Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers

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Abstract: The ability of fish to migrate past velocity barriers results from both attempt rate and swimming capacity. Here, I formalize this relationship, providing equations for estimating the proportion of a population successfully passing a barrier over a range of distances and times. These equations take into account the cumulative effect of multiple attempts, the time required to stage those attempts, and both the distance traversed on each attempt and its variability. I apply these equations to models of white sucker (*Catostomus commersoni*) and walleye (*Stizostedion vitreum*) ascending a 23-m-long flume against flows ranging from 1.5 to 4.5 $m \cdot s^{-1}$. Attempt rate varied between species, attempts, and over time and was influenced by hydraulic variables (velocity of flow and discharge). Distance of ascent was primarily influenced by flow velocity. Although swimming capacity was similar, white sucker had greater attempt rates, and consequently better passage success, than walleye. Over short distances, models for both species predict greater passage success against higher velocities owing to the associated increased attempt rate. These results highlight the importance of attraction to fish passage and the need for further investigation into the hydraulic and other environmental conditions required to simultaneously optimize both attempt rate and passage success.

Résumé : La capacité des poissons de migrer à travers une barrière d'eau rapide résulte à la fois de la fréquence des tentatives et de la capacité de nage. Cette relation apparaît ici de façon formelle et des équations permettent d'estimer la proportion de la population qui réussit à traverser une barrière sur une gamme de distances et de temps. Ces équations tiennent compte de l'effet cumulatif de tentatives répétées, du temps requis pour organiser ces tentatives, ainsi que de la distance traversée à chaque tentative et sa variabilité. Les équations ont été appliquées à des modèles de meuniers noirs (*Catostomus commersoni*) et de dorés *(Stizostedion vitreum*) qui remontent une canalisation de 23 m contre des courants variant de 1,5 à 4,5 $m \cdot s^{-1}$. La fréquence des tentatives varie en fonction de l'espèce, et du temps, ainsi que d'une tentative à l'autre, et elle est influencée par les variables hydrauliques (vitesse du courant et débit). La distance de la remontée est surtout influencée par la vitesse du courant. Bien que la capacité de nage soit semblable chez les deux espèces, les meuniers noirs font plus de tentatives de remontée et leur taux de réussite est plus élevé que celui des dorés. Sur de courtes distances, les modèles des deux espèces prédisent un taux de réussite plus élevé dans les vitesses de courant plus fortes, parce qu'il y a, dans ces conditions, une fréquence plus grande de tentatives. Ces résultats mettent en lumière l'importance de l'attraction exercée par les passes migratoires et la nécessité d'études plus poussées sur les conditions environnementales et hydrauliques qui optimisent à la fois la fréquence des tentatives et la réussite des traversées.

[Traduit par la Rédaction]

Introduction

Studies on swimming performance of fishes are of intrinsic biological interest, and in the case of diadromous migrants, they also have an important applied component. The relevance of swimming performance to fish passage issues motivated some of the pioneering work of the last century in this field (Denil 1937; Bainbridge 1960; Brett 1962) and continues to receive attention today (Peake et al. 1997; Hinch and Bratty 2000; Haro et al. 2004).

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One factor that has limited the study of swimming capacity has been the challenge of observing fishes under controlled conditions that mimic their natural environments, making it difficult to formulate relevant hypotheses. For example, many carefully controlled studies have shown that critical swimming speed (U_{crit}) and other measures of performance increase with both temperature and length (Beamish 1978; Videler 1993). This has a broad physiological basis, yet may not accurately reflect the behavior of fish in the wild (Rome et al. 2000; Swank and Rome 2000). This is because volitional behavior is not governed exclusively by metabolism and biomechanics but, at least ideally, reflects a fitness-maximizing response to both environmental and endogenous cues. For example, the total discharge (Winstone et al. 1985; Aadland 1993; Holm et al. 2001) or chemical signatures issuing from a stream (Hasler 1971) may be as important a cue to the quality of upstream habitat as flow velocity or temperature. Given the appropriate stimulus, migrants of a range of sizes may be induced to swim upstream,

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even against currents or at temperatures that force them to swim at energetically costly prolonged or sprint speeds (Collins 1952; Weaver 1963; Webb 1975).

