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A Model of Steelhead Movement in Relation to Water Temperature in Two Lake Michigan Tributaries

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Abstract.—We used movement data from two Lake Michigan tributaries to develop a new approach for analyzing upstream adult steelhead migration. Our data included 28 radio-tagged steelhead *Oncorhynchus mykiss* in the Pere Marquette River and a larger (5,876–10,083-steelhead), multiyear (1993–1999) data set of camera-recorded steelhead passages through a fishway on the St. Joseph River. To quantitatively predict the probability of upstream movement, our model used a rule for temperature-based movements developed from the data. Exponential, logistic, and power functions were evaluated as possible ways to express the probability of movement. Of these, the power function resulted in the closest fit between observed and predicted movements. The probability of movement increased with increasing water temperatures above a movement-threshold water temperature. Stream flow was incorporated into the temperature-based movement (TBM) model but did not add substantially to the model's ability to describe the migratory behavior of steelhead in the Pere Marquette and St. Joseph rivers. The TBM modeling approach is broadly applicable and transferable to other Great Lakes tributaries and may work well for describing the migratory behavior of other species having migrations that depend on water temperature.

Several approaches have commonly been used to characterize fish movements in response to exogenous (environmental) cues. One approach is to collect sequential descriptions of the location of individual fish while taking note of environmental conditions such as water temperature, pH, dissolved oxygen, and stream flow (Doerzbacher 1980; Schulz and Berg 1992; Workman 1994). Descriptive statistics (e.g., mean and range) are then used to characterize observed movement patterns of fish. The information gained from this approach tends to be fish specific and largely descriptive in nature. Another approach is to determine the timing of movements relative to environmental thresholds (Geen et al. 1966; Bailey 1969; Power 1981; Jonsson 1991). Environmental thresholds (e.g., water temperature, dissolved oxygen level, etc.) can be thought of as cues that trigger fish movement. Typically, little or no movement is associated with levels below a minimum threshold; movements begin at the threshold and increase until a maximum movement rate is reached. Other approaches make use of regression analyses, analysis of variance (ANOVA), and multivariate analyses to identify environmental cues and their relation to fish movement (Clapp et al. 1990; Trepanier et al. 1996; Giorgi et al. 1997; White and Knights 1997). The information gained from these studies partially describes fish movement by linking exogenous cues to movement or identifying a range of conditions in which many fish are likely to move. However, these analyses generally provide a static description of fish movement and do not provide a base for predictive models across the range of one or many environmental cues.

Because of the important role migration plays in fish population dynamics, improvements to our understanding are critical to the management of migratory fishes. One aspect of fish migratory behavior that is of particular interest is the timing of migration and its relation to environmental cues. Understanding migratory behavior thus may help fishery biologists better manage these species by limiting exposure to mortality sources.

Our objective was to develop an alternative approach for describing fish migratory behavior, based on a dynamic model that treats migratory behavior in a probabilistic manner. Here, we illustrate the application of this modeling approach using a case study of steelhead *Oncorhynchus mykiss* in two Lake Michigan tributaries. Through this modeling approach, we gain a better understanding of how water temperature and stream flow affect the probability of upstream movement of steelhead in these streams. We also evaluate how the model

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performs for two different types of steelhead migration data collected from discrete Michigan streams: radiotelemetry passage data on the Pere Marquette River and fishway-passage observational data on the St. Joseph River.

Steelhead were chosen because they are highly valued by anglers, they require a scientific basis for management, and their migratory behavior has been documented. Previous migratory studies have focused on a variety of topics: the energetic cost of migration (Hinch and Rand 1998), migration timing of separate runs of the same species in the same river (Burger et al. 1984), factors that influence the migration of juveniles (Northcote 1962; Muir et al. 1994; Zabel et al. 1998), and factors that influence upstream migrations of adults (Shepard 1972; Miller 1974; Jensen et al. 1986; Trepanier et al. 1996).

Our study focused on adult steelhead movement behavior as affected by two exogenous cues, temperature and discharge. These are the most frequently cited exogenous cues that initiate upstream migration (Peters et al. 1973; Miller 1974; Power and McCleave 1980; Power 1981; Jensen et al. 1986; Trepanier et al. 1996).

Methods

Study sites.—The model was developed using two data sources: movement data from radio-tagged steelhead in the Pere Marquette River and counts of fish passing through a fish ladder on the St. Joseph River (Figure 1). The Pere Marquette River is located in west-central Michigan and the main stem of the river is approximately 154 km long (Pere Marquette River Watershed Council 1999). The river drains 1,955 km^2 of watershed and is one of the last, large free-flowing Great Lakes tributary streams in Michigan. The Pere Marquette River is primarily predominated by a coldwater fish community and hosts spawning runs of steelhead during the spring and fall and coho salmon *O. kisutch* and chinook salmon *O. tshawytscha* during the fall. There is also a substantial population of resident brown trout *Salmo trutta*.

