

**A multiple reach model describing the migratory behavior of
Snake River yearling chinook salmon (*Oncorhynchus tshawytscha*)**

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Abstract

A multiple reach model was developed to describe the downstream migration of juvenile salmonids in the Columbia River system. Migration rate for cohorts of fish was allowed to vary by reach and time step. A nested sequence of linear and nonlinear models related the variation in migration rates to river flow, date in season, and experience in the river. By comparing predicted to observed travel times at multiple observation sites along the migration route, the relative performance of the migration rate models was assessed. The analysis was applied to cohorts of yearling chinook captured at the Snake River Trap near Lewiston, Idaho and fitted with passive integrated transponder (PIT) tags over the eight year period 1989-1996. The fish were observed at Lower Granite and Little Goose Dams on the Snake River and McNary Dam on the Columbia River covering a migration distance of 277 km. The data supported a model containing two behavioral components: a flow term related to season – fish spend more time in regions of higher river velocity later in the season; and a flow-independent experience effect where the fish migrate faster the longer they have been in the river.

Introduction

The behavior of juvenile salmon during their migration from tributary streams to the ocean is highly variable (Groot and Margolis 1991) and depends on a variety of factors. These factors may be inherent to the fish's condition such as size (Washington 1982) and level of smoltification (Hoar 1976; Folmar and Dickhoff 1981), and they may be external factors such as river flow (Berggren and Filardo 1993) and river temperature (Brett et al. 1958). The knowledge of migration behavior and the ability to predict migration speed has practical value in rivers with hydroelectric systems. Such information can be used to partially mitigate the impacts of hydroelectric dams on the fish and thus improve migration survival.

For some stocks of juvenile salmon, travel times through the Snake and Columbia Rivers have doubled since the development of dams (Raymond 1979), and thus mitigation efforts have focused on improving fish migration speed under the assumption that faster migration results in higher survival. One strategy to improve migration speed is to increase water velocity by either: (1) increasing flow from the storage reservoirs in the upper Columbia and Snake Rivers, or (2) lowering the reservoir levels (drawdown) behind the dams on the mainstem Columbia and Snake Rivers (NMFS 1995). The first approach increases water velocity by increasing river flow while maintaining reservoir volumes. The second approach increases velocity by decreasing the cross-sectional area of the river. Both actions have ecological and economic consequences. Draining the up-river storage reservoirs for the spring migration adversely affects resident fish in the storage reservoirs and uses water that could otherwise be used for power generation, irrigation, or augmenting flow for summer migrants. Drawdown has a number of unknown ecological impacts on the riverine habitat and complicates the dam passage of both juvenile and adult salmon. Thus, which ever method is used to improve fish migration rate it is essential that the action be used in the most effective manner possible.

The focus of this paper is to present a mathematical model for fish migration behavior that captures many of the basic factors controlling juvenile salmonid migration rate. The paper builds

on earlier work (Zabel and Anderson 1996) that details an equation to determine the distribution of travel times for a cohort of fish migrating through a single river reach. In this earlier paper the downstream movement of a group of fish is characterized in terms of two parameters: an average migration rate and a rate of population spreading. In this paper we extend the model to multiple reaches and identify environment and fish specific factors that determine the migration rate for juvenile spring chinook. In addition, we develop statistical methods to extract parameters from data on the arrival times of cohort of fish through a series of dams.

Factors affecting migration timing of juvenile salmon have been the focus of several studies. In particular, flow has been demonstrated to be an important factor in determining travel times of yearling and subyearling chinook and steelhead through the Columbia and Snake Rivers (Berggren and Filardo 1993; Smith et al. 1993). From a mechanistic standpoint, the magnitude of the flow effect is determined by the fish's position in the river and the proportion of the day spent migrating. In the Hanford reach of the mid-Columbia, Dauble et al. (1989) found that subyearling chinook preferred shallow near-shore locations in slower river velocities, and yearling chinook smolts preferred deeper mid-channel locations where river velocities are greater. Bax (1982) determined that juvenile salmonids in the Hood Canal in Washington migrate close to the shore early in the season and further offshore later in the season. Mains and Smith (1964) demonstrated that the majority of subyearling chinook migration occurs at night in the Columbia and Snake Rivers. Yearling chinook have less of a tendency for strictly nocturnal migration (Bell 1958; Healy 1991). It is also clear that migration behavior varies during the season. Several researchers have demonstrated the importance of photoperiod (Hoar 1976; Giorgi et al. 1990; Muir et al. 1994) to migration rate and timing; accelerated photoperiod resulted in faster migration rates. Also, Johnson and Groot (1963) determined that migrating sockeye increased migration speed later in the season. They attributed this to an increased "migration drive."

This paper formulates migration models based on these studies and others in an effort to relate juvenile salmon travel times to measurable factors. We apply the models to a multi-reach system

in which fish are observed at several points along the migration route. This allows determination of the change in migration rate as the fish migrate down the river. Model predicted travel times are compared to observed travel times at several points along the river. Using a nested sequence of nonlinear models, we relate migration rate to river flow, date in the season, and length of time in the river and determine the importance of these factors as formulated in the models.

The simplest model has a constant migration rate throughout the season. In most cases this is too simplistic, but the model serves as a comparison to other models. The second model assumes migration rate is linearly related to river velocity. The third model introduces a season/flow interaction that assumes the effect of river velocity increases as the season progresses. The fourth model adds a non-flow related experience effect. As the fish spend more time in the river, they migrate faster.

The migration model is applied to yearling chinook (*Oncorhynchus tshawytscha*) originating in the Snake River and its tributaries. The fish were captured at the Lewiston trap on the Snake River, fitted with PIT (passive integrated transponder) tags (Prentice et al. 1990), and released daily during the seven year period 1989-1996. PIT tags are small electronic tags that allow for individual fish to be identified as they pass each detection site. The fish were observed at Lower Granite and Little Goose Dams on the Snake River and McNary Dam on the Columbia River.