Another characteristic of laboratory studies that undermines their relevance to natural situations is the selective use of cooperative individuals (Brett 1964; Dewar and Graham 1994; Leonard et al. 1999). This practice tends to bias predictions of ability to traverse barriers (Castro-Santos and Haro 2003). Also, test fish are often of hatchery or cultured origin (Brett 1967; Peake et al. 1997) and are coerced into swimming, with either electric shock, prodding, confinement, or other external form of stimulation. Finally, laboratory studies typically attempt to generate a uniform flow profile, which reduces turbulence structure and low-velocity zones that fish might make use of in a natural setting. Although often necessary to obtain the desired data, each of these practices casts doubt on the accuracy of the predictions they are used to generate (Hammer 1995).

A similar criticism can be applied to the analysis presented in our companion paper (Haro et al. 2004) in which we analyzed data on swimming performance, quantified as the distance that fish were able to swim against a velocity challenge in an open channel. Fish were collected from a variety of sources and run over a range of dates and temperatures. We did this in part to guarantee a sampling of populations and conditions that represent the diversity of the region in which the tests were done. The resulting predictions of maximum distance of ascent ($D_{\max}$), however, were based on the observed maxima of fish that entered during the first hour of each trial, ignoring the rate or frequency of attempt, the presence of individuals that staged no attempts, and the effects of successive attempts on ascent distance. Thus, effects of variability in motivation were largely excluded from our analyses. Here, I further develop the idea of swimming performance to include motivation, measured as attempt rate, and explore the implications of this variable on predictions of passage success.

Methods

A new model of swimming performance

Consider a scenario in which a group of fish with a common start time ($T_0 = 0$) is able to stage only one attempt to traverse a velocity barrier of distance D. The expected proportion of the population that will have passed by time T is equal to the proportion attempting multiplied by the proportion succeeding:

$$(1) \qquad P(T,D) = A(T)\cdot S(D)$$

(see Table 1 for notation). The proportion blocked by the barrier equals the product of the proportion attempting and the proportion failing to pass:

$$(2) \qquad B(T,D) = A(T)\cdot F(D)$$

The resulting functions increase with time as $A(T)$ approaches unity, but the proportion passing can never exceed $S(D)$.

A third population component comprises those fish that are available to pass but do not stage an attempt by time T.

$$(3) \qquad N(T) = 1 - A(T)$$

Thus, the proportion of the population remaining below the obstacle consists of those that did not attempt to pass the obstacle as well as those that tried and failed to pass.

$$(4) \qquad R(T,D) = N(T) + B(T,D)$$

When fish are allowed to stage successive attempts, however (as is generally the case), the probability of a given fish traversing a barrier becomes $1 - [F(D)]^n$, where n is the total number of attempts. As n increases, this value approaches unity for passable distances and zero for impassable distances (Fig. 1). In nature, the population of fish available to pass a barrier consists of individuals that have already staged one or more attempts and failed to pass as well as those that have yet to stage their first attempt. Of fish staging their first attempt before time T (or $t_1 < T$), the proportion that stages a second attempt will depend on the time t of their first attempt, i.e.,

$$(5) \qquad A_2(T) = \int_{t=0}^{T} f_1(t)\,\hat{A}_2(T-t)$$

where t is time, incrementing by an arbitrarily small step Δt, $f_1(t)$ is the probability density function of attempt time, or the probability of staging a first attempt on the interval $(t - \Delta t, t)$, and $\hat{A}_2(T)$ is the cumulative distribution function of attempt time, conditional on fish having staged one attempt. Note that as the time of the first attempt approaches T, the probability of staging a second attempt goes to zero ($A(T)$ is, by definition, an increasing function with origin at zero and maximum of 1; Table 1). This logic can be extrapolated to successive attempts such that