The St. Joseph River is located in southwestern Michigan and northwestern Indiana. The mouth of the St. Joseph River is approximately 200 km south of the Pere Marquette River; the two are separated by three major tributaries (Muskegon, Grand, and Kalamazoo rivers) of Lake Michigan. The St. Joseph River is 493 km long and drains a watershed of approximately 11,098 km^2 (Brown 1944). The St. Joseph River has hosted runs of hatchery-reared salmonines from Lake Michigan since the

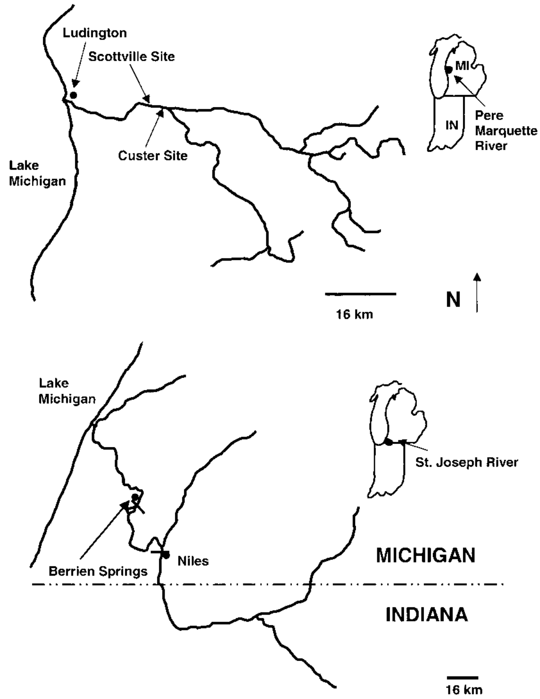

FIGURE 1.—Locations on the Pere Marquette and St. Joseph rivers in Michigan where data on steelhead migration, water temperature, and stream flow were collected. Data on the passage of radio-tagged steelhead and water temperature were collected at the Custer site and stream flow data at the Scottville site on the Pere Marquette River. The bars on the St. Joseph River map indicate where camera-recorded steelhead passage and water temperaturedata (Berrien Springs, Michigan) and stream flow (Niles, Michigan) were collected.

inception of a stocking program in the late 1960s (Dexter and Ledet 1997). Six dams located along the river's main stem regulate stream flow. In 1975, a fishway was constructed at Berrien Springs, the dam furthest downstream and 39 km upstream of Lake Michigan (Figure 1). Fish passage has been noted each year at the Berrien Springs dam since 1977, and since 1993, fish passage has been monitored continuously during the spawning migrations (via a lighted fishway and a camera mounted in a viewing window; Dexter and Ledet 1994, 1997).

Migration data sources.— Fifty-four steelhead (all >1 kg) in the lower Pere Marquette River were implanted with radio transmitters between 15 October 1997 and 11 April 1998. The radio tags (16.0 mm in diameter, 83.0 mm long) weighed 29 gm in air and 12.8 gm in water and were rated to last for 282 d at a 5-s burst rate.

Fyke nets and angling were used to capture the fish. Steelhead were anesthetized in a tank filled with 60 mg/L tricaine methanesulfonate (MS-222) dissolved in river water, and a digitally encoded radio transmitter (CFRT-7A, LOTEK Engineering, Inc.) was surgically implanted into the peritoneal cavity (Winter 1996). The gills of the fish were irrigated with river water during the surgical procedure. The incisions were closed with 000 gut suture, and the radio-tagged fish were transferred to another tub with fresh river water, where they remained until regaining an upright posture within the tub. Radio-tagged fish were released as close to their point of capture as possible. Fish captured in the fyke nets were released approximately 200 m upstream of the nets.

Radio-tagged fish were continually monitored for passage at a fixed location at the Custer public access site approximately 29 km upstream of Pere Marquette Lake, the downstream terminus of the Pere Marquette River (Figure 1). The Custer public access site has an electric barrier for sea lampreys *Petromyzon marinus* and a fishway that is designed to block sea lamprey spawning migrations but not impede salmonine spawning migrations; this fishway did not go into operation until this study was concluded.

Stream temperature was monitored at 90-min intervals using an Onset HOBO Temp Logger at the Custer site. Stream flow was monitored hourly at a U.S. Geological Survey flow recording station located in the river in Scottville, Michigan.

The Michigan Department of Natural Resources provided us with 7 years (1993–1999) of steelhead passage data through the fish ladder at Berrien Springs on the St. Joseph River (Figure 1). Fish passage was continually recorded over 24 h using a camera mounted in a viewing window of the fishway. Monitoring typically beginning on 1 March and continued through April. In 1999, fish passage was monitored for a 1-week period, 12–19 February, and resumed on 1 March; monitoring began on 23 February in 1998 and on 18 February in 1997. Because of the gap in data collection during the month of February 1999, we only used data that had been collected beginning on 1 March 1999 for purposes of model simulation. Water temperatures were recorded once daily (0800 hours) at 1.2 km below the Berrien Springs fish ladder. Annual steelhead migrations enumerated for the St. Joseph River ranged from 5,876 in 1994 to 10,083 in 1997.

Model development.—Upstream migration begins when exogenous and endogenous conditions are appropriate to stimulate the movement of fish into a river from a source location, such as a lake or ocean. The model portrays the passage of fish upstream beyond a detection site to spawning locations, based upon changes in water temperature and stream flow, by drawing daily from a population of fish from the source. The source population of fish (N_t) includes individuals that will migrate upstream to the spawning area, but it does not include the portion that will remain in the lake and not participate in spawning migrations during a given year. Once upstream migration begins, the source population continually declines until there are no more fish left to move upstream. The number of fish available to move upstream each successive day (N_{t+1}) is determined from the number of fish available to move the previous day (N_t) minus the number of fish passing the detection site. The number of fish passing the detection site varies daily and is expressed as the number of fish available to move (N_t) times a probability of movement (PM_t). For the purposes of this model, the probability of movement is based upon a function of water temperature alone or water temperature and stream flow.