To demonstrate the utility of the model as a predictive tool, we compare our predictions of 1996 arrival distributions to the observations. The predictions are based on release distributions at Snake Trap, flow information, and model parameters obtained from the 1989-1995 data.

Methods

single reach model

The single reach model determines the travel time distribution for a group of fish migrating through a single reach and is described elsewhere (Zabel and Anderson 1996; Zabel 1994). This model starts with a point release of fish at time = t_0 . The travel time distribution is based on the

length of the reach (L) and two parameters: r , which determines the downstream migration rate, and σ^2 , which determines the rate of population spreading.

For this application, the discrete time version of the model is used. The travel time distribution is described in terms of

$$p_t = \text{Prob}(\text{arriving during } t\text{-th time period, given values } r, \sigma^2, \text{ and } L), \quad (1)$$

with $t = (1, 2, 3, \dots)$. If there are N recaptured individuals in the cohort, then

$$\hat{n}_t = N \cdot p_t = \text{expected number of individuals arriving during } t\text{-th time period.} \quad (2)$$

The travel time distribution has a long right tail (Figure 1) and fits well to observed travel time distributions (Zabel and Anderson 1996).

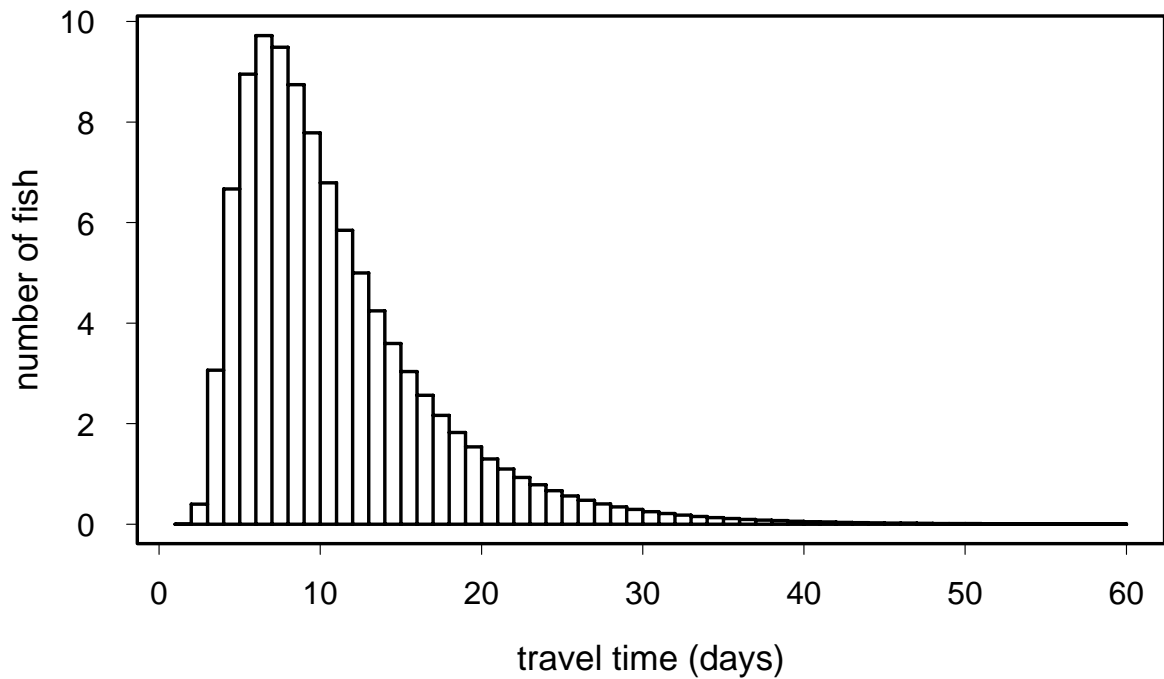


Figure 1. Travel time distribution from the single reach model. For this plot, $r = 5$ $\text{km}\cdot\text{day}^{-1}$, $\sigma^2 = 100$ $\text{km}^2\cdot\text{day}^{-1}$, reach length = 50 km, and population size = 100 fish.

multiple reach model

The multiple reach model moves a cohort of fish through a series of reaches. The model begins with a point release at t_0 . Based on the reach model, the arrival time distribution is determined at the next downstream site. This arrival distribution is then used as a departure distribution for the next reach. The model iterates through each departure time and distributes these fish at the next downstream site according to the reach travel time model. All fish that arrive at a site in the same time interval but departed during different time intervals from the upstream site are combined together in the arrival time distribution. The new arrival time distribution is then used as a departure distribution for the next reach. This cohort of fish is moved from reach to reach in this manner until the end of the river is reached.

This algorithm can be described in terms of $P_{i,t}$, which is the probability of arriving at the i -th site during t -th time period. This is calculated as

$$P_{i,t} = \sum_{j=1}^{t-1} P_{i-1,j} \cdot P_{t-j}. \quad (3)$$

The terms inside of the summation multiply the probability of a fish departing from the upstream site during the j -th time period by the probability of the fish taking exactly $t-j$ time periods to travel through the reach. The summation is over all the possible combinations of departure times and travel times that result in fish arriving at the i -th site during the t -th time period.

The expected number of individuals observed at the i -th site during the t -th time step is computed as

$$\hat{n}_{i,t} = N_i \cdot P_{i,t}, \quad (4)$$

where N_i is the total number of fish observed at the i -th site. The average travel time to the i -th site is computed as

$$\hat{T}_i = \sum_{t=1}^S t \cdot P_{i,t}, \quad (5)$$

where S is the length of the migratory season. These expected average travel times are compared to the observed ones in the statistical analysis.