$$(6) \qquad A_a(T) = \int_{t=0}^{T} f^*_{a-1}(t)\,\hat{A}_2(T-t)$$

where a is the attempt number and $f^*_a(t)$ is the probability density function of attempt time, conditional on the probability density function of the previous attempt

$$(7) \qquad f^*_a(t) = \int_{i=0}^{t} f^*_{a-1}(i) f_a(t-i) \mid a \geq 2$$

$$f^*_1(i) = f_1(i)$$

Given information on timing and success rates of multiple attempts, eq. 6 can be combined with eqs. 2, 3, and 4 to predict the overall proportion of a population remaining below an obstacle. For example, allowing for two attempts:

$$(8) \qquad R(T,D) = N_1(T) + N_2(T)\cdot B_1(T,D) + B_1(T,D)\cdot B_2(T,D)$$

The proportion remaining comprises those fish that staged no attempts, those that staged only one attempt and were blocked, and those that staged two attempts but were blocked on both. Note that, as with $A_a(T)$, $N_a(T)$ is the proportion failing to stage an attempt, conditional on having staged the previous attempt, and $B_a(T,D)$ is the conditional proportion that staged an attempt but failed to pass. Over k attempts, eq. 8 can be expressed as follows:

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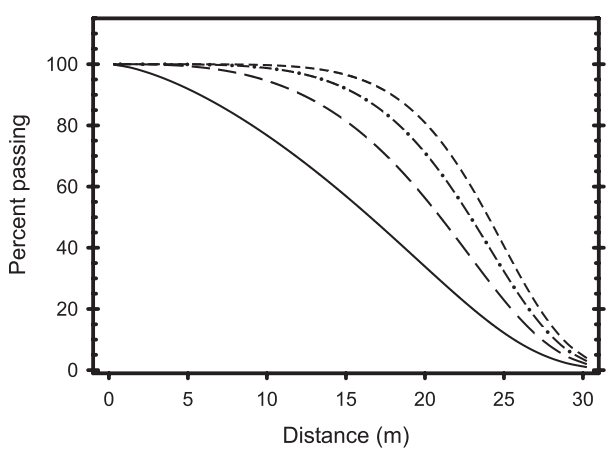
Table 1. Glossary of terms used throughout this paper.

Term	Meaning
D_{max}	Maximum distance of ascent within the flume (m)
U_f	Speed of flow (m·s^{-1})
Q	Volume of flow (i.e., discharge) (m^3·s^{-1})
$A_a(T)$	Cumulative distribution function of attempt a at time T, i.e., probability of staging an attempt at time $t \leq T$. For $a > 1$, this function is conditional on having staged the previous attempt, and so $0 \leq A_a(T) \leq 1$
$N_a(T)$	Proportion of fish not staging attempt a by time T, i.e., the complement of $A_a(T)$
$f_a(t)$	Probability density function of attempt a at time t, i.e., unconditional probability of staging attempt a at time t
$F_a(D)$	Cumulative distribution function of attempt a at distance D, i.e., probability of failing at distance $d \leq D$; $0 \leq F_a(D) \leq 1$
$S_a(D)$	Survivorship function of attempt a at distance D; equal to $1 - F_a(D)$ or the proportion successfully passing at distance D; $0 \leq S_a(D) \leq 1$
$B_a(T,D)$	Proportion of the population that attempts to pass the barrier but is unsuccessful on attempt a
$R(T,D)$	Proportion of the population that remains below the barrier because of either unsuccessful passage attempts or failure to stage attempts
$P(T,D)$	Joint probability of passage through distance D at time T

Fig. 1. Effect of multiple attempts on passage success. The prediction from the first attempt is for the expected distance of ascent by American shad (*Alosa sapidissima*) against 3 m·s^{-1} flow (Haro et al. 2004). The proportion of population passing increases exponentially with attempt number as $1 - [F(D)^n]$. Attempts (a): solid line, 1; long-dashed line, 2; dashed–dotted line, 3; short-dashed line, 4.