The initial model development included water temperature as the exogenous factor upon which movement was based. A time-step of 1 d, which was in accordance with the data collected from the Pere Marquette River study, was used for the simulation. The differential equation representing movement was solved using a fourth-order Runga–Kutta integration (Press et al. 1992). Three functions were evaluated as a means to express the relationship between temperature and the probability of upstream movement (PM). These functions represented the general concept that as water temperature increases, fish are more likely to migrate upstream. An assumption of our model is that steelhead will migrate before stream temperatures are warm enough to inhibit upstream spawning migrations. Therefore, the functions we used to depict the probability of movement do not account for a decreasing probability of movement as water temperature increases. Using the definitions a = rate parameter, b = rate parameter, T = mean daily water temperature, and h = minimum water temperature threshold for steelhead movement, three functions were explored, namely, the exponential function, $\text{PM} = ae^{b(T-h)}$; the power function, $\text{PM} = a(T-h)^b$; and the logistic function, $\text{PM} = 1[1 + e^{-b(T-h)+a}]^{-1}$.

The Solver feature in Excel was used to minimize the sum of squared differences between the observed and predicted numbers, moving residual sum of squares (RSS) by varying the natural logarithmic ($\log_e$) values of h and the a and b parameters in the migration functions. By varying the $\log_e$ values of our model parameters, the model parameters were constrained to positive values. Best-fitting parameter values were determined by performing a nonlinear search to minimize RSS. The nonlinear search was initiated with several different values to ensure that the search had achieved a global minimum. The functions tested were compared for goodness of fit by evaluating the sum of squares of differences between the observed and predicted number of steelhead moving.

After selecting the best-fitting function, we examined how the effect of water temperature varied among years for the St. Joseph River data using an F-test based on extra sum of squares (Neter and Wasserman 1974). A temperature-based movement (TBM) model with a set of parameters representing each year (full model) from 1993 to 1999 was compared with a model wherein one set of parameters was used to represent the data among all years (reduced model).

Approximate standard errors for the model parameters were estimated using a likelihood approach (Ratkowsky 1983). The standard errors were approximated because we assumed that our data were normally distributed. The concentrated likelihood for each parameter was calculated according to methods described in Seber and Wild (1989), namely,

$$\text{concentrated } [\log_e \text{ likelihood}] = \left(\frac{\nu}{2}\right)\left[\log_e\left(\frac{2\pi \mathrm{RSS}}{\nu}\right) + \frac{\nu}{2}\right],$$

where $\nu = N - k$ is the degrees of freedom (N = the sample size and k = the number of model parameters).

Standard errors for parameters were calculated by perturbing the best-fit parameter estimates by 1% and determining the change in the concentrated likelihood. We estimated the standard error of each parameter estimate (i.e., $\sqrt{\mathrm{var}(S_x)}$) from the variance–covariance matrix for the parameter estimates (Ratkowsky 1983):

$$\text{variance–covariance matrix} = \begin{bmatrix} s_h^2 & \mathrm{cov}(h, a) & \mathrm{cov}(h, b) \\ \mathrm{cov}(h, a) & s_a^2 & \mathrm{cov}(a, b) \\ \mathrm{cov}(h, b) & \mathrm{cov}(a, b) & s_b^2 \end{bmatrix},$$

where h = minimum water temperature threshold for steelhead movement, a = rate parameter, and b = rate parameter.

We derived the variance–covariance matrix from the inverse of the information matrix (Ratkowsky 1983):

$$\text{information matrix} = \begin{bmatrix} \frac{\partial^2 L}{\partial^2 h} & \frac{\partial^2 L}{\partial h \partial a} & \frac{\partial^2 L}{\partial h \partial b} \\ \frac{\partial^2 L}{\partial h \partial a} & \frac{\partial^2 L}{\partial^2 a} & \frac{\partial^2 L}{\partial a \partial b} \\ \frac{\partial^2 L}{\partial h \partial b} & \frac{\partial^2 L}{\partial a \partial b} & \frac{\partial^2 L}{\partial^2 b} \end{bmatrix},$$

where L is the concentrated likelihood value for the best-fitting parameter values.

We estimated the second derivatives numerically for the h, a, and b parameters from the following equation:

$$\frac{\partial^2 L}{\partial x^2} = \frac{\frac{\partial L}{\partial x}}{0.5(x_1 - x)},$$

where x = the best-fitting value for parameter estimate (h, a, or b) from the TBM model and x_1 = the value of each parameter (h, a, or b) when it is perturbed 1% above the best-fitting estimate. The numerator on the right-hand side is defined as

$$\frac{\partial L}{\partial x} = \frac{L_1 - L}{x_1 - x},$$

where L_1 = the concentrated likelihood value when one model parameter (h, a, or b) is perturbed 1% above the best-fitting estimate.

The second derivatives for the covarying parameters were derived from the general equation,

$$\frac{\partial^2 L}{\partial x^2 \partial y^2} = \frac{L_{x+y} - L}{(x_1 - x) + (y_1 - y)},$$

where y = the best-fitting value for one of the two remaining parameter estimates (h, a, or b) from the TBM model that were not used to determine the value of x in this equation; y_1 = the value of one of the two remaining parameters (h, a, or b from the TBM model) perturbed 1% above the best-fitting estimate of y that was not used determine the value of x in this equation; and L_{x+y} = the concentrated likelihood value when two parameters (h, a, or b from the TBM model) are perturbed 1% above the best-fitting values.

