

Effects of Water Temperature and Flow on Adult Salmon Migration Swim Speed and Delay

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Abstract.—The effects of temperature and flow on the migration of adult Chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* through the Columbia River hydrosystem were determined with a novel technique that fits a broken linear model of swim speed versus temperature and flow by partitioning data into speed ranks. Using the migration times of passive integrated transponder (PIT)-tagged adult Chinook salmon upstream between Bonneville and Lower Granite dams (462 km) over the years 1998–2002, we found that a maximum swim speed of about 1 body length/s occurred at 16.3°C. Speed was less above and below this optimum temperature. For PIT-tagged steelhead, migration speed uniformly decreased with increasing temperature, suggesting that the fish migrated at temperatures above the optimum. Migration delay was also a unimodal function of temperature, the minimum delay occurring around 16–17°C. The broken linear model was compared with seven alternative models of unimodal and monotonic speed versus temperature and flow. The unimodal models fit the data better than the monotonic models (when ranked by the Akaike information criterion), and the broken linear model fit the data best. Flow was insignificant in all of the monotonic models and only marginally significant in the unimodal models. The findings of this study have significance in evaluating the effects of hydrosystem operations and climate change on salmon and steelhead fitness.

Because salmon *Oncorhynchus* spp. cease feeding during their upstream migration, the speed and efficiency of the migration can significantly affect their energy reserves and consequently their spawning fitness (Brett 1995). Flow and temperature, thought to be significant determinants of migration speed and delays at dams, further complicate upstream migration and could increase energetic cost and stress. The Columbia–Snake River system is of particular interest since the listing of 12 stocks of salmon and steelhead *O. mykiss* as threatened or endangered under the Endangered Species Act (Good et al. 2005). This system also presents a unique opportunity to explore the effects of river flow and temperature on fish migration because thousands of adults that were tagged with passive integrated transponder (PIT) tags as juveniles are detected as they pass dams on their journey to spawning grounds in the Snake River basin. Thus, a better understanding of how temperature and flow affect the upstream migration is of value to resource managers charged with minimizing hydro-system impacts on migrating salmon and steelhead.

An equation for the effect of temperature on fish swimming speed was first proposed by Ware (1978) and parameterized by Stewart et al. (1983) and Stewart and Iberra (1991), who assumed that the optimal swim

speed, V_s , of various salmonid species is an exponential function of temperature, that is,

$$V_s = 9.7W^{0.13} \cdot e^{0.0405\theta}, \quad (1)$$

where θ is temperature (capped at 25°C) and W is the fish mass in grams. Stewart et al. (1983) presented the exponential equation as an approximation of swim speed data of juvenile coho salmon *O. kisutch* published by Griffiths and Alderdice (1972). The data exhibited a unimodal pattern in which the highest speed occurred below the maximum temperature tested. The exponential equation generally fits the speed–temperature relationship up to the maximum speed, but above that the equation deviates from the data because the equation then increases monotonically. Nevertheless, the exponential equation has become a standard way to characterize adult salmon swim speed (Beauchamp et al. 1989; Hanson et al. 1997; Hinch and Rand 1998; Rand and Hinch 1998; Hinch and Rand 2000; Standen et al. 2002; Standen et al. 2004). It is noteworthy that other studies also found unimodal swim speed–temperature patterns. For juvenile sockeye salmon *O. nerka*, the critical swim speed (the speed at which a fish fatigued in a swim chamber) reached a maximum at about 15°C (Brett 1964; Brett and Glass 1973). For juvenile coho salmon, the “optimal swimming speed” (the speed that minimizes the oxygen consumption per unit distance traveled) occurred at nearly 20°C (Griffiths and Alderdice 1972). For juvenile brown trout *Salmo trutta*, Ojanguren and Brana (2000) found that “endurance time” (the time to

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Received October 13, 2004; accepted October 5, 2005.
Published online December 14, 2005

fatigue of fish swimming at 36.6 cm/s) was a quadratic function of temperature, with a maximum at 16°C. While different measures of swimming performance as a function of temperature cannot be compared directly, they are probably related through mechanisms that limit oxygen metabolism. Taken together, the studies indicate that the exponential model (or any monotonic model) is inadequate to characterize swim speed across the full range of temperatures fish experience.

Although, in principle, river flow must also affect swim speed, the findings are mixed. Trepanier et al. (1996) reviewed 18 studies of the effects of river flow and temperature on salmonid upstream migration. Five of the studies were based on telemetry data but reached mixed conclusions on the effects of flow on migration timing and rate. Quinn et al. (1997) found that the upstream migration rate of sockeye salmon in the Columbia River increased with increasing temperature and decreasing flow. However, the study used seasonally averaged temperatures and flows, which were inversely correlated, making it impossible to separate their effects. A weak and variable relationship between migration rate and river velocity is not unexpected because anadromous fish are efficient at exploiting locally slow or reverse currents during migration (Hinch and Rand 2000; Standen et al. 2004). Using this logic, we expect that the current speed that fish encounter may be significantly less than the average current speed; however, the average flow may be a useful, if not the only widely available proxy for the current speeds encountered by fish during upstream migration. Using "stereovideography" and bankside observations to estimate swimming speeds from tail beat frequency, Hinch and Rand (2000) determined that the optimal swim speed of sockeye salmon increased by 0.75 times the current speed encountered.

In the Columbia–Snake River system, as in other impounded rivers, upstream migration may be significantly delayed by in-river structures. Using telemetry, Bjornn et al. (2000) found that the migration time of Chinook salmon *O. tshawytscha* from Bonneville Dam to upriver dams was strongly correlated to the time it took to pass the dams. Evidence that the time required for fish to pass an in-river structure depends on temperature is mixed. Keefer et al. (2003) found that dam passage times for Chinook salmon and steelhead decreased with increased temperature at John Day and the Dalles dams in the Columbia River, but Peery et al. (2003) and Keefer et al. (2004) found that dam passage times were not significantly related to temperature. Quinn et al. (1997) found evidence that temperatures above 21°C blocked sockeye salmon at Columbia River dams and tributary entrances. Jensen et al. (1989) found that below 8°C, Atlantic salmon *Salmo salar*

were unable to pass waterfalls on the Vefsna River in Norway. Salmon ascending a fish ladder or a high-velocity region of a structure may use anaerobic burst swimming and thus accumulate an oxygen debt. While anaerobic swim performance is not temperature dependent, the time to repay the debt is (e.g., Beamish 1978; Kieffer 2000), and so temperature could indirectly affect the delay in passing structures.