$$R(T,D) = \sum_{a=1}^{k}\left[N_a(T)\prod_{b=1}^{a}B_{b-1}(T,D)\right] + \prod_{a=1}^{k}B_a(T,D) \tag{9}$$

$$B_0(T,D) = 1$$

The complement of $R(T, D)$ is the cumulative proportion passing an obstacle.

$$P(T,D) = 1 - \sum_{a=1}^{k}\left[N_a(T)\prod_{b=1}^{a}B_{b-1}(T,D)\right] + \prod_{a=1}^{k}B_a(T,D) \tag{10}$$

This means that as the proportion of a population staging multiple attempts grows, the overall probability of passage also grows, even exceeding $S(D)$ (Fig. 1). Here, I demonstrate these methods using data from fish volitionally sprinting against controlled velocities in a large, open-channel flume.

Facilities, apparatus, and study animals

This study was conducted in the flume facility of the S.O. Conte Anadromous Fish Research Center (U.S. Geological Survey, Biological Resources Division) in Turners Falls, Massachusetts, located on the Connecticut River at river kilometre (rkm) 193. Details of the facility, the flume apparatus, hydraulics, and instrumentation as well as tagging, handling, and transport are described in Haro et al. (2004).

During the migratory seasons of 1997–1999, white sucker (*Catostomus commersoni*) and walleye (*Stizostedion vitreum*) were electrofished from the mainstem Connecticut River at rkm 278. Additional suckers were electrofished from the mainstem Connecticut River at rkm 183 and 98 or were collected from a fishway trap on the Westfield River (rkm 6, a tributary to the Connecticut with confluence at Connecticut River rkm 114). Fish were conveyed to the facility using a fish transport truck. There they were measured (fork length), sexed, externally tagged with uniquely coded passive integrated transponder (PIT) tags (Castro-Santos et al. 1996), held for 1–7 days in open, outdoor, flow-through holding ponds, and fed ad libitum pelletized feed (suckers) or shiners (walleye).

Before each trial, individual batches of fish were corralled (not handled) into the staging area below the swimming speed flume, where they were confined until the hydraulics were brought to the desired conditions (velocity, depth, etc.), usually for about 10 min. Trials lasted from 60 to 420 min and were assigned to a single nominal velocity condition of 1.5, 2.5, or 3.5 m·s^{-1}. White suckers were also subject to 4.5 m·s^{-1} (actual velocities varied; see Haro et al. (2004) and Table 2 for details). Because entry rates during the 1st hour were low for both species, trial duration was generally set to 360 min. During some trials, however, multiple species were present. In these cases, trials were of shorter duration, ranging from 60 to 180 min. This did not constitute a problem for these analyses, however, as will be shown below.

Velocity treatments were only semirandom, with greater emphasis placed on the 2.5 and 3.5 m·s^{-1} conditions, where large proportions of available fish entered the flume but failed to traverse its full length. Owing to the properties of flowing water and our desire to maintain uniform flow characteristics along the length of the flume, depths of flow dif-

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Table 2. Target and measured flow velocities (U_f, m·s^{-1}) and their SDs with associated discharge (Q, m^3·s^{-1}) (in parentheses). Also included are characteristics of white sucker and walleye trials, along with their SDs.

Nominal velocity	U_f (Q)	N	% attempting	Length (mm)	Temperature (°C)	Days held	Trial duration (h)
White sucker							
1.5	1.71 (1.64)±0.00	54	75.9	390±37	11.5±0.8	2.9±1.4	6.1±0.1
2.5	2.64 (0.69)±0.04	81	76.5	391±33	13.6±3.4	3.1±2.0	6.1±0.2
3.5	3.38 (1.52)±0.03	51	62.7	391±35	19.3±4.8	2.9±2.2	3.2±2.9
4.5	4.50 (2.07)±0.03	63	50.8	396±26	15.0±4.2	5.9±2.3	4.1±2.2
Walleye							
1.5	1.64 (1.57)±0.04	54	46.3	313±55	11.4±2.4	2.0±0.0	4.8±1.4
2.5	2.65 (0.69)±0.11	80	48.8	304±48	13.4±3.3	2.2±0.8	5.8±1.7
3.5	3.35 (1.51)±0.02	54	53.7	313±48	10.1±0.6	3.3±0.0	5.1±1.7

