to water temperature, river flow, and spill proportion. The two species, however, exhibited different patterns in their response. Such information is crucial for managers to effectively restore migratory fish populations in regulated rivers.

Keywords Ecological modeling · Salmon · Migration · Survival · Hydropower

Guest editors: R. L. Welcomme & G. Marmulla
Hydropower, Flood Control and Water Abstraction: Implications for Fish and Fisheries

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Introduction

How do migratory fish populations respond to varying river conditions? This question is particularly relevant in regulated rivers because river impoundments have impacted migratory populations worldwide (McCully, 2001) and because management operations can have substantial effects on population survival and migration timing. Thus, efforts to restore migratory fish populations in regulated rivers will benefit greatly from a clear understanding of survival and migration processes over a wide-range of river conditions and dam operations.

In the Columbia River basin in northwestern United States (Fig. 1), this issue is critical because 13 "Evolutionarily Significant Units" (ESUs) of Pacific salmon (*Oncorhynchus* spp.) that spawn within the basin are listed as threatened or endangered under the US Endangered Species Act. Further, the basin provides irrigation for millions of acres of farmland and has traditionally supported sport, commercial, and tribal fisheries for salmon and steelhead. In addition, the Columbia River and its tributaries is one of the most hydroelectrically developed river system in the world (capacity of approximately 20,000 megawatts), and dams allow for river navigation and provide flood control. Consequently, actions to mitigate effects on fish can cost tens of millions of US dollars per year.

The social and economic importance of these conflicting interests has led to an effort to develop a model to describe juvenile salmon passage through the Columbia River and Snake River (the largest tributary to the Columbia). Scientists from throughout the northwestern United States have developed the Comprehensive Passage (COMPASS) model to predict the effects of alternative hydropower operations on salmon survival rates.

The model has a variety of applications, including developing management plans for the highly regulated Columbia and Snake rivers and monitoring intra seasonal progress of migrating populations to determine if timely adjustments to river operations are required. The model simulates several types of management actions: spill scheduling (for many dams, the spillway is the safest and quickest passage route for juvenile salmon), timing of water releases from storage reservoirs (which can alter water velocity and temperature downstream), transportation timing (many juvenile salmon are collected at upstream dams and transported in barges and trucks

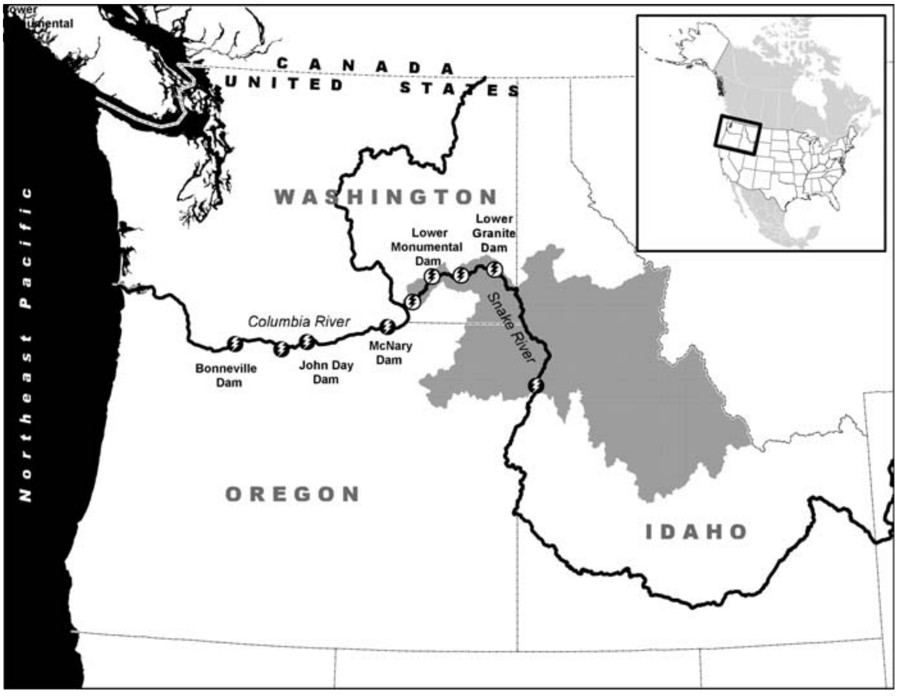

Fig. 1 Columbia and Snake Rivers, with major dams on the Snake and lower Columbia rivers identified with lightning bolts. The Snake River basin is highlighted in grey

and released below the hydropower system). In the future, we may also use the model to address more dramatic actions, such as reservoir drawdown and dam removal.

This article focuses on the dynamics of the seaward migration of juvenile anadromous salmonids. We present overviews of the model components, data to support the model, and range of predictions produced by the model. Due to space limitations, we cannot provide all model details, but more details are available upon request to the lead author. This article presents results for two ESUs: Snake River spring/summer Chinook salmon (*O. tshawytscha* Walbaum) and Snake River steelhead (*O. mykiss* Walbaum).