Overall, the studies suggest that migration rate depends on swim speed and delays from various causes. While swim speed is demonstrably related to temperature, delay is not. Thus, it is reasonable to assume that the fish with the highest migration rates experience the least delay and exhibit the strongest relationships with temperature and river flow. From these assumptions, we develop a new analysis method based on swim speed-ranked data partitioning to estimate the effect of temperature on migration swim speed, ground speed, and delay. The analysis uses data on adult salmon and steelhead migration between Bonneville Dam on the Columbia River and Lower Granite Dam on the Snake River, a 462-km route passing seven dams (Figure 1).

Methods

To characterize the factors determining migration speed, sequential subgroups of fish passing Bonneville Dam are first partitioned into four rank quartiles according to their migration speeds between Bonneville and Lower Granite dams. Second, each quartile is combined across the migration season to produce yearly patterns of migration speed for the quartiles. Third, the relationship of migration speed to temperature and flow in each quartile is determined by regression. Fourth, the coefficients of the migration speed and delay equations are expressed as linear functions of quartile rank. Last, the coefficients of the swim speed model are defined as the coefficients of the zero rank, which represents fish migration without delay.

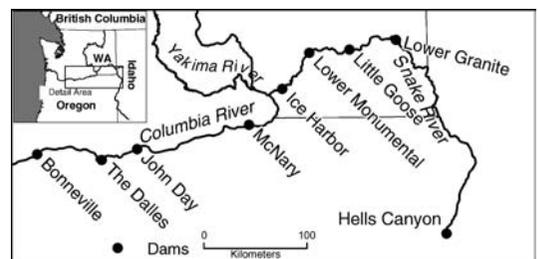


FIGURE 1.—Map showing the Columbia and Snake rivers and the locations of dams on the migration route from Bonneville Dam to Lower Granite Dam.

Model.—Because swim speed increases with temperature up to some optimum, $\check{\theta}$, and then decreases at higher temperatures, we express swim speed as a broken linear function of temperature (θ), that is,

$$V_S = \begin{cases} \alpha_0 + \alpha_1\theta & \text{if } \theta \leq \check{\theta} \\ \alpha_0 + \alpha_1\check{\theta} + \alpha_2(\theta - \check{\theta}) & \text{if } \theta > \check{\theta}. \end{cases} \quad (2)$$

To include the effect of flow, we apply the Hinch and Rand (2000) finding that sockeye salmon swim speed increased by κV_C in low-to-moderate flows, where V_C is the encountered current speed and κ is the ratio of swim speed increase to current speed increase (0.75 for sockeye salmon). Since fish may use eddies and low-flow regions when moving against a current, we cannot specify the actual current speed encountered. Therefore, we assume that the current speed encountered is linearly related to river flow F by the equation $V_C = \alpha_3 \cdot F$, where α_3 is a model coefficient dependent on river geometry and fish behavior. Swim speed, as a function of flow and temperature, becomes

$$V_S = \kappa\alpha_3 F + \begin{cases} \alpha_0 + \alpha_1\theta & \text{if } \theta \leq \check{\theta} \\ \alpha_0 + \alpha_1\check{\theta} + \alpha_2(\theta - \check{\theta}) & \text{if } \theta > \check{\theta}. \end{cases} \quad (3)$$

The upstream ground (V_U) speed is the difference between the swim speed and the encountered current speed, so

$$V_U = V_S - V_C = V_S - \alpha_3 F. \quad (4)$$

The total migration time (T_M) is

$$T_M = T_U + T_D, \quad (5)$$

where T_U is the active upstream migration time and T_D is total delay time associated with dam passage, excursions into tributaries, downstream movement, or simply stopping during the migration. Noting that the observed migration rate over distance L (V_M) is given by $V_M = L/T_M$ and that the ground speed V_U is given by $V_U = L/T_U$, then the migration rate and upstream ground speed are related as follows:

$$V_M = V_U \left(1 - \frac{T_D}{T_M} \right). \quad (6)$$

In this expression the migration rate, as a function of temperature and flow, is

$$V_M = \begin{cases} \beta_0 + \beta_1\theta + \beta_3 F & \text{if } \theta \leq \check{\theta} \\ \beta_0 + \beta_1\check{\theta} + \beta_2(\theta - \check{\theta}) + \beta_3 F & \text{if } \theta > \check{\theta}. \end{cases} \quad (7)$$

where the migration rate coefficients of equation (7) and swim speed coefficients of equation (3) are related by $\beta_j = \alpha_j(1 - T_D/T_M)$ for $j=0, 1$, and 2 , and $\beta_3 = (\kappa - 1)\alpha_3(1 - T_D/T_M)$. Equation (7) characterizes the effects of temperature and flow on both swim speed and delay time.