Migration rate model

To implement the multiple reach model, migration rates (r_t) must be provided on a per reach and per time step basis. The general model assumes fish velocity depends on a flow related and a flow independent term. Both terms are time dependent, reflecting the change in fish behavior through time. The general form of the full model is

$$r_t = r_{\text{flow-ind}}(t, T_{RLS}) + r_{\text{flow}}(t, T_{SEASN}, \bar{V}_t). \quad (6)$$

The first term characterizes the flow independent component of migration which is related to the fish maturity relative to release time, T_{RLS} . The second terms characterizes the flow dependent component of migration as expressed by the average water velocity (\bar{V}_t) and a seasonal factor T_{SEASN} that characterizes how the fish's behavior relative to water velocity changes over time.

Any number of mathematical equations can be used to express how the two migration components evolve over time. We formulated the sequence of models below to reflect the mechanisms that determine variability in migration rate.

model 1) The null model assumes that r is constant over time with an average value β_0 :

$$r_t = \beta_0 + \varepsilon_t. \quad (7)$$

Variation about the average rate is expressed by ε_t .

model 2) This model assumes a linear relationship between migration rate and river velocity:

$$r_t = \beta_0 + \beta_1 \bar{V}_t + \varepsilon_t. \quad (8)$$

\bar{V}_t is the average velocity during the average migration period for each of the reaches. River velocity is assumed to be proportional to river flow through a dimensional argument:

$$V_t = \frac{F_t}{X}, \quad (9)$$

where X is the cross sectional area of the reservoir.

The intercept (β_0) is a combination of directed movement independent of flow and a potential non-zero intercept from the river velocity/river flow relationship.

model 3) This model assumes that fish migrate more actively later in the season by migrating in the higher flow regions of the river and/or by spending a greater proportion of the day in the river flow versus holding up along the shore. The equation is formulated as

$$r_t = \beta_0 + \beta_{FLOW} \bar{V}_t \left[\frac{1}{1 + \exp(-\alpha(t - T_{SEASN}))} \right] + \varepsilon_t, \quad (10)$$

where t is the Julian date in the season. Equation (10) is based on the following four parameters:

β_0 – determines the flow independent migration (km/day);

β_{FLOW} – determines the proportion of the river velocity used for downstream migration when the fish are full smolted (non-dimensional);

α – slope parameter that determines how quickly the flow effects shift from early season to late season behavior (1/days);

T_{SEASN} – inflection point of the flow dependent term that has the effect of shifting the flow effect through the season (Julian date)

model 4) The model has the same terms as model 3 but also includes a flow independent experience factor – as fish spend more time in the river, migration speed is increased. Migration rate for the i th release group is modeled as

$$r_t = \beta_0 + \beta_1 \left[\frac{1}{1 + \exp(-\alpha_1(t - T_{RLS}))} \right] + \beta_{FLOW} \bar{V}_t \left[\frac{1}{1 + \exp(-\alpha_2(t - T_{SEASN}))} \right]. \quad (11)$$

Equation (11) introduces the following terms:

T_{RLS} – the release date (Julian date) for the cohort;

α_j – slope parameter that determines rate of change of the experience effect (1/days);

β_0 and β_1 – determine the magnitude of the flow independent migration rate (km/day).

β_0 and β_1 are combined in the following way to determine the flow-independent contribution to migration rate:

$\beta_{MIN} = \beta_0 + \beta_1/2$ (minimum flow independent migration rate);

$\beta_{MAX} = \beta_0 + \beta_1$ (maximum flow independent migration rate).

When fitting model 4, we set $\alpha_j = 0.15$, which guarantees that 95 percent of the difference between β_{MAX} and β_{MIN} is attained within 25 days. This choice was based on the data analyzed in this application and ensured that unrealistically high migration rates would not be obtained when applying the model to lower reaches.

Both models 3 and 4 use the nonlinear logistic equation in which upper and lower bounds can be set, creating a threshold effect. This appears to be consistent with some types of juvenile salmon migratory behavior and eliminates unrealistically high or low migration rates that can occur with linear equations applied outside the range of observations. The flow related term determines the seasonally varying proportion of river velocity used for fish migration; the threshold equation ensures that this proportion is realistic. The flow independent term is based on the fish's contribution to downstream migration, which increases with time spent in the river. Clearly there is an upper bound to this contribution. Also, for suitable parameter values, the logistic equation effectively mimics a linear relationship.

Model implementation

The models were run utilizing the Columbia River Salmon Passage (CRiSP) model, a management tool for evaluating the effect of Columbia River hydrosystem operations on juvenile salmon (Anderson et al. 1996). The CRiSP model imposes mortality due to dam passage and in the reservoirs due to predation and gas bubble disease. The modeled survival was calibrated to survival studies (Iwamoto et al. 1994; Muir et al. 1995; Muir et al. 1996) based on fish of similar origin and migrating through the same reaches as the ones we analyze below. In addition, the model keeps track of the numbers of fish collected at dams and barged through the system for release below the last dam on the river. These factors can cause slight changes in modeled travel times, so they were incorporated into the model predictions.

Statistical methods

The objectives of the statistical analysis were to estimate parameters and standard errors, assess how well the models compare to the data, and determine the appropriate level of complexity for the migration rate models.

estimating parameters

The modeled average travel times are a function of the model chosen and the particular parameter values selected. The migration rate parameters are estimated by a least-squares minimization (with respect to the parameters) of the following equation:

$$SS = \sum_{i=1}^O \sum_{k=1}^C (\hat{T}_{i,k} - \overline{T}_{i,k})^2 \quad (12)$$

where O is the total number of observation sites, C is the total number of cohorts, $\hat{T}_{i,k}$ is the modeled average travel time to the i -th site by the k -th cohort, and $\overline{T}_{i,k}$ is the observed average travel time to the i -th site by the k -th cohort. This equation is fit using a Levenberg-Marquardt routine (Fletcher 1990; Press, et al. 1994), with derivatives calculated numerically using a finite

element method (Gill 1981; Seber and Wild 1989).

standard errors

Approximate standard errors of the parameters were calculated following procedures for nonlinear least squares regression (Bates and Watts 1988). The model function was linearized at the optimal parameter values, and then linear least squares calculations were implemented (Weisberg 1980). Approximate 95 per cent confidence intervals can be constructed by adding and subtracting twice the standard errors from the parameter values. Since these values are approximate, they are not used for inference but characterize the stability of the parameter estimates.

estimating rate of population spreading

While the purpose of this paper is to study the variability in migration rate, in order to implement the reach model, the rate of spreading (σ^2) of the cohorts must also be specified. The units for σ^2 are km^2/day . Although σ^2 is also variable from cohort to cohort (Zabel and Anderson 1996), for this paper we treat it as constant among all cohorts to simplify the analysis. Also, the travel time model predictions are not as sensitive to variability in σ^2 as to variability in migration rate (Zabel 1994).