Model description

The downstream passage component of COMPASS is written in the C programming language and was derived from CRiSP (Anderson et al., 2000), a previous salmon passage model. The model is composed of four submodels: dam passage, reservoir survival, travel time, and hydrological processes.

The model is initiated with a simulated release of fish at a particular release site, with the timing of this release typically corresponding to the migration of wild populations. Releases may be distributed across days with varying numbers of fish per day. All fish in a release group share common travel time, survival, and dam passage behaviors. The model moves fish in half-daily time increments through river segments and dams following a sequence of steps (Fig. 2). Step 1 releases all fish into a reservoir on a given day and Step 2 distributes their exit time at the bottom of the reservoir according to the travel time model, described below. Step 3 applies a reservoir survival function to the fish before they move to the dam passage algorithm. At the dam, arriving fish are distributed across passage routes according to specified passage probabilities (Step 4). Step 5 applies route-specific survival probabilities. Step 6 recombines fish that passed through the various passage routes. Fish that enter the bypass system in collector dams may be transported, according to transportation schedules (Step 7); the remaining fish are released to the next downstream reservoir (Step 8). Note that because travel time and dam passage algorithms disperse fish, the daily groups exiting a dam are composed of fish from different release groups within or at the top of the reservoir. Fish move through the system until they pass the lowermost dam and enter the estuary.

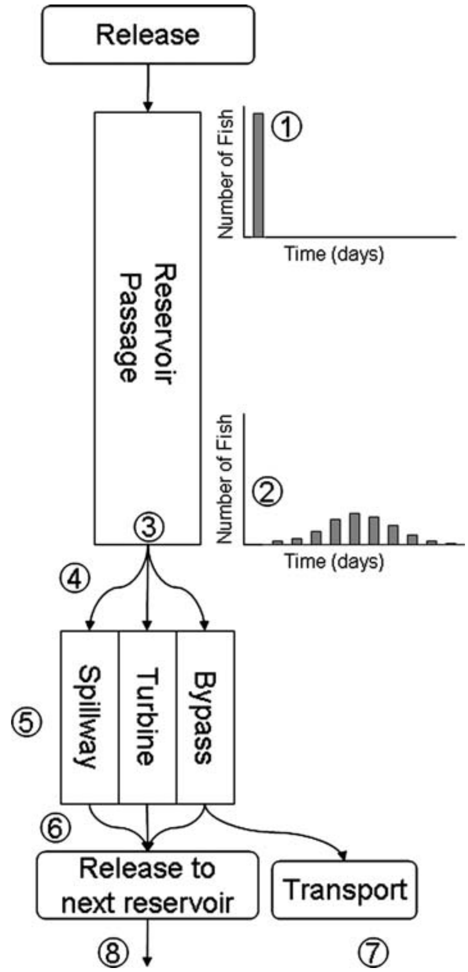

Fig. 2 Passage model algorithm, features the steps taken to move a daily release of fish through a project. See text for description

Dam passage

Fish pass from the reservoir module to the dam module on half-daily time steps corresponding to a daytime and nighttime period. Dam passage is represented as a sequence of passage probabilities which are derived from dam passage studies using radio and acoustic tagged fish (e.g., Skalski et al., 2002). First, the typically nonlinear spill efficiency relationship between the portion of fish passing through a spillway and the proportion of river flow passing through the spillway (e.g., Wilson et al., 1991) determines a portion of the fish are diverted to spillway passage (Fig. 3). Each dam and species has a unique spill efficiency relationship.

Fish that do not pass via the spillway enter the turbine intakes at the powerhouse. At most dams, turbine intake screens divert a large proportion of the fish to a juvenile bypass system, with this proportion defined as Fish Guidance Efficiency (FGE). FGE can be specified separately for day and night at each dam, if sufficient data exist. At some dams, fish can pass via sluiceways or alternate surface bypass routes not associated with turbine intakes or the spillways. These passage routes also have specified passage probabilities.

Reservoir survival

The primary data for calibrating model survival are PIT-tag (Prentice et al., 1990) data. Most dams in the lower Columbia and Snake rivers have automatic PIT-tag detectors in their juvenile bypass systems. PIT-tagged fish are also detected downstream from Bonneville Dam in the Columbia River estuary. Using standard mark-recapture methods (Burnham et al., 1987) we estimated survival and standard errors through four river segments delineated by dams (Fig. 1): Lower Granite (release site) to Lower Monumental; Lower Monumental to McNary; McNary to John Day; and John Day to Bonneville.