Alternative migration rate models.—Because equa-

tion (7) has not been applied to swim speed-temperature data previously, we compare its fit with that of the following alternative migration rate models: linear flow model:

$$V_M = c_0 + c_f F; \quad (8)$$

linear flow temperature model:

$$V_M = c_0 + c_1\theta + c_f F; \quad (9)$$

exponential model (equation 1 without the weight component):

$$V_M = c_0 e^{c_1\theta} + c_f F; \quad (10)$$

quadratic model:

$$V_M = c_0 + c_1\theta + c_2\theta^2 + c_f F; \quad (11)$$

difference of sigmoids model (after Thornton and Lessem 1978):

$$V_M = \frac{c_0}{\left\{ 1 + \exp[-c_1(\theta - \hat{\theta})] \right\} \left\{ 1 + \exp[c_1(\theta - \hat{\theta})] \right\}} + c_f F; \quad (12)$$

broken linear-quadratic model (with continuous derivative at the break point):

$$V_M = \begin{cases} c_0 + c_1\theta + c_f F & \text{if } \theta \leq \check{\theta} \\ c_0 + c_1\check{\theta} + c_2(\theta - \check{\theta})^2 + c_f F & \text{if } \theta > \check{\theta}; \end{cases} \quad (13)$$

and the Logan temperature curve (Logan et al. 1976):

$$V_M = c_0 \left\{ \exp(c_1\theta) - \exp[c_1\hat{\theta} - (\hat{\theta} - \theta)/c_2] \right\} + c_f F. \quad (14)$$

Estimating model coefficients.—To estimate the coefficients β_j and α_j as well as the delay T_D , we partition the fish into speed-rank quartiles and applied equation (7) to each partition. That is, we define groups according to the sequential arrival of fish at the initial detection point and partition each group into four rank quartiles according to migration speed to the upstream detection point. This resulted in each group's generally corresponding with the number of fish arriving on a given day. Combining each quartile across all groups, we obtain four series representing fish according to their relative migration rates. Bjornm et al. (2000) showed that migration times were strongly correlated to delay times at dams, so we assume that the fastest fish experienced the shortest delays.

The following derivation is specific to equation (7), but a similar approach could be taken for the alternative models. Denoting the speed rank quartiles from fastest ($i = 1$) to slowest ($i = 4$), equation (7) becomes

$$V_M^i = \begin{cases} \beta_0^i + \beta_1^i\theta + \beta_3^i F & \text{if } \theta \leq \check{\theta}^i \\ \beta_0^i + \beta_1^i\check{\theta}^i + \beta_2^i(\theta - \check{\theta}^i) + \beta_3^i F & \text{if } \theta > \check{\theta}^i, \end{cases} \quad (15)$$

where the coefficients $\beta_0^i, \beta_1^i, \beta_2^i, \beta_3^i$, and θ^i are specific to quartile i .

To characterize speed variations with rank, the rank-specific coefficients β_j^i were regressed against the midpoint of each rank quartile Q^i (0.125, 0.375, 0.625, and 0.875) and replaced by the regressions

$$\beta_j^i = a_j + b_j Q \quad (16)$$

for $j = 0, 1, 2$, and 3 . Assuming that the fish in all quartiles have the same optimal swimming temperature, θ^i , we can use the mean $\theta^* = 1/4 \sum \theta^i$ to characterize the optimum swimming temperature. Combining the results of the regressions from equation (16) with equation (15), migration rate as a continuous function of rank Q , temperature θ , and flow F is

$$V_M(Q) = \begin{cases} (a_0 + b_0 Q) + (a_1 + b_1 Q)\theta \\ \quad + (a_3 + b_3 Q)F & \text{if } \theta \leq \theta^* \\ (a_0 + b_0 Q) + (a_1 + b_1 Q)\theta^* \\ \quad + (a_2 + b_2 Q)(\theta - \theta^*) \\ \quad + (a_3 + b_3 Q)F & \text{if } \theta > \theta^* \end{cases} \quad (17)$$

where Q varies continuously between 0 (maximum speed and no delay) and 1 (minimum speed and maximum delay).

Note that $V_M(Q = 0)$ represents the migration rate without delay or the ground speed V_U , so that

$$V_U = \begin{cases} a_0 + a_1\theta + a_3F & \text{if } \theta \leq \theta^* \\ a_0 + a_1\theta^* + a_2(\theta - \theta^*) + a_3F & \text{if } \theta > \theta^* \end{cases} \quad (18)$$

gives coefficients for equations (3) and (4) with $\alpha_j = a_j$, for $j = 0, 1$, and 2 and $\alpha_3 = a_3/(\kappa - 1)$.

Writing equation (17) for speed-ranked migration time gives

$$T_M(Q) = \begin{cases} L/((a_0 + b_0 Q) + (a_1 + b_1 Q)\theta \\ \quad + (a_3 + b_3 Q)F) & \text{if } \theta \leq \theta^* \\ L/((a_0 + b_0 Q) + (a_1 + b_1 Q)\theta^* \\ \quad + (a_2 + b_2 Q)(\theta - \theta^*) \\ \quad + (a_3 + b_3 Q)F). & \text{if } \theta > \theta^* \end{cases} \quad (19)$$

Note that because $T_M(Q = 0)$ represents the migration time without delay (T_U), the delay time as a function of rank, temperature, and flow is approximated as

$$T_D(Q) = T_M(Q) - T_M(0). \quad (20)$$

The cumulative delay distribution can be illustrated by plotting Q versus T_D for fixed values of θ and F .

Reiterating, we partition the data into quartile ranked subsets and obtain model coefficients from each subset. We then regress the model coefficients against rank to

approximate delay T_D and obtain the equation (7) coefficients.

Data.—Fish migration times from Bonneville Dam to Lower Granite Dam, a distance of $L = 462$ km (see Figure 1), were constructed from 8,489 records of individually tagged adult Chinook salmon and steelhead detected at both Bonneville and Lower Granite dams. As juveniles, the fish were tagged with PIT tags (Prentice et al. 1990) and represent both hatchery and wild rearing types. Table 1 shows the number of spring, summer, and fall Chinook salmon and steelhead detected at both dams in the study period (1998–2002) as well as the range of detection dates at Bonneville Dam and the median and range of migration times to Lower Granite Dam. The data were obtained from the University of Washington's Columbia basin research database, DART (University of Washington 2003), and as a courtesy by the Pacific States Marine Fisheries Commission (PSMFC) Columbia Basin PIT tag Information System (PTAGIS). The adult PIT tag detectors at Bonneville Dam came online in 1998 and were upgraded in subsequent years, accounting for much of the increase in detections in later years. Like telemetry tags, PIT tags provide migration times for individual fish. However, telemetry tags are large (4.3–9 cm long) and are implanted in the fish as adults so that they may affect fish behavior (Bernard et al. 1999), while PIT tags are small (1.2 mm long) and are implanted in the fish as juveniles so that they have no appreciable effect on fish behavior. In addition, radio tags are more invasive (being intragastric with a 43-cm antenna extending out the fish's mouth), whereas PIT tags are subcutaneous. In fact, radio-tagged fish appear to be much more affected than PIT-tagged fish. Median travel times between Bonneville and Lower Granite dams were 0.1–5.2 d longer for radio-tagged Chinook salmon and 1.9–8.7 d longer for radio-tagged steelhead (Table 1).