fered among velocity treatments. At 1.5 m·s^{-1}, the depth was 0.96 m; at 2.5 m·s^{-1}, it was 0.26 m; at 3.5 m·s^{-1}, it was 0.45 m; and at 4.5 m·s^{-1}, it was 0.46 m. Because the flume was 1.00 m wide and rectangular in cross section, the discharge (Q, cubic metres per second) was equal to the product of measured flow velocity U_f and flow depth. Also, because of the differing depths, the U_f:Q ratio varied by test condition, allowing for preliminary analysis of the separate effects of the two variables (Table 2).

Once the velocities had stabilized at the desired levels, an entrance gate was opened, the time was recorded, and fish were allowed to enter the flume of their own volition. Time of entry and maximum distance of ascent of each fish were logged using an array of PIT readers. These readers were spaced every 2.5 m from 0.5 m into the flume and interfaced with a central computer recording at 14 Hz. Although some fish were capable of exiting the top of the flume, the jet of water issuing from beneath the headgate (Haro et al. 2004) created a behavioral barrier through which most fish refused to pass; instead, fish that ascended to the top of the flume either lingered there or quickly fell back to the staging area.

At the end of each trial, the entrance gate was closed and fish were returned to the holding ponds. Tags were removed from the fish and they were returned to the river to continue their migrations. Thus, all fish used in this study were naïve, and cumulative effects from prolonged holding times were minimized.

Attempt rate

In part to maximize the number of fish and test conditions run, trials were terminated whether or not all individuals had staged attempts. This constitutes censoring with respect to time (Hosmer and Lemeshow 1999) and has important implications for the analysis of factors affecting attempt timing (Castro-Santos and Haro 2003). Regression models developed primarily for survival studies (accelerated failure time models: Allison 1995; Meeker and Escobar 1998) can be used to evaluate multiple covariate effects on data that include censored observations; I apply them here to quantify covariate effects on attempt timing.

For those fish that staged at least one attempt, the time elapsed between opening the gate and first detection by the PIT readers constituted the first attempt time: this is a complete (uncensored) observation. Those that never staged an attempt before the end of a trial (regardless of the duration of the trial) were included in the analysis, with attempt time set to trial duration, and designated as censored (incomplete) observations. In this way, all fish are included in the analyses, regardless of trial duration, and contribute to the estimates of $A(T)$ up until the time of censoring (Hosmer and Lemeshow 1999; Castro-Santos and Haro 2003). Similarly, subsequent attempt times were calculated as the time elapsed between their initiation and that of the previous attempt, i.e., the time between first detections of successive attempts. Censored observations were calculated as the time elapsed between the initiation of the previous attempt and the end of the trial. Thus, censoring times of the first attempts were mostly fixed at 6 h, but on subsequent attempts, censoring times were random.

The maximum read range of each reader was 0.5 m, so fish had to enter the flume to be detected. Individual attempts were defined as sequences of continuous records separated by no more than 30 s. This value was established empirically by reviewing preliminary data and was found to accurately describe the behavior of the fish: very rarely were fish present in the flume for more than 30 s without being logged by the nearest PIT reader. This method did, however, allow fish to probe the entrance of the flume multiple times before entering without generating a new attempt every time. This is a realistic criterion because fish swimming near the entrance may not be detected by the first reader for a short time but may still experience substantially greater velocities of flow (U_f) than in the rest of the staging area.

Because the intent of this paper is to illustrate the combined effects of attempt rate and maximum distance of ascent (D_{max}, metres), the regression models are as simple as possible, including only hydraulic variables (flow velocity (U_f, metres per second), discharge (Q, cubic metres per second), and U_fQ)), temperature, length, and time elapsed between collections and trials (holding time) as candidate covariates. Discharge is included instead of depth in the analyses of hydraulic variables because it provides a more meaningful measure of the hydraulic characteristics of the staging area and therefore more accurately describes conditions that the fish were likely to perceive before entering the flume.