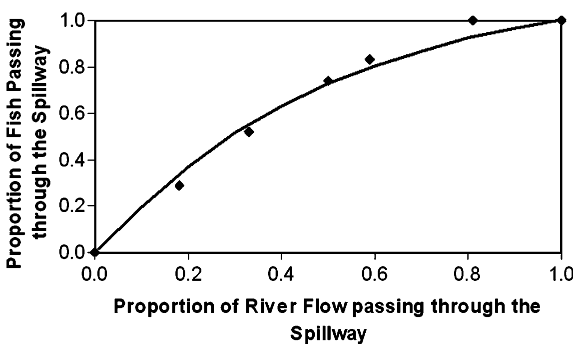

Fig. 3 Sample spill efficiency curve (see text for definition) fit to data (points). The data are based on radio-tagged Snake River spring/summer Chinook salmon passing Lower Granite Dam in 2002 and 2003

Reservoir survival estimates were based on fish PIT-tagged from 1995 through 2005. Juvenile wild Snake River spring/summer Chinook salmon and steelhead were captured, PIT tagged, and released at Lower Granite Dam or upstream from the dam. Tagged fish were placed into weekly release groups based on either day of release or day of passage at Lower Granite Dam. Because groups of fish spread out as they migrate downstream, we formed new weekly cohorts (of Snake River origin) at McNary Dam based on when fish were detected there for survival estimation through the lower Columbia River.

PIT-tag survival estimates represent survival through an entire "project" (reservoir and dam), or two such projects in some cases (e.g., Lower Monumental Dam to McNary Dam, which includes Ice Harbor Dam (Fig. 1)):

$$S_{\mathrm{PROJECT}} = S_{\mathrm{RESERVOIR}} \cdot S_{\mathrm{DAM}} \tag{1}$$

In order to estimate the components of survival, we used independent data, primarily radio telemetry data, to estimate dam survival, as described above. We divided this out of project survival and then treated the remaining survival as reservoir survival. We related this remaining survival to river conditions in the reservoir. Therefore, some of the variability in our model fits described below reflects variability in dam survival in addition to variability in reservoir survival.

A standard form for survival functions is

$$S(t) = \exp(-r \cdot t) \tag{2}$$

where $S(t)$ is the probability of surviving through t units of time and r is the mortality rate, with units time^{-1} (Hosmer & Lemeshow, 1999). The parameter r is interpreted as the instantaneous probability that an individual will die in the next time increment given that the individual has survived to the current time (Ross, 1993). Thus, as r increases, survival across a time period decreases (Fig. 4).

However, a strict exposure time model is not consistent with the PIT-tag survival data (Smith et al., 2002). Both observations (Muir et al., 2001) and theory (Anderson et al., 2005) indicate that survival is also related to distance travelled. As the exposure, in this case, is to distance traveled, we modified the exposure model accordingly:

$$S(d) = \exp(-r \cdot d) \tag{3}$$

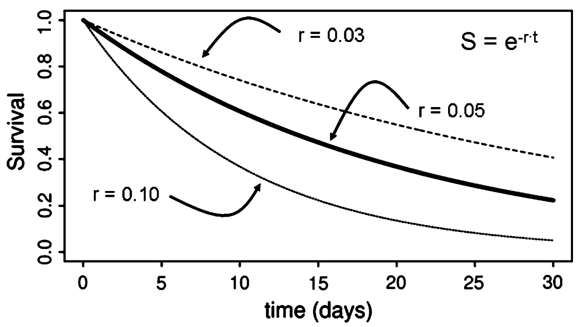

Fig. 4 Exponential survival relationships as a function of exposure time for various values of the parameter *r* (instantaneous mortality). As *r* increases, survival decreases at a greater rate

To accommodate both survival processes, we implemented a hybrid model where survival is a function of travel time and distance traveled:

$$S(t,d) = \exp(-(r_t \cdot t + r_d \cdot d)) \quad (4)$$

In order to relate reservoir survival to river conditions we modeled the instantaneous mortality rates, r_t and r_d, as a function of predictor variables and assumed that predation is the primary cause of mortality in the reservoir. Since predator activity has a nonlinear response to temperature (e.g., Vigg & Burley, 1991), we expressed the predation rates as quadratic functions of temperature. Evidence exists to support the hypothesis that predation rate is negatively related to river flow, perhaps through turbidity, which could decrease the predators–prey encounter rate (Gregory & Levings, 1998, Anderson et al., 2005). Finally, we included proportion of fish passing a spillway as a potential variable, based on the assumption that increased spill leads to increased reservoir survival due to a quicker and safer dam passage. Including these covariates in both the distance and time mortality rates and taking the log transform of Eq. 4 yields a simple linear model (Hosmer & Lemeshow 1999):

$$\begin{aligned} -\log(S_{g,s}) = {} & (\alpha_0 + \alpha_1 \cdot \text{Flow} + \alpha_2 \cdot \text{Temp} \\ & + \alpha_3 \cdot \text{Temp}^2 + \alpha_4 \cdot \text{Spill}) \cdot d \\ & + (\beta_0 + \beta_1 \cdot \text{Flow} + \beta_2 \cdot \text{Temp} \\ & + \beta_3 \cdot \text{Temp}^2 + \beta_4 \cdot \text{Spill}) \cdot t + \varepsilon_{g,s} \end{aligned} \quad (5)$$

where survival and the error term are referenced to a particular release group (g) and river segment (s), *Spill* is the proportion of fish passing the spillway at the upstream dam, *Flow* and Temperature (*Temp*) are the mean across the time the fish were in the reservoir, t is the average reservoir travel time of the release group, d is the reservoir length, and ε is a normally distributed error term with zero mean. Note that this is just one possible form of the survival relationship. COMPASS accommodates alternative hypotheses of reservoir survival.