Temperature and flow data were obtained from the DART (University of Washington 2003) database. The few missing flow and temperature records were replaced by interpolation from data for surrounding dates. Figure 2 shows temperatures and flows for Bonneville Dam during the spring, summer, and fall Chinook salmon migrations.

Analysis.—In the absence of the water temperatures and current speeds that fish actually encountered, we derived temperature and flow indices by exploring the relationship between daily average temperature and flow profiles at Bonneville and Lower Granite dams. We also performed regressions of the index flows on temperature to study the relationship between those variables.

In the absence of migration delay data, we could not

TABLE 1.—Number of PIT-tagged adult Chinook salmon and steelhead detected at both Bonneville and Lower Granite dams, Bonneville Dam detection dates and median date of detection, and migration time range and median (d). Median travel times (d) and number of radio tag detections are given where available for comparison (Keefer et al. 2004).

Run	Year	Number	PIT tags				Radio tags	
			Arrival		Travel time		Number	Median travel time
			Range	Median	Range	Median		
Spring Chinook salmon	1998	13	Apr 25–May 30	Apr 30	11.5–36.9	18.2	173	21.8
	1999	20	Apr 15–May 29	May 13	15.0–43.3	21.3		
	2000	193	Apr 5–May 31	Apr 28	8.9–75.0	15.1	144	17.7
	2001	1,222	Mar 31–May 31	Apr 26	7.6–58.3	14.0	271	14.1
	2002	1,478	Mar 5–May 31	May 5	8.5–59.1	14.7		
Summer Chinook salmon	1998	14	Jun 3–July 16	Jun 30	9.6–25.8	13.3	35	16.8
	1999	18	Jun 2–July 29	Jun 30	9.9–22.1	15.6		
	2000	45	Jun 1–July 14	Jun 16	7.7–20.1	10.0	23	14.8
	2001	467	Jun 1–Aug 1	Jun 19	7.0–43.4	11.1	48	12.3
	2002	1,148	Jun 1–Aug 1	Jun 13	7.7–129.6	12.6		
Fall Chinook salmon	1998	38	Sep 3–Oct 3	Sep 22	9.0–32.5	12.2	8	16.5
	1999	16	Aug 25–Oct 2	Sep 13	9.9–29.0	15.3		
	2000	84	Aug 19–Oct 19	Sep 15	9.3–27.1	12.9	17	18.1
	2001	143	Aug 3–Oct 22	Sep 11	9.2–73.7	12.9	24	15.1
	2002	202	Aug 3–Oct 17	Sep 16	8.9–65.6	12.9		
Steelhead	1998	38	July 14–Oct 14	Sep 15	11.3–81.0	31.8		
	1999	15	July 27–Sep 23	Aug 27	13.9–54.4	32.9		
	2000	134	May 29–Oct 23	Aug 19	9.0–106.9	36.0	219	43.7
	2001	1,896	Apr 29–Nov 7	Aug 4	9.9–160.1	47.0	259	48.9
	2002	1,305	Mar 22–Oct 23	Aug 27	10.0–151.6	33.3		

directly determine the coefficients for the ground speed (equation 4). Instead, as described in the section on estimating model coefficients, we first determined coefficients for the speed-ranked migration rate equation (15) and then used equation (16) to estimate the coefficients for the ground speed equation (4).

We partitioned the migration rate data to produce four speed-ranked data sets by grouping sequential arrivals of 12–40 fish (depending on run size) at Bonneville Dam and partitioning each arrival group into four speed ranks. To partition the data without first creating sequential subgroups would obscure correlations. Each year’s data were partitioned separately before being combined for the multiyear analysis.

For each speed rank quartile i ($i = 1, 2, 3,$ and 4), we used a Gauss–Newton nonlinear least-squares regression algorithm to estimate the coefficients β_j^i ($j = 0, 1, 2,$ and 3) in equation (15) as well as the optimum temperature or breakpoint, θ^i . Histograms provided visual confirmation that the residuals were approximately normally distributed. Multiple starting values confirmed a global optimum. We assessed the resulting model fit by a linear regression on each segment of the broken linear model, one regression using only data with $\theta \leq \theta^i$ and a second regression using data with $\theta > \theta^i$. These regressions reproduced the β_j^i coefficients

obtained from the Gauss–Newton algorithm and provided r^2 and P -values.

Results

Water Temperature and Flow Indices

During the Chinook salmon migration, water temperatures at Bonneville Dam correlated closely with those at points upriver (lagged by the number of days it would take the median fish to reach each point). Regression of Bonneville Dam temperatures for April 1–October 31 of 1998–2002 on Lower Granite Dam temperatures 14 d later (the median migration time for Chinook salmon) showed strong correlation ($r^2 = 0.74$, $P < 0.00001$). Further, the slope (0.96) and intercept (1.44) showed a similarity between temperature profiles. Due to these strong correlations, we simply used the water temperature at the Bonneville Dam forebay on the date of detection at Bonneville Dam as the index temperature. We opted not to use temperatures and flows corresponding to the Lower Granite Dam detection dates because this would skew the results by associating a fish that may have experienced lengthy delays at some lower-river dam with a later-season Lower Granite Dam temperature and flow profile.