When fish staged multiple attempts, time (minutes) from the beginning of the trial to the beginning of each time interval (i.e., time to the previous attempt) was included as a covariate (start time). This allowed testing for correlations in

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attempt rate within individuals that were not adequately accounted for by other covariates. Such correlations can arise from informative censoring, which these statistical methods assume does not occur. Informative censoring means that censoring is not random with respect to the covariates, i.e., had censored observations been complete, they would not have had the same covariate response as the complete observations. The incomplete nature of censored observations means that there is no way to test for informative censoring statistically. However, inclusion of the time variable can help to offset any effect of informative censoring on the rest of the model (Allison 1995).

Methods of model selection and inference detailed in Burnham and Anderson (1998) were used to select the most parsimonious models from suites of models containing meaningful combinations of covariates. Thus, the U_fQ interaction effect was only included in models that also included either or both of the main effects. Start times for attempts other than the first (i.e., time of the previous attempt) were included in all models, regardless of significance. Replicates of each model were constructed using lognormal, Weibull, and generalized gamma distributions (SAS Institute Inc. 1999; Meeker and Escobar 1998). Having generated the full series of models, the best one was selected using the adjusted Akaike's information criterion. This approach to model building has a strong foundation in information theory and avoids ambiguous and over- and under-fit models generated by stepwise methods (see Burnham and Anderson (1998) for an interesting review of this problem).

Distance of ascent

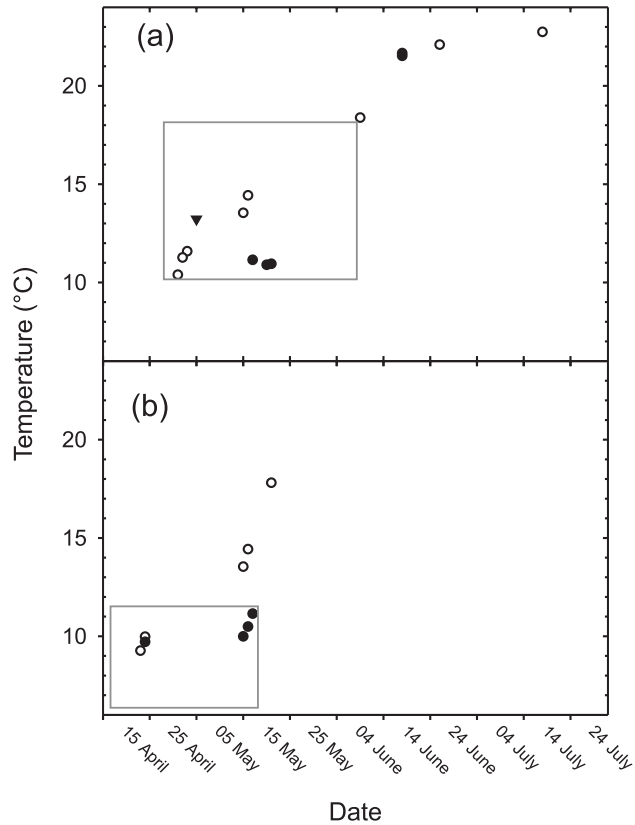
An analogous, but less conventional, approach to censoring is applied here in the analysis of swimming capacity, measured as the maximum distance (D_{max}) that fish swam once they entered the flume. The PIT readers used to log D_{max} were arrayed up to 18 m in 1997 and up to 23 m in 1998 and 1999. However, because fish may have been able to detect changing hydraulics and lighting at the head of the flume, all detections at or above 18 m were censored, regardless of year. Those that stopped before that distance were considered complete observations representing fatigue; censored observations indicate nonfatigue (throughout this paper, fatigue is defined by the decision to abandon an attempt, with no assumptions that fish are fatiguing in any physiological sense).