Equation (5) parameters were estimated by fitting the COMPASS model to the 1995–2005 PIT-tag survival data using a maximum likelihood optimization routine that drew on the historical hydrosystem and river conditions for each year. We removed insignificant parameters based on their Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). Since the Snake and Columbia rivers are physically different, we developed separate reservoir survival relationships for each river. Further, because the survival estimates varied considerably in precision, we weighted the estimates by their inverse "relative" variance (coefficient-of-variation squared) because the variance of log(S) is equal to relative variance (Burnham et al., 1987).

We imposed the following constraints on model selection: (1) a quadratic term must include its corresponding linear term; (2) a time intercept (β_0) must be included with time-exposure variables; (3) a distance intercept (α_0) must be included with distance-exposure variables. Also, to protect against overfitting, we rejected models with coefficients whose signs were inconsistent with the mechanisms outlined above. For example, we rejected models with negative flow coefficients, based on the hypothesis that survival is positively related to flow. We calculated a weighted R^2 for each model fit.

Although no consensus exists on how to calculate R^2 in cases of no intercept, we applied the following calculation:

$$R^2 = \frac{\sum_{i=1}^{N} w_i \cdot d_i^2}{\sum_{i=1}^{N} w_i \cdot (S_i - \bar{S})^2} \quad (6)$$

where i indexes each group/river segment survival, N is total number of group/river segment combinations, w is the weight (inverse relative variance), d is the deviance between observed and predicted survival, S is the observed survival, and $\bar{S}$ is the mean of the observed survivals.

Travel time

Fish reservoir travel time is based on a model developed by Zabel & Anderson (1997) and is governed by two parameters: fish velocity, v, and population spread rate, σ. The predicted travel time distribution is right-skewed, which is consistent with the data (Fig. 5).

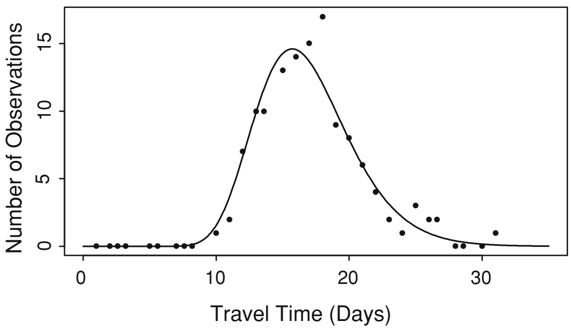

Fig. 5 Examples of the fish travel time model fit to PIT-tag data for Snake River spring/summer Chinook salmon migrating from Lower Granite Dam to McNary Dam, 225 km downstream. Points represent data; solid line is model fit

Zabel et al. (1998) determined that fish velocity is related to river velocity and date in the season. In the current version of the model, fish velocity is also related to percentage of fish passing through the spillway. This accounts for the fact that spilled fish pass over dams more quickly than nonspilled fish (or, spilled fish experience less delay than nonspilled fish). For COMPASS we modified the Zabel et al. model to include spill effects. The resulting fish velocity (km day^{-1}) is:

$$v_i = \beta_0 + \beta_1 \cdot \text{velocity}_i + \beta_2 \cdot \text{date}_i + \beta_3 \cdot \text{velocity}_i \cdot \text{date}_i + \beta_4 \cdot \text{spill}_i + \beta_5 + \varepsilon_i \quad (7)$$

where v_i is the fish velocity of the ith cohort, $velocity_i$ is mean water velocity over the migration period, spill is the percentage of fish passing the spillway and is measured on the day the fish pass the upstream dam, $date_i$ is the date the cohort enters a reservoir, and ε_i, is a normally distributed error term. As with the reservoir survival modeling, we began with the "full" model above and selected the best fit model based on AIC. We compared model-predicted fish

Table 1 Regression results for −log (survival) versus environmental covariates, distance and travel time

Coefficient	Variables	Value	s.e.	t-value	P-value
Chinook Salmon/Upper River		*N = 236 AIC = −326.52 R^2 = 0.882*			
α_0	Distance	0.0167	0.00166	10.02	<0.00001
α_1	Distance · flow	−0.0000117	0.0000026	−4.45	0.00001
α_2	Distance · temp	−0.00284	0.000289	−9.84	<0.00001
α_3	Distance · temp^2	0.000140	0.0000128	10.90	<0.00001
α_4	Distance · spill	−0.00195	0.000574	−3.39	0.00082
Chinook Salmon/Lower River		*N = 126 AIC = 61.06 R^2 = 0.627*			
α_0	Distance	0.0105	0.00414	2.53	0.01271
α_2	Distance · temp	−0.00184	0.000650	−2.83	0.0055
α_3	Distance · temp^2	0.0000812	0.0000257	3.17	0.00196
β_0	Time	0.0118	0.00363	3.26	0.00145
Steelhead/Upper River		*N = 225 AIC = −53.83 R^2 = 0.756*			
α_0	Distance	−0.00317	0.00108	−2.95	0.00354
α_2	Distance · temp	0.000956	0.0000865	11.05	<0.00001
β_0	Time	0.0476	0.00397	11.98	<0.00001
β_1	Time · flow	−0.00105	0.0000811	−12.94	<0.00001
Steelhead/Lower River		*N = 104 AIC = 145.30 R^2 = 0.749*			
β_0	Time	0.0179	0.0352	0.51	0.61218
β_1	Time · flow	−0.000358	0.0000586	−6.10	<0.00001
β_2	Time · temp	0.00793	0.00206	3.86	0.00021