Flows at Bonneville Dam for April 1–October 31 of 1998–2002 and those 14 d later at Lower Granite Dam

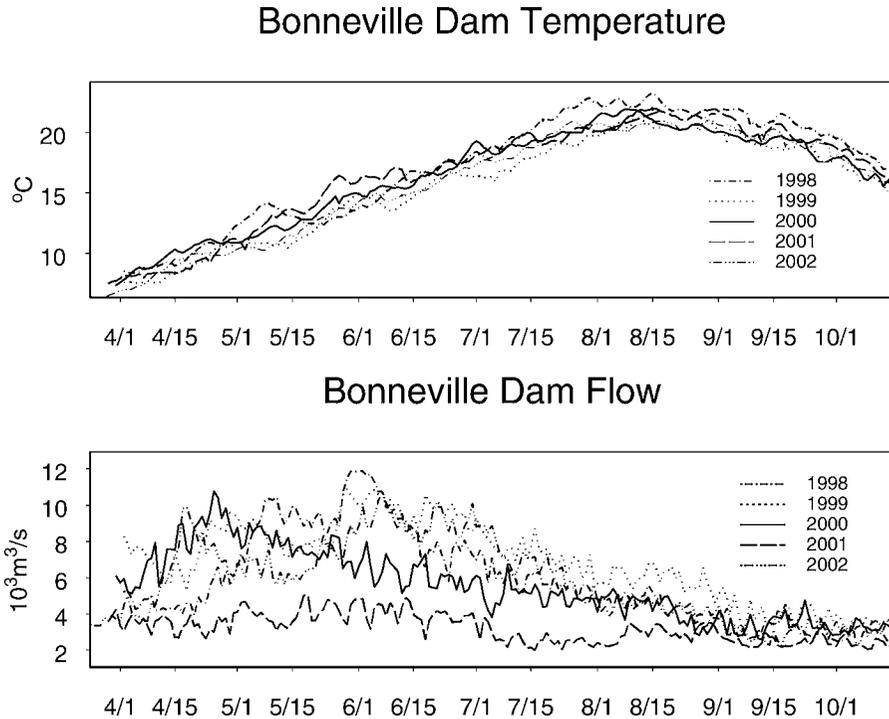


FIGURE 2.—Water temperature and flow at Bonneville Dam on selected dates during the Chinook salmon and steelhead migration periods. See Table 1 for passage dates.

were less correlated ($r^2 = 0.52$, $P < 0.00001$). In addition, the mean flows ($5.3 \times 10^3 \text{ m}^3/\text{s}$ at Bonneville versus $1.4 \times 10^3 \text{ m}^3/\text{s}$ at Lower Granite) were disparate due to the dams' positions in the river (see Figure 1). As a result, we defined the index flow as the average flow at Bonneville Dam on the detection date and the flow 14 d later at Lower Granite Dam. Index temperatures and flows corresponding with dam arrival times were uncorrelated ($r^2 = 0.03$, $P < 0.00001$). Figure 3 shows histograms of the temperatures, flows, migration times, and migration rates associated with the PIT-tagged spring, summer, and fall Chinook salmon.

For steelhead, we used the Bonneville Dam temperature on the detection date and defined the index flow as the average of the flows at Bonneville Dam on the detection date and the flow 25 d later at Lower Granite Dam. These index temperatures and flows were uncorrelated ($r^2 = 0.03$, $P < 0.00001$). Temperatures during the steelhead migration season were limited to a small range of high temperatures.

The temperature data were collected daily in the forebay and tailrace of each dam as part of the U.S. Army Corps of Engineers water quality monitoring program. These measures are highly representative of the temperatures experienced by the migrating fish

because the water mixes in passing through the dams so there was no appreciable temperature stratification in the reservoirs.

Alternative Migration Rate Models

Table 2 compares the broken linear and alternative migration rate models as fit to the Chinook salmon migration data. In this comparison, the models were fit to all data, that is, the fits were not applied to speed-ranked data quartiles. We judged the fits according to the Akaike information criterion (AIC), where a lower value indicates a better fit. The broken linear model with a flow term (equation 7) exhibited the best fit of the models. The broken linear–quadratic model (with flow) and the Logan curve (with flow) also fit the data well and significantly better than the linear and exponential models. Interestingly, flow was only important in the unimodal speed–temperature models and not in the linear and exponential models. We also noted that the exponential and linear models differed by less than 3% over 6–23°C.

Chinook Salmon Swim Speed and Delay

Table 3 shows the regression results for the broken linear model migration rate for combined spring,

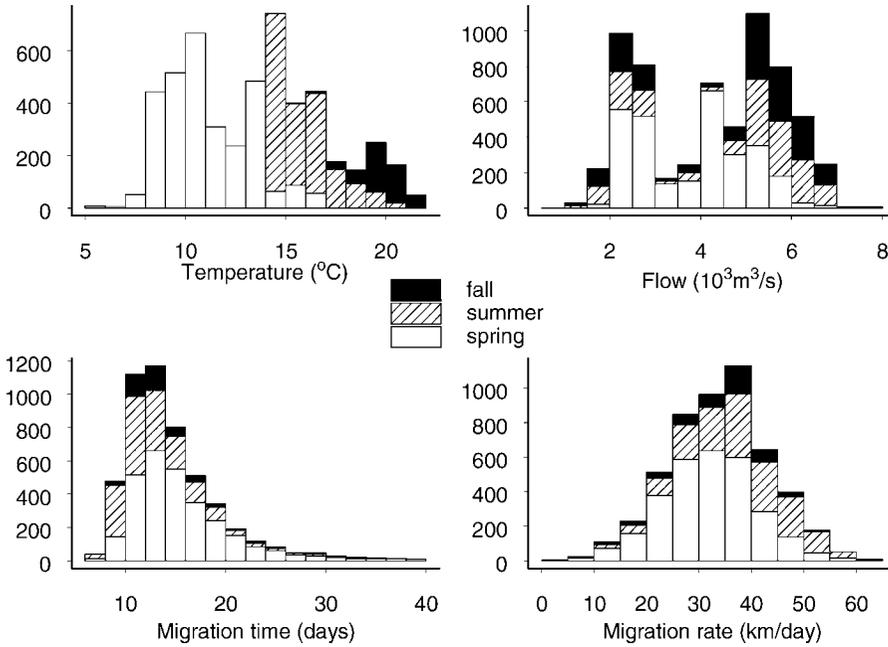


FIGURE 3.—Histograms of index temperature and flow as well as migration time and rate for 1998–2002 for spring, summer, and fall Chinook salmon. The migration rates were computed from the migration time data.

summer, and fall Chinook salmon in 1998–2002 for the four speed ranks of groups arriving sequentially at Bonneville Dam. The final two columns of Table 3 give r^2 values for the equation (15) regressions with flow omitted.