The effects of stream flow on migratory behavior were incorporated into the TBM model, fol-

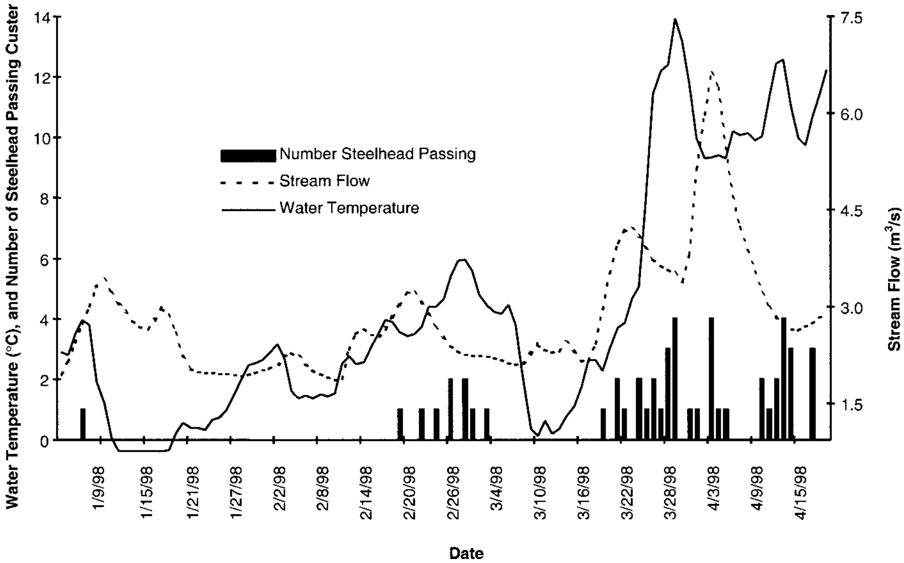

FIGURE 2.—Passage of radio-tagged steelhead per day at the Custer reception site on the Pere Marquette River, Michigan (left scale), coincident stream flow at the U.S. Geological Survey stream flow gauge downstream in Scottville (right scale), and mean daily mean water temperature recorded at the Custer reception site (left scale), 1998.

lowing initial evaluations of the effect of water temperature alone. To determine the qualitative relationship between flow and movement, we examined plots of the residuals from the TBM versus flow. For these models, three functions were evaluated to describe the probability of upstream movement (PM) as a combination of stream flow (F) and water temperature. These functions were a linear $\times$ power function, $\mathrm{PM} = (c \cdot F + d) \cdot a(T - h)^b$; a power $\times$ power function, $\mathrm{PM} = (c \cdot F^d) \cdot a(T - h)^b$; and a logistic $\times$ power function, $\mathrm{PM} = (1 + e^{-d \cdot F + c})^{-1} \cdot a(T - h)^b$, where c and d are additional rate parameters.

Because stream flow is affected by the size of the watershed, stream channel width, streambed gradient, and other factors, the effect of flow on the probability of movement is likely to vary among watersheds. Therefore, we represented stream flow in the TBM model using the relative deviation from the mean daily flow $(Q - \overline{Q})/\overline{Q}$, where Q represents flow and $\overline{Q}$ represents the mean seasonal flow). Stream flow data from the U.S. Geologic Survey were obtained for the Pere Marquette River from a monitoring station located approximately 8 km downstream of the Custer site, near the Scottville public access site, and for the St. Joseph River, from a gauging station located approximately 71.6 km upstream of Berrien Springs in Niles, Michigan (Figure 1). The Solver feature in Excel was used to determine the best-fitting parameter values as determined by the smallest sum-of-squares differences between the observed and predicted movement.

Results

Of the 54 radio-tagged steelhead, 28 were recorded moving upstream at the Custer monitoring site and were subsequently used in this study. Of the 26 fish not recorded at Custer, 7 were recorded moving out of the Pere Marquette River; status of the remainder was unknown.

The number of fish passing by the Custer monitoring site each day showed a general correspondence to stream flow and water temperature (Figure 2). Incidence of higher numbers of fish passing generally occurred when stream flow and water temperature were increasing. However, it is difficult to quantitatively describe movement behavior based on stream flow and water temperature using this figure alone. In the St. Joseph River, few fish migrated upstream early in the migration period when water temperature was low (Figure 3). As water temperature increased, the number of upstream migrants increased. Later in the migrating season, when the water temperature continued to increase, the number of upstream migrants decreased.

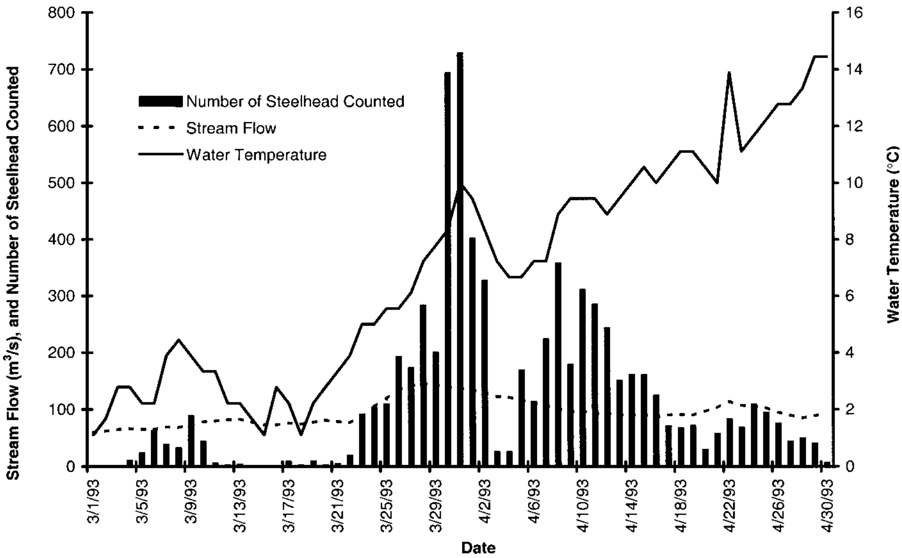

FIGURE 3.—Number of steelhead counted per day using camera-recorded fish passage videos at Berrien Springs on the St. Joseph River, Michigan, coincident stream flow at the U.S. Geological Survey stream flow gauge upstream in Niles (both left scale), and mean daily mean water temperature recorded at Berrien Springs (right scale), 1993.