The estimate of σ is based on the spread of the travel time distribution; this information is lost when computing average travel times. Thus σ^2 is estimated separately after the migration rate parameters are estimated using equation (12). To estimate σ^2 , a finer resolution of the data is used. The unit of comparison between the model and the data is the number of individuals from each cohort observed per time step at each of the observation sites. Since the variance associated with this measure is highly variable, generalized least squares (Draper and Smith 1981; Seber and Wild 1989) is used, with each element of the summation weighted by the variance. The equation to be minimized is

$$SS = \sum_{i=1}^O \sum_{j=1}^C \sum_{t=1}^S \frac{1}{V_{ijt}} (n_{ijt} - \hat{n}_{ijt})^2, \quad (13)$$

where n_{ijt} is the observed number of fish arriving at the i th site from the j -th cohort during the t -th time period and \hat{n}_{ijt} is the expected number. V_{ijt} is the variance (under a multinomial model see (Zabel 1994)) associated with this group and is calculated as

$$V_{ijt} = n_{ij} \cdot \hat{p}_{ijt} \cdot (1 - \hat{p}_{ijt}), \quad (14)$$

where n_{ij} is the number of fish from the j th cohort observed at the i th site. Equation (13) is also fit using a Levenberg-Marquardt routine, and the standard errors are calculated in the same manner as with the migration rate parameters.

model comparisons

To compare the performance of the models, a modified R^2 value is reported as the sum of squares of each model as compared to the sum of squares of the mean model (model 1):

$$R^2 = \frac{SS_1 - SS_A}{SS_1} \quad (15)$$

where SS_1 is the sum of squares for the mean model, and SS_A is the sum of squares for the more complex (alternative) model. The R^2 values gives the percent reduction in the sum of squares for the alternative model as compared to the null model.

Standard statistical analysis of the results is not possible. In most cases, the residuals are not normally distributed, serial trends exist, and average travel times are not independent from site to site within cohorts, making traditional F -tests invalid. However, many conclusions can be drawn about the models' performances based on the R^2 values and the standard errors of the parameter estimates.

Data

Passive integrated transponder (PIT) tags are used to monitor individual fish. The tag, 12 mm long, is inserted in the fish's body cavity and contains a microchip that is programmed with individual fish identification codes (Prentice et al. 1990). The system yields information about passage times of individuals at interrogation sites. The tags do not seem to adversely affect the fish in terms of survival or swimming performance (Prentice et al. 1990).

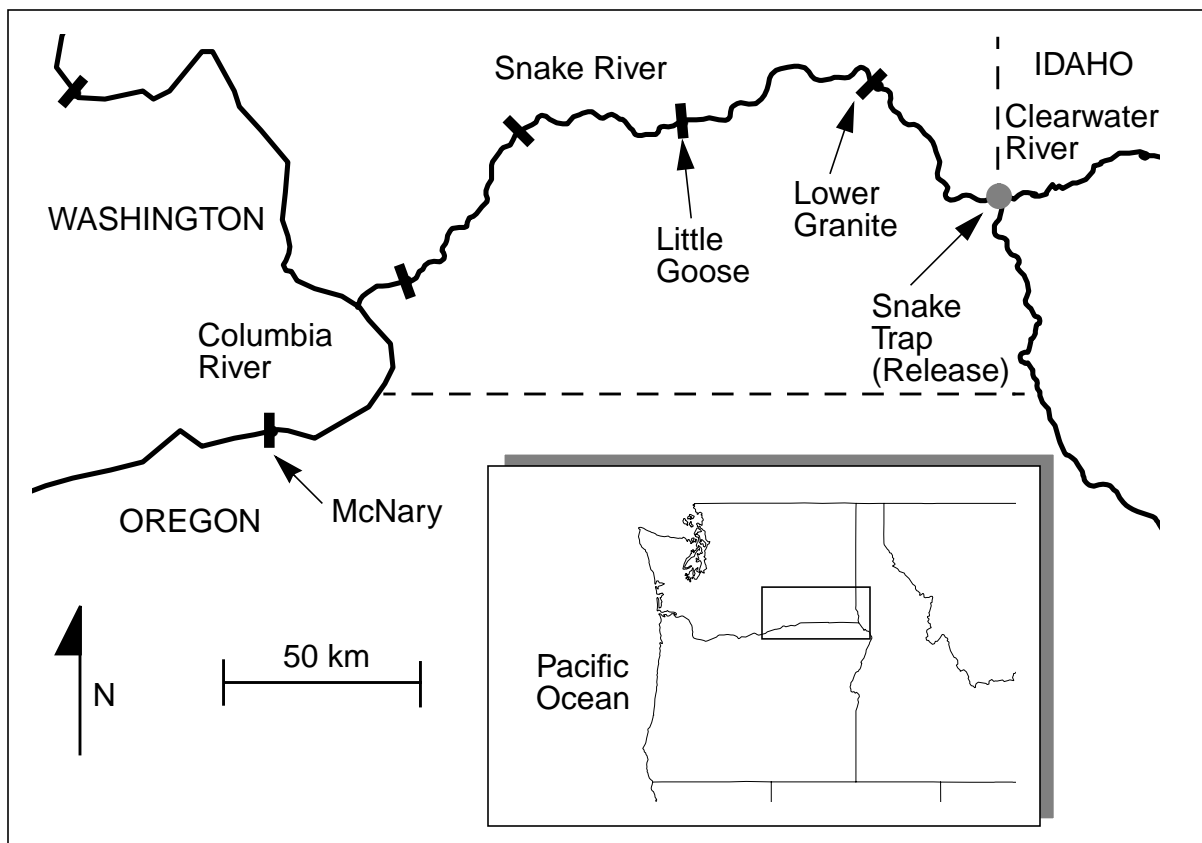


Figure 2. A map of the migratory route along the Snake and Columbia Rivers in Washington, Oregon, and Idaho (state boundaries shown by dashed lines). The bars represent dams. Included are the release point (grey dot) and observation points (labeled dams). The river flow, in general, is from east to west. The area of detail is delineated by the rectangle in the inset map of the northwestern United States.