Table 4 gives the coefficients a_j and b_j for the equation (16) regressions, which linearly correlate the speed-ranked coefficients (from Table 3) with rank midpoints. The a_j and b_j coefficients are used in equation (17) to generate the speed-ranked migration rate, $V_M(Q)$, as a function of temperature and flow and in equation (19) to generate the speed-ranked migration time from Bonneville to Lower Granite Dam, $T_M(Q)$, as a function of temperature and flow. Figure 4 shows the migration times of the four speed ranks as a function of

temperature. Notice that the slowest ranked fish experience large delays at both the high and low temperature extremes.

Using $T_M(Q)$ in equation (20) provides speed-ranked delay times. Figure 5, the plot of rank Q versus T_D (equation 20), illustrates the cumulative delay distribution for the Chinook salmon migration at various temperatures and the mean flow. For example, at 17°C, 50% of fish have a cumulative delay less than 3.3 d or, assuming that delays primarily occur in dam passage, less than about 0.5 d at each dam. At 8°C, 50% of fish have a cumulative delay less than 4.7 d or less than about 0.67 d per dam. These results are consistent with dam delay times of radio-tagged Chinook salmon (0.5–1.25 d at each of the four Lower Columbia River dams

TABLE 2.—Comparison of alternative migration rate models fitted to all Chinook salmon data, with number of temperature model parameters (N) and the Akaike information criterion (AIC) value and rank for each model with and without flow.

Model	Equation	Without flow		With flow	
		N	AIC (rank)	N	AIC (rank)
Broken linear	7	4	37,603.2 (4)	5	37,521.3 (1)
Linear flow	8	1		2	38,305.7 (14)
Linear flow temperature	9	2	37,860.0 (10)	3	37,861.4 (11)
Exponential	10	2	37,883.4 (12)	3	37,884.5 (13)
Quadratic	11	3	37,694.9 (9)	4	37,603.4 (5)
Thornton and Lessem (1978)	12	3	37,685.0 (8)	4	43,356.7 (15)
Linear-quadratic	13	4	37,608.1 (6)	5	37,543.0 (2)
Logan et al. (1976)	14	4	37,631.2 (7)	5	37,569.0 (3)

TABLE 3.—Regression results (SEs in parentheses) for equation (15) for spring, summer, and fall Chinook salmon combined (1998–2002) for fastest ($i = 1$) to slowest ($i = 4$) ranked fish. The models were fit using nonlinear methods; $P < 0.00001$ for all regressions. Coefficients and r^2 values are shown for the model with flow; only r^2 values are shown for the model without flow. Variables are as follows: Q^i , the midpoint of the rank quartile; β_0^i , intercept (km/d); β_1^i , temperature coefficient (km·d⁻¹·°C⁻¹) for temperature (θ) up to the optimum temperature ($\check{\theta}^i$); β_2^i , temperature coefficient for temperatures above the optimum temperature; and β_3^i , flow coefficient (1,000 × m³/s).

i	Q^i	β_0^i	β_1^i	β_2^i	β_3^i	$\check{\theta}^i$	r^2			
							Flow model		No-flow model	
							$\theta \leq \check{\theta}^i$	$\theta > \check{\theta}^i$	$\theta \leq \check{\theta}^i$	$\theta > \check{\theta}^i$
1	0.125	25.03 (0.78)	1.87 (0.07)	-2.38 (0.20)	-1.29 (0.012)	16.35 (0.15)	0.46	0.59	0.39	0.39
2	0.375	21.24 (0.59)	1.57 (0.05)	-1.93 (0.15)	-1.04 (0.088)	16.41 (0.14)	0.52	0.63	0.44	0.40
3	0.625	17.55 (0.56)	1.42 (0.05)	-1.69 (0.15)	-0.879 (0.083)	16.39 (0.15)	0.50	0.57	0.44	0.37
4	0.875	12.60 (0.85)	1.06 (0.08)	-1.33 (0.18)	-0.488 (0.133)	15.99 (0.27)	0.19	0.26	0.17	0.18
All		19.08 (0.69)	1.47 (0.06)	-1.81 (0.17)	-0.898 (0.102)	16.35 (0.17)	0.16	0.20	0.14	0.13

and 0.5–1 d at each of the Lower Snake River dams; Keefer et al. 2004). Figure 5, however, lacks the long tail of the small percentage of exceptionally delayed fish observed in that study.

From equation (18), the ground speed (km/d) is

$$V_U = \begin{cases} 27.3 + 2.0\theta - 1.5F & \text{if } \theta \leq 16.3 \\ 100.7 - 2.5\theta - 1.5F & \text{if } \theta > 16.3, \end{cases} \quad (21)$$

where F is in 10³ m³/s, and from equation (4) the swim speed is

$$V_S = V_U + 6F, \quad (22)$$

where we assumed that $\kappa = 0.75$ as was derived from sockeye salmon (Hinch and Rand 2000) because no corresponding value for Chinook salmon has been determined. While Trudel et al. (2004) warn against cross-species parameter borrowing, this assumption has only a small effect on the estimated swim speeds.

Using a mean flow of 3.9×10^3 m³/s, these equations translate to ground speeds of 0.43–0.62 m/s over 8–16°C, diminishing to 0.52 m/s at 20°C. The

swim speeds are 0.70–0.88 m/s over 8–16°C, diminishing to 0.79 m/s at 20°C.