See text (Eq. 5) for definitions of coefficients. Abbreviations: temp = temperature; s.e. = standard error; N = sample size (number of cohorts) velocities to PIT-tag data. As with the reservoir survival modeling, we developed separate relationships for the Snake and Columbia rivers. Also, model fits were weighted by the inverse variance of the fish velocity and, the spread parameter, σ, was set to its (analytical) maximum likelihood values (see Zabel & Anderson, 1997).

Hydrological processes

Daily river flow, water velocity, and water temperature are represented through a detailed hydrological submodel, which we briefly describe. Flow and temperature, specified at system headwaters, are propagated downstream according to water velocity, which is determined by river flow and reservoir geometry. Flow and temperature are adjusted at downstream sites to be consistent with monitoring sites, which reflect evaporative loss, irrigation withdrawals, tributary flows, and heating and cooling.

Implementing the model

We used parameters from the best fit survival and travel time models (presented in *Results*) to run COMPASS in a prospective, predictive mode. In this mode, we used the current dam passage parameters to predict hydropower system survival under current conditions. In order to characterize model sensitivity we varied river flow, water temperature, and spill proportion and modeled expected survival and travel time through the entire hydrosystem, and survival through the dams (removing reservoir survival). We only used combinations of river conditions that were observed during 1995–2005; the period over which the model was fit.

Results

The model-predicted survival relationships for Chinook salmon and steelhead from Lower Granite Dam to McNary Dam and from McNary Dam to

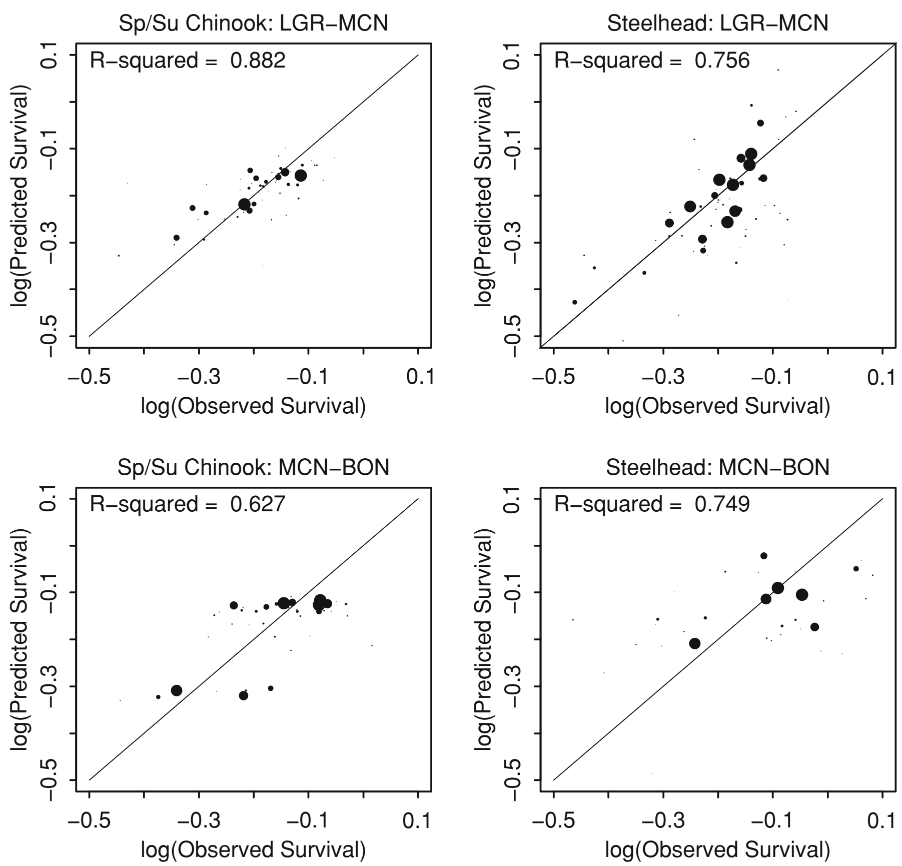

Fig. 6 Predicted log (survival) versus observed log (survival) for cohorts of Chinook and Steelhead migrating through the upper (Lower Granite (LGR) Dam to McNary (MCN) Dam) and lower (McNary Dam to Bonneville (BON) Dam) river reaches. The size of the point represents its weight, with maximum size set equal to 2/3 of the greatest weight