The model was evaluated with run-of-the-river fish (hatchery and wild stocks) yearling chinook. The fish were captured tagged and released at the Snake River trap and observed at Lower Granite, Little Goose and McNary Dams over a migratory route of 277 km (Figure 2). Separate releases were made daily during the from early April to early May. Although these fish are classified as run-of-the-river fish, it is likely that the vast majority were yearling chinooks based on the distribution of lengths (most fish longer than 110 millimeters) and the timing of migration (early spring). This is consistent with other treatments of these fish (e.g., Fish Passage Center 1991). We did not analyze fish released after May 10 because reduced length distributions after this date indicate a possible presence of subyearling chinook which have different migratory behavior.

Release cohorts were formed by combining releases from up to three consecutive days to achieve sample sizes of at least 80 individuals observed at Lower Granite Dam. 78 cohorts are analyzed representing releases from 1989-1996. Table 1 contains release dates, average travel times to the three observation sites, and sample sizes for all the cohorts. Flow and temperature information was obtained from the Army Corps of Engineers, Portland, Oregon.

Predictions

Predicted cumulative passage distributions were generated at the three downstream observation sites for the 1996 fish. These predictions were derived from parameters estimated from the 1989-1995 data, so the predictions are independent of the 1996 data. The downstream passage distributions for the 1996 cohorts were combined to generate one distribution for all the cohorts at each of the observation sites. The predicted cumulative passage distributions were then compared to the observed cumulative passage distributions.

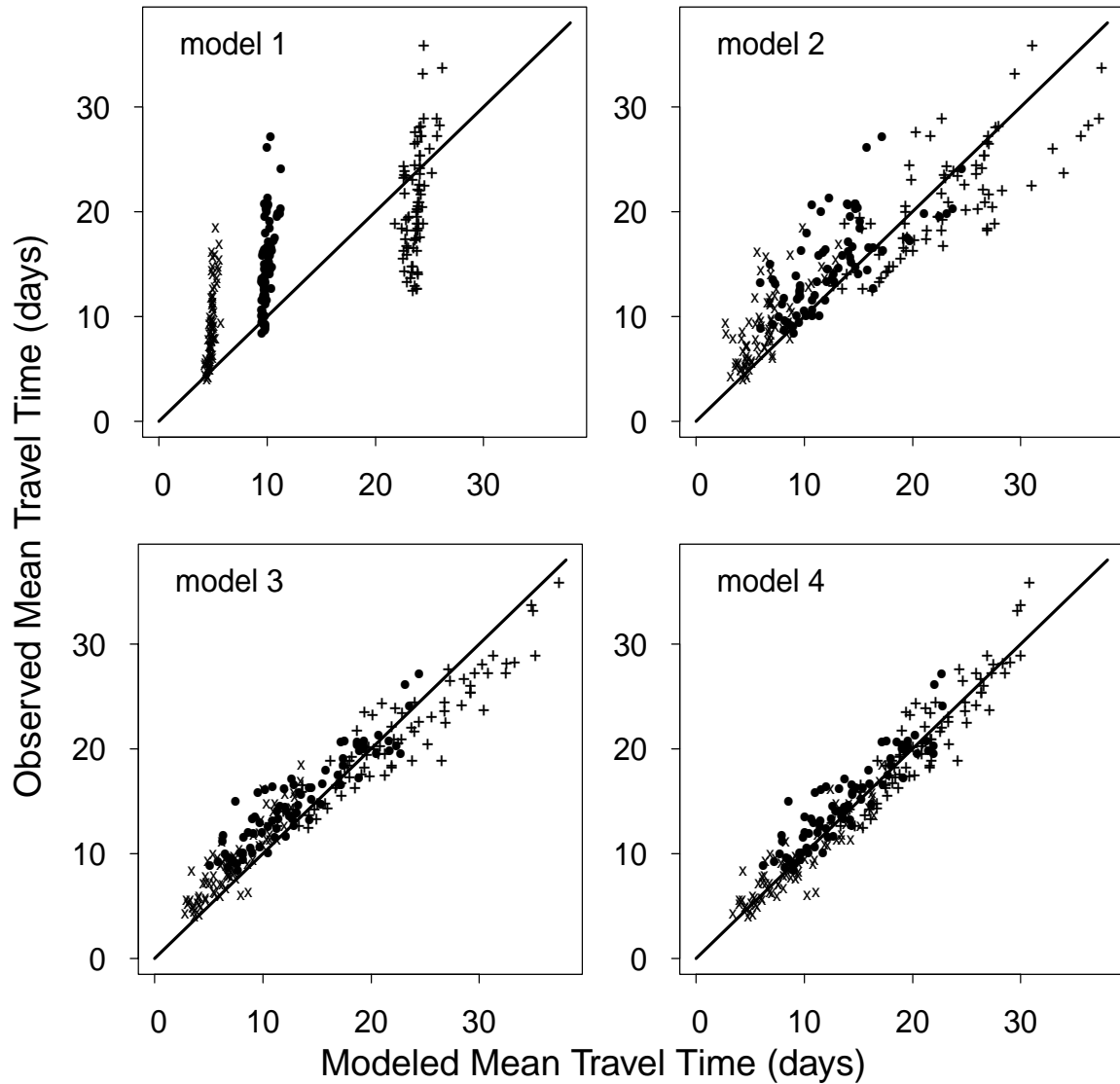


Figure 3. Observed mean travel times versus modeled mean travel time for each of the four migration rate models for 1989-1996. The travel times are from Snake Trap to each of the observation sites – Lower Granite, Little Goose, and McNary Dams. Each point represents a cohort at a single observation site; therefore, each cohort is represented three times in each plot. x = mean travel time to Lower Granite. • = mean travel time to Little Goose. + = mean travel time to McNary.