While flow is a statistically significant predictor of migration rate, the effect of flow in equation (21) is minimal. At 15°C and for flows ranging from 2.4 to 5.4×10^3 m³/s—one standard deviation above and below the mean index flow—the resulting ground speed ranged only from 0.57 to 0.62 m/s. However, the effect on swim speed was greater, the latter ranging from 0.79 to 0.95 m/s. With a typical body length of 0.8 m (University of Washington 2003), the swim speed is on the order of 1 body length per second.

Steelhead Swim Speed and Delay

Over 93% of steelhead detections occurred in the 18.5–22°C range at Bonneville Dam, which was probably above the temperature for optimal migration. Therefore, a linear version of the ground and swim speeds, equations (4) and (3) without α_2 and $\check{\theta}$, are appropriate. Tables 5 and 6 give coefficients for linear versions of the migration rate, ground speed, and migration time equations (15–19). The ground speed

TABLE 4.—Equation (16) regression coefficients for spring, summer, and fall Chinook salmon found by regressing the corresponding speed-ranked coefficients (j) in Table 3 on their rank quartile midpoint (Q^j). See text and Table 3 for more details.

Parameter or statistic	j				
	0	1	2	3	$\check{\theta}^i$
Intercept	27.30 (0.48)	1.99 (0.06)	-2.53 (0.06)	-1.46 (0.09)	16.28
Slope	-16.40 (0.83)	-1.04 (0.10)	1.41 (0.11)	1.09 (0.17)	
r^2	0.995	0.98	0.99	0.95	
P	0.003	0.011	0.006	0.024	

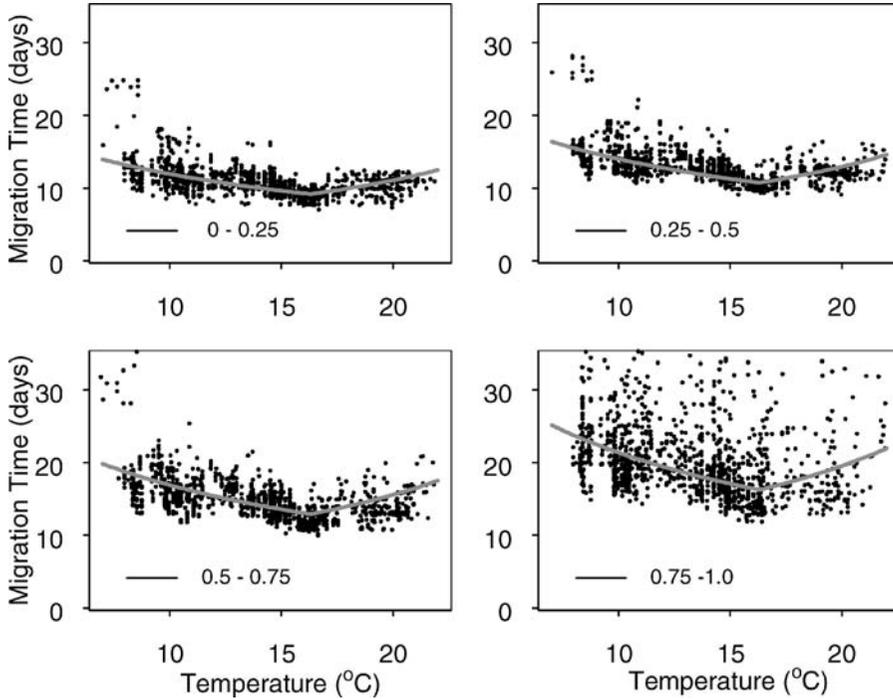


FIGURE 4.—Modeled and observed migration times of Chinook salmon from Bonneville Dam to Lower Granite Dam, 1998–2002, versus temperature for the four fish migration time rank quartiles (from fastest [0–0.25] to slowest [0.75–1.0]). Modeled results are based on equation (19) with coefficients from Table 4 and $F = 3.9 \times 10^3 \text{ m}^3/\text{s}$ (mean flow). Note that 80 out of 5,101 data points, representing the slowest fish, fall outside the scale of the graphs.

(km/d) equation for steelhead is then

$$V_U = 103.9 - 3.6\theta - 3.3F, \tag{23}$$

and the swim speed is

$$V_S = V_U + 13.2F, \tag{24}$$

where we assumed that $\kappa = 0.75$ as was derived from sockeye salmon (Hinch and Rand 2000) because no corresponding value for steelhead has been determined. This assumption has only a small effect on the resulting swim speeds. Notice that the temperature coefficient is negative, indicating that speed diminishes with temperature at the high temperatures encountered by migrating steelhead.

Using a mean flow of $2.0 \times 10^3 \text{ m}^3/\text{s}$, these equations translate to ground speeds of 0.42–0.21 m/s over 17–22°C and swim speeds of 0.73–0.52 m/s over the same temperature range. With a typical body length of 0.7 m (University of Washington 2003), the swim speed is on the order of 1 body length per second.

Discussion

Our analysis indicates that the swim speed of Chinook salmon and steelhead in migrating from Bonneville to Lower Granite Dam in 1998–2002 exhibits a unimodal relationship with temperature. The swim speed of Chinook salmon increased with temperature below an optimal temperature (16°C) and decreased with temperature above the optimum. The

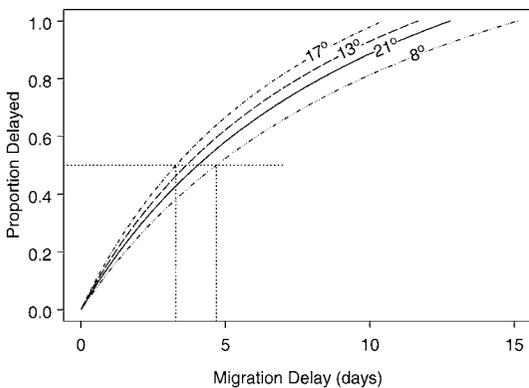


FIGURE 5.—The cumulative distribution of total migration delay for Chinook salmon passage at seven dams as a function of temperature (°C) from equation (20) with coefficients from Table 4 and $F = 3.9 \times 10^3 \text{ m}^3/\text{s}$.