Table 2 Regression results for fish velocity versus environmental covariates and date in the season

Coefficient	Factors	Value	s.e.	*t*-value	*P*-value
Chinook Salmon/Upper River		*N = 383 AIC = 948.80 R^2 = 0.704*			
β_0	Intercept	−3.545	0.0601	−59.00	<0.00001
β_1	Velocity	0.403	0.0219	18.43	<0.00001
β_2	Date	0.0309	0.00014	226.41	<0.00001
β_3	Date · velocity	−0.00043	0.00018	−2.32	0.02082
Chinook Salmon/Lower River		*N = 148 AIC = 639.02 R^2 = 0.869*			
β_0	Intercept	14.171	0.813	17.43	<0.00001
β_1	Velocity	−2.287	0.0690	−33.14	<0.00001
β_2	Date	−0.117	0.00491	−23.82	<0.00001
β_3	Date · velocity	0.0222	0.00061	36.15	<0.00001
β_4	Spill	7.593	0.759	10.01	<0.00001
Steelhead/Upper River		*N 371 AIC = 992.12 R^2 = 0.739*			
β_0	Intercept	−2.797	0.0249	−112.41	<0.00001
β_1	Velocity	0.403	0.0331	12.19	<0.00001
β_2	Date	0.0197	0.00131	15.03	<0.00001
β_3	Date · velocity	0.000577	0.00024	2.41	0.01667
Steelhead/Lower River		*N = 147 AIC = 643.36 R^2 = 0.742*			
β_0	Intercept	−2.850	0.159	−17.91	<0.00001
β_1	Velocity	0.756	0.0365	20.73	<0.00001
β_4	Spill	4.919	1.0315	4.77	<0.00001

See text (Eq. 7) for definitions of coefficients. Abbreviations: s.e. = standard error; *N* = sample size (number of cohorts). "Velocity" refers to river velocity

Bonneville Dam conformed well with the PIT-tag survival data (weighted R^2 ranged from 0.627 to 0.882, Table 1, Fig. 6). In all cases, the "best fit" model was reduced (at most five parameters) from the full ten parameter model. The upper river models included more parameters, probably because of larger sample sizes and greater precision of survival estimates. Both distance traveled and travel time were important factors, which justifies including both in the model. Temperature appeared in all four models, and flow appeared in three out of four; flow was not significant for survival of Chinook through the lower river. Spill was important for Chinook (upper river) but not for steelhead.

In all cases, model-predicted fish velocity was significantly influenced by water velocity (Table 2), with significant water velocity/date interactions in three out of four cases. The proportion of fish passing through spillways was important in the lower river but not in the upper river. Date was important in three of the models, and combined with the water velocity interaction, fish velocity generally increased through the season. Overall, model fits were strong with weighted R^2 ranging from 0.704 to 0.869 (Table 2, Fig. 7).

Chinook salmon hydropower system survival was much more sensitive to water temperature than river flow (Fig. 8). The survival and temperature relationship was notably nonlinear, with the highest survival occurring at approximately 11°C. Chinook salmon hydropower system survival was also sensitive to percentage of river passing spillways, particularly when spill increased from 0 to 25% of the river flow. Survival through the dams was also sensitive to spill proportion; increasing approximately 10% when spill increased from 0 to 50%. Chinook salmon hydropower system travel time had a strong inverse relation to river flow, decreasing by over 30 d in high flow compared to low flow conditions. Increased spill also decreased travel time by 5–10 d at lower flows.

Steelhead hydropower system survival was much more sensitive to river flow than was that for Chinook salmon (Fig. 9). Survival decreased consistently with