Results

The results of the data analysis are contained in Table 2 and presented graphically in Figure 3. The results of model 1 give the average migration rate through the entire system (10.52 km per day). It is clear from the plot of observed versus modeled average travel time (Figure 3) that this model is inadequate for describing migration rate. The model predicts roughly the same travel times for all of the cohorts to each of the observation sites.

The linear flow component (model 2) explains 52.2 percent of the variability in the first model. This model yields a flow-independent migration rate of 0.686 km per day, and the fish utilize 89.3 percent of the river velocity. The plot in Figure 3 shows that although this model offers an improvement over the first, quite a bit of spread and bias is evident.

Introducing a flow/season interaction (model 3) substantially improves model performance; The R^2 increases to 0.782. With this model, the fish use less river flow before the seasonal inflection point (day 116 or April 26 in non-leap years) and substantially more later in the season. It is clear from Figure 3 that this model underestimates shorter travel times and overestimates longer travel times.

The experience factor added to the non-flow term (model 4) corrects the bias of model 3, with the R^2 increasing to 0.872. The flow-independent maximum migration rate (β_{MAX}) is over 11 km per day faster than the minimum rate (β_{MIN}). Model 4 yields essentially unbiased predictions over the entire range of observed travel times, and the standard errors are relatively small compared to the parameter values indicating that this model is stable.

Another interesting feature is that as model performance improves, the estimated value for σ^2 decreases. Recall that σ^2 describes the rate of spreading of the cohort as it moves downstream. Some of the variability ascribed to population spreading in the less complex models is really due to lack of fit of the migration rate model. As the ability to predict migration rate improves, so does the precision of predicting the individual cohort's behavior.

The results of the 1996 passage predictions are contained in Figure 4. Model 4 successfully predicts the arrival distributions at the first two sites, Lower Granite and Little Goose. At McNary Dam, the early fish migrate faster than expected, but after 80 per cent passage, the model is very consistent with the data.

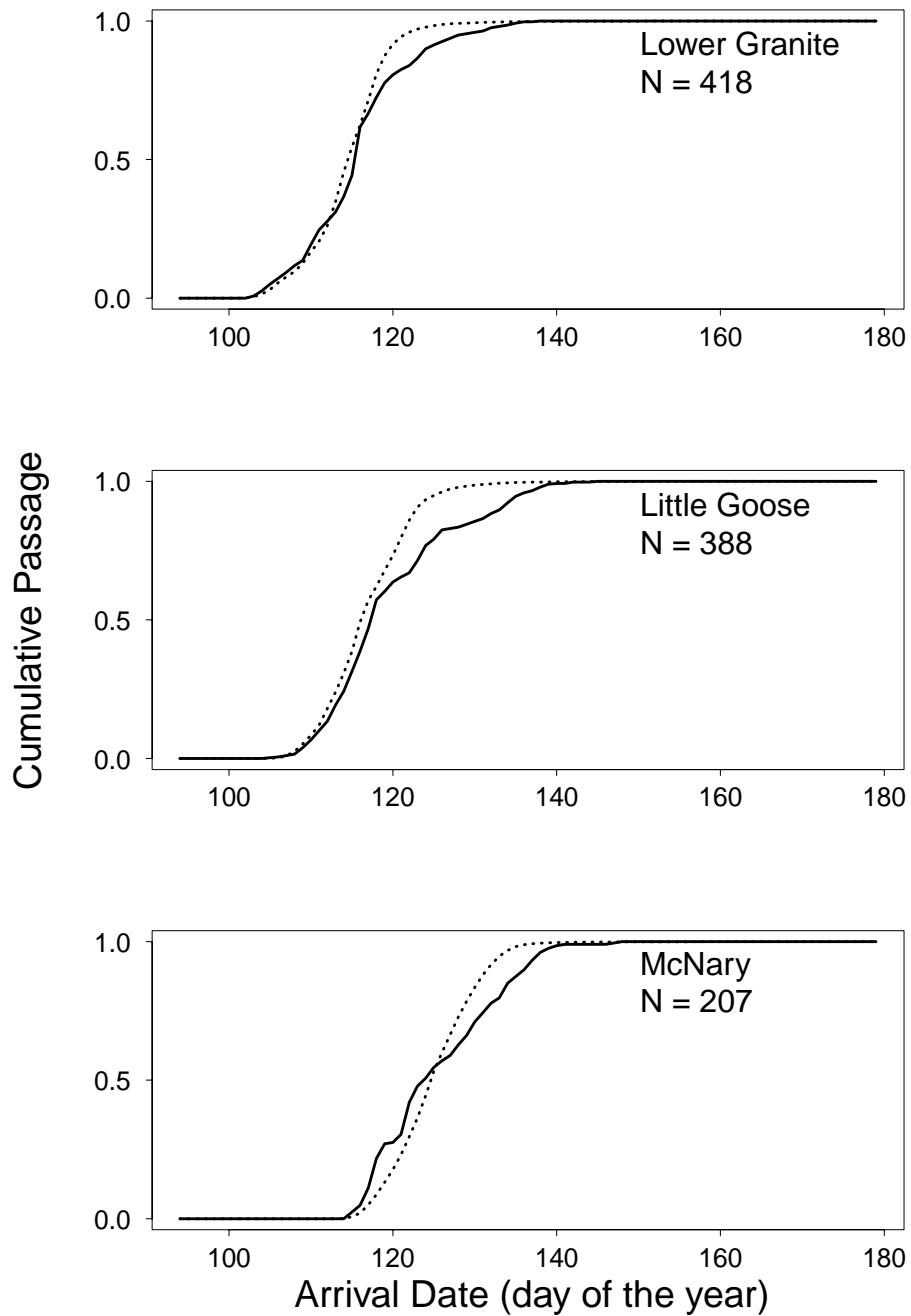


Figure 4. Comparisons of predicted and observed cumulative passage versus date at the three observation sites for the 1996 migration year. The solid line represents the data, and the dotted line represents the model prediction. The prediction was based on parameters derived from 1989-1995 data. One set of parameters was used to generate predictions to all three sites. Day 100 is April 10 in non-leap years.