Water Temperature

Three functions were compared for their ability to represent the relationship between water temperature and the probability of movement. The power function provided the best fit for the Pere Marquette River telemetry data and for 6 of 7 years of count data for the St. Joseph River (i.e., in 1995 the exponential function provided the best fit; Table 1). The mean sum of squared residuals for the power function was smaller than for the exponential and logistic functions for the St. Joseph River data. Using the 1996 St. Joseph River data as a typical example, all three functions predicted trends of fish movement that generally corresponded to periods when steelhead were observed to move (Figure 4). The observed steelhead movement was variable from day to day, and all three functions did not consistently predict to the observed maximum and minimum numbers of fish moving. The power function was the best predictor of movement early in the migration period, when there was less week-to-week variation in movement, and it consistently did the best job of approximating the observed data. Based on these results, we used the power function for the remaining analyses.

The minimum temperature threshold for movement in the St. Joseph River varied from 0.0°C in 1995 to 6.1°C in 1996. Across years, the minimum temperature threshold for movement averaged

TABLE 1.—The residual sum of squares (RSS) values for the power, logistic, and exponential forms of the temperature-based movement model for steelhead in the Pere Marquette (1998) and St. Joseph (1993–1999) rivers, Michigan. The lowest values indicate the best fists, which are marked by asterisks.

Data source	Year	RSS: Power	RSS: Logistic	RSS: Exponential
Pere Marquette River	1998	21*	23	23
St. Joseph River	1993	232,411*	262,736	290,192
	1994	323,337*	339,036	340,647
	1995	480,621	470,424	470,114*
	1996	369,816*	482,955	518,423
	1997	1,163,361*	1,284,841	1,326,333
	1998	396,918*	607,810	574,139
	1999	582,682*	694,935	694,935
Mean		507,021	591,820	602,112

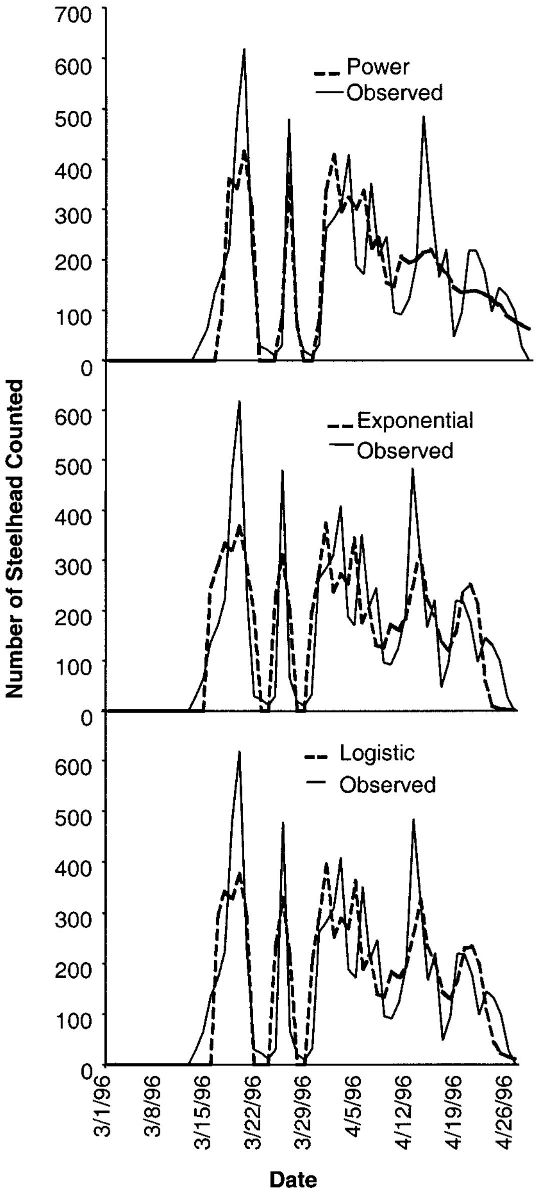

FIGURE 4.—Observed and predicted steelhead movement data in the St. Joseph River, Michigan, 1996, based on power (top panel), exponential (middle panel), and logistic (lower panel) models of temperature-based movement.

3.8°C (Table 2). The lowest temperature threshold value (h = 0.0°C) occurred in 1995 when the logistic (h = 3.4°C) and the exponential (h = 3.9°C) functions produced a smaller sum of squares than the power function-based TBM model (Table 1). The intercept value for the power function (a) varied substantially, ranging from 0.001 in 1995 to 0.086 in 1996 (Table 2). The exponent value for the power function (b) also varied substantially from 0.34 in 1996 to 2.43 in 1993. High values of b were generally associated with low temperature thresholds and low intercept values (Table 2). Despite the variation in parameter estimates, the predicted probability of movement as a function of water temperature for the St. Joseph River was similar among years except 1993, when the probability of movement rose sharply with water temperatures in excess of 10°C (Figure 5).

A comparison of the RSS for the full TBM model (RSS = 3,549,146) and the reduced TBM model (RSS = 4,336,051) indicated that the parameter estimates for the power function TBM model varied in the St. Joseph River annually ($F_{18,\ 416}$ = 1.57, F_{Calc} = 5.12, $P < 0.001$). The full TBM model included a separate set of parameter estimates for each year and the reduced model included a single set of parameter estimates for all years. The minimum temperature threshold was 3.7°C for the reduced (Table 2). The intercept value for the reduced model was 0.001 and the exponent value was 1.25.