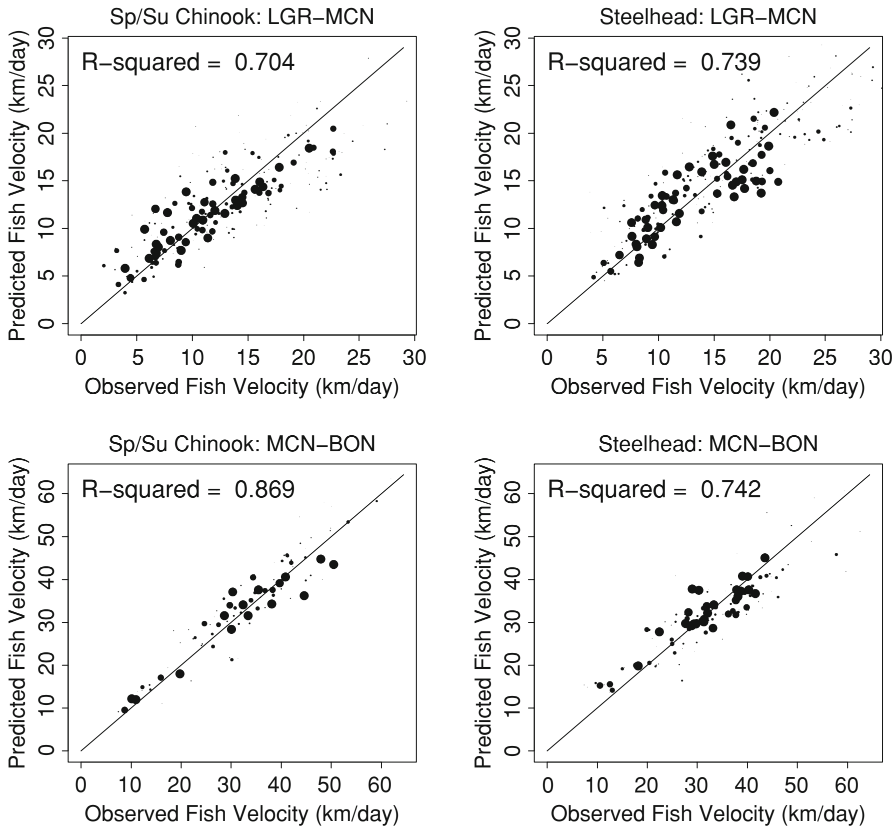

Fig. 7 Predicted migration rate versus observed migration rate for cohorts of Chinook and Steelhead migrating through the upper (Lower Granite (LGR) Dam to McNary (MCN) Dam) and lower (McNary Dam to Bonneville (BON) Dam) river reaches. The size of the point represents its weight, with maximum size set equal to 1/3 of the greatest weight

increasing water temperature, in contrast to the pattern observed with Chinook salmon. The sensitivity of steelhead survival through the dams to spill proportion was similar to that of Chinook salmon, but steelhead survival through dams was approximately 2–3% greater. Finally, the sensitivity of steelhead travel time through the hydropower system to river flow and spill was similar to that of Chinook salmon.

Discussion

Since management actions on regulated rivers are often large-scale, constricted by operating restrictions, and expensive, it is difficult to determine the benefits of various actions through manipulative experiments. Thus, models based on a sufficient understanding of the mechanisms and comprehensive data can be valuable tools for assessing the impacts of river conditions on fish populations. Recent developments in fish tagging technology (e.g., PIT tags and acoustic tags) and a strong commitment to conduct multiyear studies has provided the data on which to develop such a model. The COMPASS model described here appears to realistically portray the available data, primarily PIT-tag data, and thus can potentially serve as important tool in the management of the Columbia River hydropower system. Model results suggest that salmonid populations are responsive to river conditions and thus will respond to river manipulations. However, the results also suggest that different species will respond differentially, and thus multi-species approaches are desirable.

In any ecological modeling exercise, a tradeoff exists between increasing model complexity, with its added realism, and model simplicity, which guards against over parameterization (Johnson & Omland, 2004). We strove for a level of complexity in COMPASS appropriate to the available data. Due to the large PIT-tag data set, we were able to develop travel time and survival algorithms using standard model selection criteria. However, we do not have sufficient data to fully characterize the temporal component of dam passage, which is complex (e.g.,

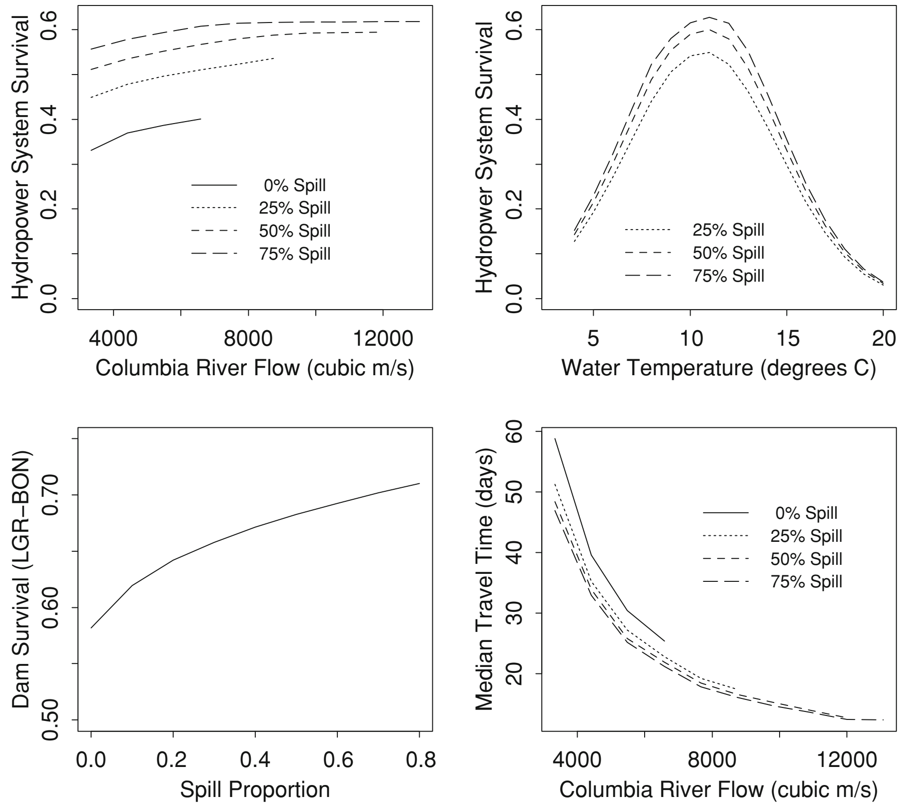

Fig. 8 Sensitivity analysis for spring/summer Chinook salmon. See text for details