Discussion

Comparing travel time data to a sequence of nested models is a powerful way to determine the appropriate level of model complexity. For the fish analyzed here, the more complex models are supported by the data. The model with the seasonal flow term (model 3) confers a considerable improvement in model fit over the model with the simpler linear flow term (model 2), indicating the effect of flow on the Snake River yearling chinook has a seasonal component. Model 4 offers improvement in model performance over model 3 by correcting the bias present in the simpler model. This is achieved by speeding up the fish as they move downstream – a difference in migration rate of more than 11 km per day in the non-flow related terms (β_{MIN} and β_{MAX}).

While the most complex model can describe a wide variety of behaviors and predict average travel times to three observation points, it is still relatively simple in terms of number of parameters – six migration rate parameters and one spread parameter. It is impressive that this model explains over 87 percent of the variability present in the constant migration rate model, especially considering the wide range of observed average travel times (observed average travel times for Snake Trap to Lower Granite ranged from 4.0 days to 18.2 days; from Snake Trap to Little Goose ranged from 8.1 to 26.9 days; from Snake Trap to McNary ranged from 12.5 to 35.8 days (Table 1)). In addition the relatively small values for the standard errors indicate that this model is stable.

It should be noted that we based our selection of the hierarchical models on our beliefs on mechanisms affecting smolt migration. Choosing models a priori to the statistical analysis is, in our opinion, more valid than multiple regressions that looks at all possible factors and potentially suffer from unplanned tests (Sokal and Rohlf 1981). The procedure of examining data at several observation sites simultaneously and using many release groups per year allows for the detection of complex migratory behavior that is not detectable with standard regression analyses that reduce data by combining reaches and using protracted releases that mask seasonal and experience effects (e.g. Berggren and Filardo 1993).

Since our method involves estimating the spread of cohorts as they move downstream, we are

able to predict entire arrival distributions at downstream sites based on departure timing at an upstream site. This predictive ability is demonstrated in Figure 4 for 1996 fish. This type of information is potentially useful for inseason management decisions such as flow augmentation and spill scheduling. The migration model can also predict the effectiveness of enhanced flows for increasing migration rates on a seasonal basis.

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Table 1. Mean release date, mean and standard deviation of travel times (days), and number of fish observed from Snake Trap to each observation site for each cohort. Minimum, maximum and mean values are given at the bottom of the table. Day 100 is April 10 in non-leap years.

Mean release date (Julian date)	mean travel time (tt), standard deviation (sd), and (number fish observed (n) from Snake Trap to:								
	Lower Granite			Little Goose			McNary		
	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
1989									
94.9	15.7	6.9	97	21.0	5.9	77	28.8	6.2	46
97.4	14.4	6.8	110	19.7	5.7	128	27.2	7.0	71
99.8	16.1	9.0	97	20.4	7.7	78	27.6	7.3	46
101.9	11.8	5.6	103	17.7	7.0	85	23.0	8.9	37
104.0	9.5	4.5	119	16.0	6.3	68	24.4	6.8	44
105.9	8.5	5.1	119	13.6	6.4	73	20.5	8.3	40
108.0	6.7	5.0	130	11.4	4.7	75	17.4	4.7	36
109.9	5.9	3.8	122	12.1	4.8	78	19.9	7.5	33
111.9	6.2	3.5	122	12.4	4.2	53	17.5	5.4	35
113.9	7.1	4.6	130	12.7	4.3	67	18.9	5.6	39
115.9	7.3	3.2	136	11.7	4.5	52	17.4	4.7	32
117.8	7.1	3.9	103	11.8	4.1	38	16.2	3.2	19

Table 1. *Continued.*

1990	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
107.3	6.3	3.0	80	16.4	8.7	39	18.8	4.2	12
109.0	6.1	2.8	93	14.9	6.4	41	20.4	6.2	32
110.9	8.2	6.5	118	15.4	6.5	44	21.6	6.9	38
112.9	8.9	5.5	128	16.9	8.3	46	20.8	5.2	30
114.7	11.2	7.5	106	15.9	5.8	32	22.1	4.6	22
1991	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
98.9	16.9	6.5	97	23.8	5.3	51	33.7	7.1	20
100.6	15.4	5.8	89	20.0	3.5	33	28.2	6.3	15
102.5	14.4	5.4	94	19.6	5.2	34	27.2	4.2	14
106.4	14.8	6.8	143	19.6	6.3	60	26.0	5.6	30
108.9	13.2	5.3	102	17.3	5.1	52	22.4	4.1	16
112.9	10.4	5.4	127	16.1	7.7	55	22.0	5.6	19
116.4	7.8	4.9	90	12.4	4.8	33	18.2	3.5	27
115.9	9.0	4.5	84	16.3	4.9	31	18.4	2.8	15
117.6	9.5	4.2	101	14.1	4.1	34	20.2	6.8	10
119.9	8.9	3.9	99	13.8	4.5	30	20.1	3.4	15
1992	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
99.2	13.6	6.7	107	19.3	6.7	53	28.8	5.7	33
105.3	12.8	6.4	115	16.9	4.7	49	23.6	6.4	25
1993	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
100.0	14.0	5.1	118	20.4	3.7	90	27.9	2.9	45
101.8	14.8	5.1	119	20.4	4.1	95	26.6	3.3	48
110.7	9.7	3.5	92	13.3	3.1	59	19.5	3.4	21
112.9	8.0	3.1	82	13.0	3.8	40	17.3	3.3	23