Water Temperature and Stream Flow

In both the Pere Marquette and St. Joseph rivers there was generally no relationship between residual errors from the TBM model and flow. This result is illustrated by the results for 1998, which was a typical year (Figure 6). The power × power, logistic × power, and linear × power stream-flow–water-temperature models had the same RSS values for the Pere Marquette River data and did not result in a substantial improvement in model fit from the power function TBM model (Tables 1, 3). The mean RSSs for the three stream-flow–water-temperature functions indicate that the logistic × power function was the best-fitting function and was only a slightly better fit than the power × power and logistic × power functions for the St. Joseph River data (Table 3). The parameter estimates of the best-fitting stream-flow–water-temperature function (logistic × power) varied from year to year, indicating no consistent effect of flow on movement. There was no significant improvement in the RSSs for the stream-flow–water-temperature models over the simple TBM model (Tables 1, 3). Based on these results, additional analyses on the effects of stream flow and water temperature on steelhead migrations were not further considered.

TABLE 2.—Parameter estimates (±1 SE) for the power function version of the temperature-based movement (TBM) model for steelhead in the St. Joseph River, Michigan, 1993–1999. Parameter values and approximate standard errors for the reduced model (combined 1993–1999 St. Joseph River data) used in the *F*-test comparing years for the St. Joseph River data are also included.

		Model parameter estimates and standard errors		
			Rate parameters	
TBM model	Year	Temperature threshold (°C)	*a*	*b*
Full model	1993	1.6 ± 0.17	0.001 ± 0.0001	2.43 ± 0.031
	1994	4.4 ± 0.07	0.028 ± 0.0029	0.67 ± 0.069
	1995	0.0 ± 0.00	0.001 ± 0.0001	2.35 ± 0.044
	1996	6.1 ± 0.03	0.053 ± 0.0045	0.34 ± 0.068
	1997	3.2 ± 0.24	0.09 ± 0.0012	1.28 ± 0.090
	1998	5.1 ± 0.15	0.018 ± 0.0016	0.98 ± 0.040
	1999	6.1 ± 0.01	0.086 ± 0.0067	0.40 ± 0.037
Reduced model		3.7 ± 0.08	0.011 ± 0.0004	1.25 ± 0.025

Discussion

Water Temperature

We found the power-function-based TBM model was the best-fitting model to represent the effect of water temperature on adult steelhead upstream migration in the Pere Marquette and for 6 of the 7 years of the St. Joseph River data. As such, the TBM model serves as a quantitative representation of the migratory behavior of steelhead in relation to water temperature. Our model indicated increasing probabilities of upstream movement over a range of water temperatures above the minimum temperature threshold for movement.

The effect of water temperature on fish migration has been clearly shown to vary among systems and species (Banks 1969; Miller 1974; Leggett 1977; Jensen et al. 1986; Jonsson 1991; Lucas and Batley 1996; White and Knights 1997). Steelhead movements have been linked to water temperature during all phases of their life cycle, including the upstream spawning migration of adults, downstream movements of juveniles, and distribution of steelhead while occupying the Great Lakes (Northcote 1962; Banks 1969; Shepard 1972; Haynes et al. 1986; Giorgi et al. 1997). Although the upstream movement of adults has been linked

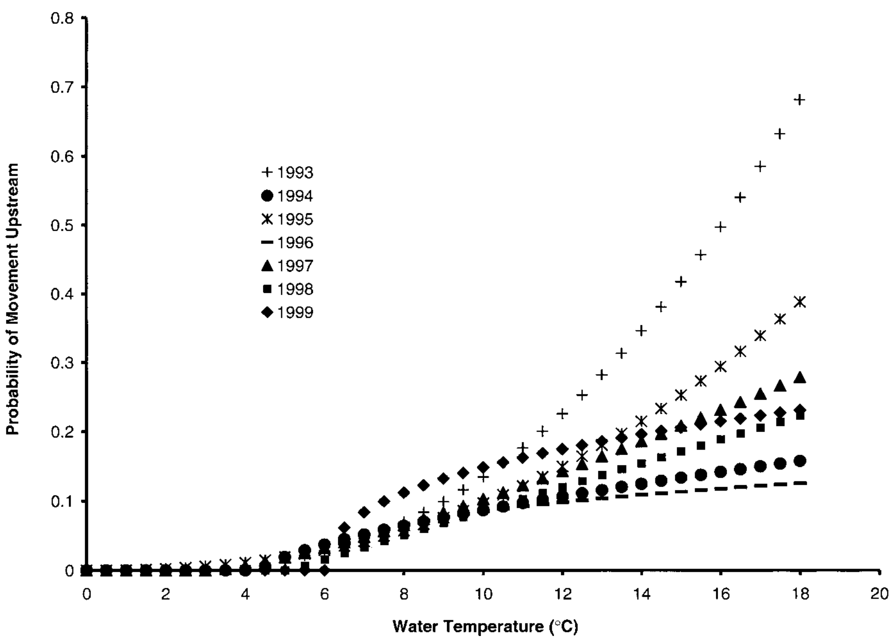

FIGURE 5.—Temperature-based probability of steelhead movement based on models developed using a power function for the St. Joseph River, Michigan, from data collected in 1993–1999.