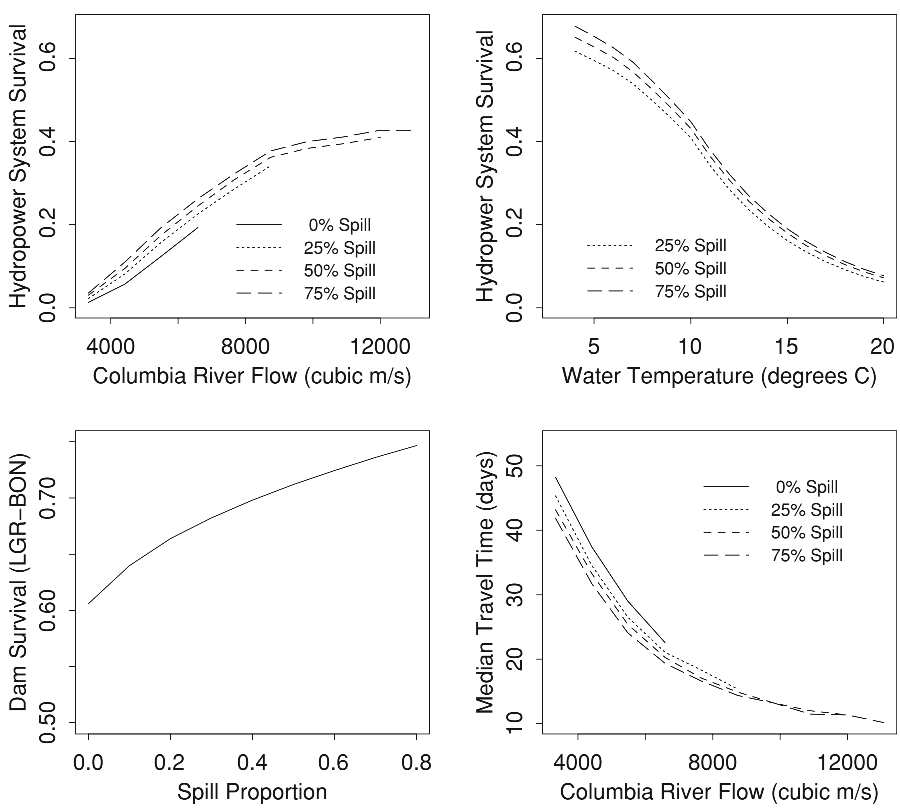

Fig. 9 Sensitivity analysis for steelhead. See text for details

Beeman & Maule, 2001, Castros-Santos and Haro, 2003). However, by relating migration rate to percentage of fish passing through the spillway, we captured an important feature: fish spillway passage is faster than powerhouse passage. We encourage more detailed studies so that we can explore the significance of dam passage behavior on fish survival. Indeed, reducing dam passage time may be a cost-effective way to improve total hydropower system survival.

We are expanding the model in several areas. First, some effects of fish passage through a hydrosystem are potentially expressed outside the hydrosystem as latent mortality due to stress, injury, and disrupted migration timing. Accordingly, to further characterize the impacts of a hydrosystem on migratory fish, we are developing algorithms that represent alternative latent mortality hypotheses. On a related note, because the most important measures of mitigation actions are population viability measures, such as population abundance or probability of quasi-extinction, the COMPASS model will be linked with a population viability model (Zabel et al., 2006) to assess the impacts of hydropower system improvements on population viability. Further, to effectively use model predictions, managers require, not only direct survival estimates, but also uncertainty about the estimates. Consequently, we are developing methods to characterize prediction uncertainty, primarily due to fitting the model to data. Finally, because one goal of our model development is to produce a management tool that is transparent and easy to use by a broad range of users, we are developing a graphical user interface that allows users to simulate management actions and predict the response of migrating fish populations.

Although COMPASS has been formulated for the Columbia and Snake rivers, it is based on a flexible geographic mapping algorithm that can be configured to any river system. Further, our general approach of developing simulation models to explore alternative management scenarios is applicable to a wide-range of river systems.

Acknowledgments Scientists throughout the northwestern United States have contributed to the COMPASS model: Ron Boyce, Dave Clugston, Brad Eppard, Kim Fodrea, Steve Grabowski, Steve Haeseker, Fred Higginbotham, Dave Hurson, Rick Kruger, Mike Langeslay, Tom Lorz, Jerry McCann, Paul Ocker, Charlie Paulsen, Charlie Petrosky, Kris Ryding, Mark Scheuerell, Ann Setter, Marvin Shutters, Earl Weber, Tim Wik, John Williams, and Paul Wilson. Valuable reviews by the Independent Scientific Advisory Board (ISAB) and two anonymous reviewers greatly improved the model and this article.

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