Table 1. *Continued.*

114.9	7.0	2.3	94	9.8	2.0	62	16.2	2.5	40
117.0	6.3	2.3	115	10.3	2.9	58	15.5	2.9	28
119.0	5.7	2.6	101	10.3	3.0	43	14.3	2.5	30
121.0	4.9	1.9	113	9.1	2.3	60	13.2	1.9	25
122.9	4.2	1.5	113	8.1	2.0	65	12.5	2.9	29
124.6	4.0	2.1	98	9.2	3.0	27	12.5	2.3	8
125.9	4.8	2.1	141	9.3	2.8	51	14.1	3.7	30
127.6	5.6	2.6	107	9.7	3.4	27	13.9	4.7	21
130.0	5.4	2.0	96	9.0	2.7	39	12.6	2.4	29
132.0	4.3	2.3	84	8.6	6.4	30	12.9	7.1	32
1994	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
104.2	10.8	4.3	80	16.3	5.3	67	26.4	5.7	70
109.9	7.6	4.1	92	14.3	6.6	28	23.3	5.7	47
111.0	7.7	4.3	149	13.0	5.4	68	23.8	5.9	106
112.9	9.1	4.7	147	14.2	4.2	54	24.3	6.1	89
115.0	9.6	3.9	120	16.1	3.8	34	23.1	3.5	80
116.9	9.9	3.2	111	15.9	3.9	39	23.5	7.9	76
118.9	9.3	2.8	106	15.5	4.1	33	21.7	5.0	79
121.3	7.8	2.2	101	13.1	3.5	47	19.2	3.9	83
124.5	5.9	2.0	80	11.3	3.0	36	18.2	5.0	65
127.8	4.4	1.7	80	9.8	2.8	42	16.7	5.8	82
1995	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
91.1	18.2	7.8	104	26.9	8.9	71	35.8	5.9	50
93.6	15.8	8.1	88	25.8	7.1	50	33.1	4.8	44
97.0	12.5	6.0	126	20.3	7.0	61	28.0	4.8	54
99.1	11.2	5.7	156	19.2	6.1	80	27.1	5.3	75

Table 1. *Continued.*

100.5	11.7	5.5	103	20.0	5.8	51	25.3	4.8	44
101.4	11.3	5.9	98	20.4	4.9	33	25.3	5.0	38
102.5	11.3	5.2	91	20.1	4.2	33	24.1	4.8	32
103.5	10.7	4.8	90	18.8	5.2	38	24.4	4.7	34
104.4	12.0	4.4	82	18.2	3.4	41	23.6	3.8	36
107.5	9.0	3.2	81	14.4	2.8	50	22.5	6.2	34
109.6	9.5	3.6	99	15.5	6.1	49	20.8	4.4	45
112.0	8.5	3.4	108	13.7	5.0	65	19.4	4.8	53
114.1	7.0	3.3	99	11.2	3.0	63	18.2	4.0	51
116.0	7.0	3.8	129	11.7	4.4	90	17.2	4.1	64
118.1	5.5	3.3	128	9.7	4.3	104	16.4	4.6	66
120.0	5.0	2.8	126	9.6	4.0	112	14.7	3.0	71
122.0	5.3	2.6	80	8.4	2.8	61	14.3	3.5	44
123.0	5.2	1.7	114	8.9	2.8	99	14.1	2.5	75
125.0	4.8	2.6	151	8.4	3.1	122	13.6	2.9	100
129.1	5.2	3.2	123	10.9	4.5	89	16.4	6.3	54
131.0	5.5	3.2	117	11.5	4.5	108	15.8	4.5	42
1996	(tt)	(sd)	(n)	(tt)	(sd)	(n)	(tt)	(sd)	(n)
101.1	9.3	5.9	98	13.0	4.4	131	18.8	3.9	66
107.5	7.9	4.9	102	12.9	5.6	96	19.3	5.2	39
109.9	7.8	3.8	128	13.2	6.4	93	18.3	6.3	61
114.9	8.3	5.5	90	14.7	6.7	68	18.8	5.9	41
mean	9.1			14.7			20.8		
minimum	4.0			8.1			12.5		
maximum	18.2			26.9			35.8		

Table 2. Parameter estimates, standard errors, sum of squares, and R^2 for the four migration rate models for all cohorts in the years 1989 - 1996. The model 4 parameter estimates for the cohorts with the 1996 data omitted are also provided. The units for β_{MIN} and β_{MAX} are $\text{km}\cdot\text{day}^{-1}$. β_{FLOW} , α_1 , and α_2 are non-dimensional. T_{SEASN} has units of Julian date, and σ^2 has units $\text{km}^2\cdot\text{day}^{-1}$. For models 1-3, β_{MIN} in this table corresponds to β_0 .

model	parameter estimates (standard error)							resid.	R^2
	β_{MIN}	β_{MAX}	α_1	β_{FLOW}	α_2	T_{SEASN}	σ^2	ss	
1	11.08 (0.38)						314.80 (9.41)	8876.96	
2	-2.86 (0.53)			1.424 (0.069)			203.16 (5.45)	4278.24	0.518
3	2.77 (0.33)			0.635 (0.046)	0.177 (0.031)	110.82 (1.22)	136.45 (3.18)	1949.91	0.780
4	0.19 (0.02)	16.78 (5.06)	0.132 (0.066)	0.452 (0.023)	0.149 (0.016)	105.92 (0.86)	160.39 (3.36)	890.24	0.900
4 ¹	0.21 (0.18)	16.78 (6.27)	0.120 (0.069)	0.468 (0.006)	0.164 (0.015)	105.93 (0.72)	152.94 (3.27)	769.44	

1. 1996 omitted