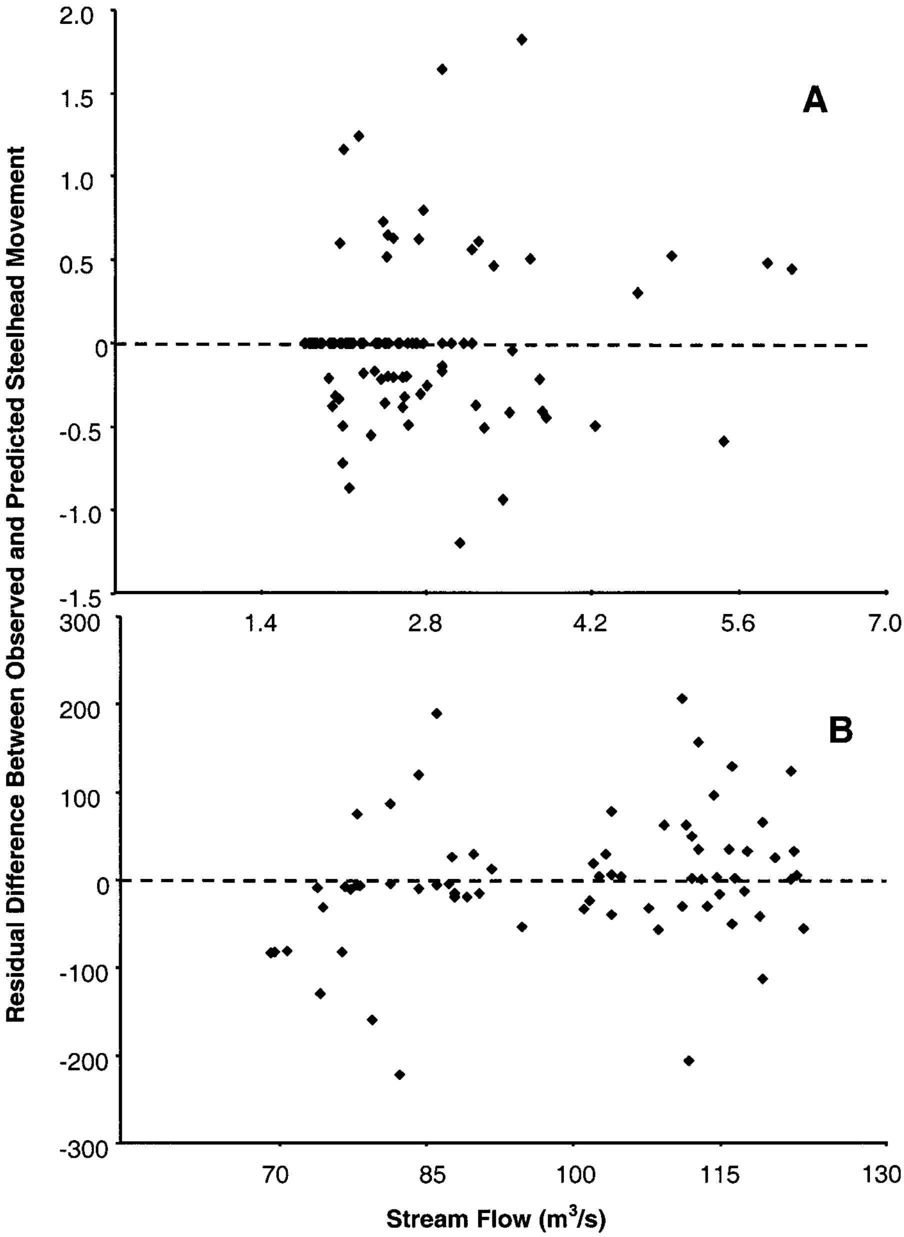

FIGURE 6.—Residual plots of differences between observed and predicted steelhead movements using a temperature-based movement model and stream flow for 1998 data from **(A)** the Pere Marquette River and **(B)** the St. Joseph River in Michigan.

to water temperature in some systems, movement has not typically been viewed as occurring over a range of temperatures (Shepard 1972; Miller 1974; Leggett 1977; Jonsson 1991). However, Power (1981) found that adult Atlantic salmon *Salmo salar* migrate within a range of temperatures and also identified a minimum temperature threshold of movement for smolts. Using our modeling approach, we view upstream migrations as a response to a continuous stimulus.

The relation between movement and water temperatures was similar between the Pere Marquette River data and the larger data set from the St. Joseph River. There was an increasing probability

TABLE 3.—The residual sum of squares (RSS) values for the power, logistic, and linear flow–temperature-based movement models for steelhead, using relative flow (Q) deviation from mean daily flow ($[Q - \bar{Q}]/\bar{Q}$) to represent flow for the Pere Marquette (1998) and St. Joseph (1993–1999) rivers, Michigan. A power function was used to describe the temperature portion of the stream-flow × water-temperature-based function. The lowest values indicate the best fits, which are marked by asterisks.

Data source	Year	RSS		
		Power[a]	Logistic[a]	Linear[a]
Pere Marquette River	1998	21*	21*	21*
St. Joseph River	1993	232,411*	232,411*	232,411*
	1994	297,682	284,663*	323,337
	1995	457,889*	459,091	479,475
	1996	396,238	369,816*	369,816*
	1997	1,163,361	1,129,662*	1,134,143
	1998	396,198*	396,853	396,918
	1999	582,682	581,180*	582,682
Mean		503,780	493,382	502,683

[a] These terms refer to the flow portion of the function.

of movement associated with increasing water temperatures for steelhead in both systems. The TBM model predicted general trends of movement during periods of observed movement for both rivers. Despite the different data types (radiotelemetry and camera-count data) and the physical separation of the two rivers (200 km of Lake Michigan shoreline), the application of the TBM modeling approach to the Pere Marquette and St. Joseph rivers suggests that this modeling approach might be applicable to spring-run steelhead in other river systems in the Great Lakes.

Although we fit both full and reduced models to explore the annual variability in movement behavior, it is important to recognize that, in practice, the reduced model would be used to predict movement in a new year. The movement predictions from the full model are more precise than the reduced model. However, it would be difficult to choose among the full-model parameter estimates to evaluate movement predictions in new years. Although the movement predictions of the reduced model are less precise than the full model, the parameter estimates from the reduced model are representative of upstream steelhead migration for all years of data in the model.