TABLE 5.—Regression results (SEs in parentheses) for equation (15) for steelhead (1998–2002) for fastest to slowest ranked fish. See the caption to Table 3 for more details. Note that the negative values of β_1^i indicate diminishing swim speeds at higher temperatures.

<i>i</i>	Q^i	β_0^i	β_1^i	β_3^i	r^2	
					Flow model	No-flow model
1	0.125	92.90 (4.48)	-3.15 (0.21)	-2.80 (0.39)	0.20	0.16
2	0.375	66.77 (3.79)	-2.28 (0.18)	-2.65 (0.32)	0.17	0.11
3	0.625	43.23 (3.35)	-1.39 (0.16)	-1.98 (0.25)	0.12	0.05
4	0.875	20.85 (2.05)	-0.55 (0.01)	-1.09 (0.14)	0.07	0.02
All		60.90 (2.69)	-2.08 (0.13)	-2.22 (0.21)	0.08	0.06

swim speed of steelhead decreased with temperature, but we note that they migrated later in the season when the river temperature was greater than 18°C. All of the unimodal swim speed models we tested fit the data better (lower AIC scores) than the monotonic models. In particular, the exponential form in the widely employed bioenergetics model of Beauchamp et al. (1989) ranked 12th and 13th out of the 15 models evaluated (Table 2).

Our unimodal swim speed–temperature model is corroborated by laboratory studies on other salmon and trout species (Griffiths and Alderdice 1972; Brett and Glass 1973; Ojanguren and Brana 2000). In particular, Lee et al. (2003) found that the critical swim speeds of adult Fraser River sockeye salmon declined between 16°C and 19°C. The broken linear swim speed–temperature relationship (equation 22) predicts a rate of change in swim speed with temperature similar to that observed in laboratory studies. For Chinook salmon, our analysis gives $dV_S/d\theta = 0.023 \text{ m}\cdot\text{s}^{-1}\cdot\text{C}^{-1}$ over 7–16°C. In comparison, the rate derived by Stewart et al. (1983) and Stewart and Iberra (1991) as expressed through equation (1) is $dV_S/d\theta = 0.022\text{--}0.025 \text{ m}\cdot\text{s}^{-1}\cdot\text{C}^{-1}$ at 15°C for a 5–15 kg fish. Additionally, in a flume study with adult Atlantic salmon, Booth et al. (1997) determined that $dV_S/d\theta = 0.067 \text{ m}\cdot\text{s}^{-1}\cdot\text{C}^{-1}$ over 12–18°C. While it is worth noting that our results are similar to laboratory results, Standen et al. (2004) noted that comparing laboratory and field studies is problematic because the flow patterns fish experience in rivers and flumes are very different.

Flow had a lesser affect on migration rate and ground speed, which was not surprising since Columbia River hydrosystem flows are moderated and salmon are efficient at exploiting locally slow or reverse currents, especially at low to moderate flow (Hinch and Rand 2000). Similar results have been found in other studies. Quinn et al. (1997) determined that the migration time of sockeye salmon between McNary and Rock Island dams on the Columbia River did not change from 1955 to 1994, despite a large decrease in water velocity over those years. In telemetry studies, Bjornn et al. (2000; their Figure 18) found that salmon dam passage times were negligibly correlated with flow or spill at seven Columbia and Snake River dams. However, for high flows the risk of delay is greatly enhanced (Hinch and Rand 2000).

A unimodal relationship between swim speed and migration delay with temperature is not unexpected. Brett (1964) referred to temperature as the “ecological master factor” for fish since temperature may influence the speed and energetic cost of upstream migration. Beamish (1978) noted that critical swim speed peaked at some intermediate temperature, and accompanying graphs showed that the “metabolic scope” (oxygen available for activities excluding basal metabolism) diminished when one moved away from the critical temperature, implicating the role of oxygen consumption in linking temperature to swim speed. Our swim speeds, approximately 1 body length/s, are similar to the minimum-cost-of-transport speed for sockeye and coho salmon in Lee et al. (2003). Additionally, at temperatures below the optimum, the rate of change of

TABLE 6.—Equation (16) regression coefficients for steelhead found by regressing the corresponding speed-ranked coefficients (*j*) in Table 5 against their rank quartile midpoint (Q^j). See text and Tables 3 and 5 for more details.

Parameter or statistic	<i>j</i>		
	0	1	2
Intercept	103.88 (1.38)	-3.58 (0.016)	-3.28 (0.28)
Slope	-95.88 (2.40)	-3.46 (0.027)	2.30 (0.48)
r^2	0.999	0.999	0.92
<i>P</i>	0.0006	0.00006	0.04

speed with temperature ($\sim 3\%$ per $^{\circ}\text{C}$) was similar to the rate of change of routine oxygen consumption ($\sim 4\%$ per $^{\circ}\text{C}$) and the scope for activity ($\sim 5\%$ per $^{\circ}\text{C}$) (Lee et al. 2003). Of particular interest, the scope of activity and maximum oxygen uptake rate were unimodal with respect to temperature and the peak values occurred at temperatures representative of the natal environments of the individual stocks.

These cross-species similarities plus the well-established effect of temperature on fish performance (e.g., Kieffer 2000) support the possibility that temperature, via physiological processes, determines the upstream swimming behavior of salmon and steelhead in the Columbia and Snake rivers. That is, the unimodal form of migration rate with temperature may be physiologically constrained, for example, by the rate of oxygen consumption. Furthermore, if the scope of activity and swim speed are physiologically linked, then we may expect that, like the scope of activity (Lee et al. 2003), the temperature of the peak swim speed is stock specific. The ecological significance of such a linkage is speculative; however, it could be one way climate change induces natural selection in salmon. In particular, climate change resulting in above-optimum migration temperatures could increase the energetic cost of migration and decrease fish fitness (Johnston and Ball 1997). In any case, monotonic swim performance–temperature models should be avoided when considering the impacts of climate change on salmon and other fish species.

Acknowledgments

This work was supported by the Bonneville Power Administration.

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