The same approach described above for attempt rate was used to develop models describing D_{max} for each attempt. Hydraulic variables pertaining to discharge were removed, and the time variable was removed from the repeat attempts, retaining only U_f, length, temperature, and holding time. Because it is unrealistic to expect U_f not to affect D_{max}, it was included in all models.

Combined effects of attempt rate and distance of ascent

After estimating attempt rates and distance of ascent for those fish that staged attempts, the combined effect of these functions was calculated using eqs. 6, 7, and 10 to generate an overall prediction of passage success at three velocities (2, 3, and 4 m·s^{-1}) and at five evaluation times (30, 60, 120, 240, and 360 min).

Fig. 2. Dates and temperatures of trials of (*a*) white sucker and (*b*) walleye. Boxes indicate the expected range of spawning dates and temperatures.



Predictions of $A_a(T)$, $S_a(D)$, and $F_a(D)$ (Table 1) were generated using SAS software (SAS Institute Inc. 1999) for the first five (walleye) or six (sucker) attempts at each of these three velocities. Except for the hydraulic parameters (U_f, Q, and U_fQ), predictions were based on mean covariate values at each attempt. The cumulative effects were then calculated at each evaluation time and velocity to generate predicted passage curves based on both attempt rate and swimming capacity.

Results

In all, 249 suckers and 188 walleye were run during their respective migratory periods from 1997 to 1999 (Table 2). Sucker trials (N = 14) were conducted from April to July; walleye trials (N = 10) were run only during April and May (Fig. 2). For this reason, the sucker data cover a greater range of temperatures than the walleye data. Sucker trials comprised 18 ± 11 individuals (mean ± SD); walleye trials comprised 19 ± 3 individuals.

Attempt rate

The two species differed in attempt rate, with more suckers staging one or more attempts than walleye (Table 2). The percentage of suckers staging at least one attempt was similar at 1.5 and 2.5 m·s^{-1} but was less at 3.5 and 4.5 m·s^{-1}. These data ignore differences in trial duration, however, and illustrate the importance of including a time axis. Under the 4.5 m·s^{-1} condition, the mean trial duration was 67% that of

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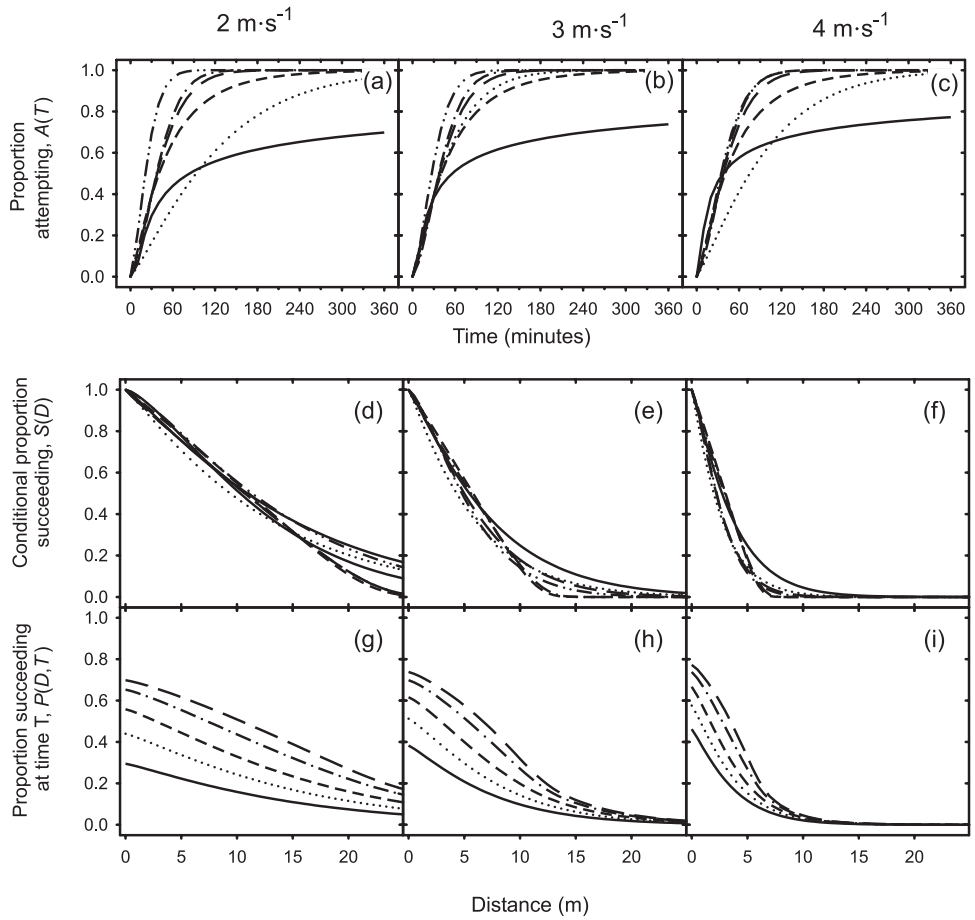
Fig. 3. Model predictions of attempt time (*a–c*), conditional success probability for the first six attempts (*d–f*), and combined probability of passage success over 6 h (*g–i*). Models are for white sucker ascending velocities of 2, 3, and 4 m·s^{-1} at 0.5 m depth. Predictions of $A(T)$ and $S(D)$ are for attempts 1 (solid line), 2 (dotted line), 3 (short-dashed line), 4 (dashed-dotted line), 5 (long-dashed line), and 6 (dashed–double-dotted line). Predictions of $P(T,D)$ are for 30 (solid line), 60 (dotted line), 120 (short-dashed line), 240 (dashed–dotted line), and 360 min (long-dashed line).