The TBM model is a useful predictor of steelhead migration, but there are several factors that were not incorporated into the model that may influence steelhead migrations. The TBM model did not generally depict the large day-to-day variability observed in movement for both rivers. Special cases (e.g. the movement of several or many steelhead together upstream at one time) may account for some day-to-day variability. Other factors such as neurological and physiological interactions may also account for daily variation in migratory behavior (Leggett 1977; Jonsson 1991). Lorz and Northcote (1965) found that onshore winds and light intensity stimulated river entry by kokanee *Oncorhynchus nerka*. The winds helped disperse creek odor along the shore, congregating greater numbers of fish in onshore areas. Spending more time in the onshore areas increased the probability of the kokanee salmon locating the river. Other studies suggest that high flow or the maturity of the fish may also facilitate river entry (Miller 1974; Smith et al. 1994).

The effect of water temperature on steelhead movement in the St. Joseph River varied among years (1993–1999). Other factors such as diurnal period may influence the year-to-year variability of the effect of water temperature on steelhead migration.

There are many possible combinations of endogenous and exogenous factors that may stimulate the upstream migration of steelhead. The TBM model demonstrates that we can simplify the complexity of influences on upstream migration by viewing the effect of one exogenous factor (water temperature) on their migratory behavior expressed as an increasing probability of upstream migration with increasing water temperature once water temperature increases above the temperature threshold for movement. Previous studies have identified the existence of a threshold for movement based on water temperature for salmonines (Menzies 1939; Power 1981; Jensen et al. 1986; Jonsson 1991). The water temperature threshold serves as a marker between little or no migration and an increasing probability of steelhead to migrate upstream with increasing water temperatures.

It is possible that the temperature threshold is a greater barrier to migration earlier in the migratory season, when water temperatures are likely to be colder for longer periods, rather than later in the season when water temperatures at or below the threshold occur over shorter durations. Our TBM model is unique in that it quantitatively predicts migration behavior over a range of water temperatures and combines the prediction with an identification of a water-temperature threshold for movement rather than the qualitative movement description.

The TBM model may work to describe the migratory behavior of other fish that move into rivers for reproductive purposes and time their movements on water temperature and other factors. For example, sea lampreys migrate into Great Lakes tributaries for spawning, and use water temperature as a migratory cue (Morman et al. 1980). Sea lampreys have significantly reduced salmonine and coregonine abundances in the Great Lakes, provoking intensive control efforts to reduce their abundance (Smith and Tibbles 1980). If a TBM model is developed for sea lampreys, it could serve to identify the timing of migration and percent passage of sea lampreys into rivers, thereby aiding the operators of control structures such as the electric lamprey barriers located on the Pere Maquette and Jordan rivers (Swink 1999).

Water Temperature and Stream Flow

The combination of stream flow and water temperature did not substantially improve the fit of the TBM model, which was consistent with an examination of the residual distribution of the TBM model compared with stream flow. Jonsson (1991) suggests upstream migration may be a response to a combination of stream flow and water temperature fluctuations, consistent with observations in the migration of Atlantic salmon (Power 1981; Jensen et al. 1986). Stream flow has been linked to migratory behavior in other salmonid populations (Ellis 1962; Alabaster 1970; Shepard 1972; Power and McCleave 1980; Smith et al. 1994). Stream flow did not appear to strongly influence steelhead migrations in our study. Neither river during the steelhead migration typically exhibits fluctuations in stream flow that are large enough to significantly affect steelhead ability to successfully migrate and subsequently affect their migratory behavior. Flow fluctuations may have been insufficient to detect how steelhead migrations would vary in response to flow in streams exhibiting greater flow variation.

Stream flow is influenced by many factors including, watershed size, streambed morphometry, surrounding topography, weather patterns, and groundwater input (Bras 1990). Hellawell et al. (1974) found that stream flow and water temperature were secondary to the effect of time-of-year or season on migratory behavior. Shepard (1972) found that stream flow and water temperature are important in steelhead migration, but their influence varied from system to system. Trepanier et al. (1996) found stream flow to be important and water temperature to have little effect on the migratory movement of Atlantic salmon. Stream flow is likely to be a greater factor in steelhead migrations in watersheds that experience drastic changes in flow, such that greater flows may promote movement by creating an avenue of passage over barriers that are typically impassable at low water periods; conversely, high flows could be so strong that upstream movement is thwarted. In rivers with small water-level fluctuations, water temperature is important in stimulating upstream migration (Jonsson 1991). The response of steelhead migratory behavior to stream flow is likely to be different among watersheds; therefore, any single model may not adequately represent steelhead having different life histories or using streams with different physical characteristics. Jonsson (1991) suggests that behaviors may differ between rivers because there is a hierarchy of environmental factors initiating migrations or because the fish adapt the timing of migration to different factors in different rivers.

In conclusion, we developed a new approach to analyzing upstream adult steelhead migrations by using a TBM model that quantitatively predicts the migratory behavior of steelhead over a range of water temperatures. This model demonstrates an increasing probability of movement over increasing stream temperatures that exceed the threshold-of-movement temperature. The TBM model predicts migratory behavior in two Lake Michigan tributaries that differ in size, location, and other factors. The success of the model in these two different tributaries suggests that the modeling approach is broadly applicable and may work well in other Great Lake tributaries, and possibly in other rivers that receive spawning migrations of steelhead that rely on water temperature as a primary cue for movement. In addition, the TBM model will probably be a useful management tool for predicting the migratory behavior of other species (such as sea lamprey) and by synthesizing fish-passage data to provide predictive migratory behavioral information on other species of fish.

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