the 1.5 and 2.5 m·s^{-1} conditions, so the observed difference was probably a function of trial duration (Table 2). Under the 3.5 m·s^{-1} condition, however, trial durations were even shorter, so the observed percentage of fish staging attempts may actually indicate a greater attempt rate under this condition. By comparison, the percent attempting and trial durations were more consistent among walleye trials, with the greatest attempt rate occurring under the 3.5 m·s^{-1} condition. Note that by quantifying attempt timing as $A(T)$ (Figs. 3*a*–3*c* and 4*a*–4*c*), the inclusion of the time axis removes the ambiguities that arise from unequal trial durations (Kaplan and Meier 1958; Lee 1992). Moreover, the methods of survival analysis applied here permit the inclusion of multiple covariates that might also contribute to variations in attempt rate.

As mentioned in Haro et al. (2004), fluctuating headpond levels occasionally caused the hydraulic jump to move beyond 1.0 m into the flume. Attempts staged during these times were excluded from the analysis, as was the succeeding attempt (to avoid misleading values of elapsed time), although later attempts were included. Of the valid observations, numbers of suckers staging one to six attempts and of walleye staging one to five attempts (Event) as well as those available to stage events (total) are included in the regression models (Tables 3 and 4). These are accelerated failure time models and indicate covariate effects on the log of time (ln *t*, minutes)

Covariate effects on attempt times differed by attempt. Among white suckers (Table 3), hydraulic conditions affected attempt times on attempts 1, 2, 4, and 6. On the first attempt, discharge alone dominated attempt time, indicating that suckers took longest to stage their first attempt under the 2.5 m·s^{-1} condition (Table 2). On the second attempt, the model suggests similar attempt times under the 1.5 and 2.5 m·s^{-1} conditions, shorter attempt times under the 3.5 m·s^{-1} condition, but longer attempt times under the 4.5 m·s^{-1} condition. On the fourth attempt, attempt times increased with velocity. The effect of discharge on the sixth attempt was the converse of that on the first: fish entered most quickly under the 2.5 m·s^{-1} condition and most slowly under the 4.5 m·s^{-1} condition. Length of fish had no effect on attempt time, and temperature affected only the first (increased attempt rate) and sixth (reduced attempt rate) attempts. The temperature effect on the first attempt is important, as it suggests that initial attempt time decreased by a factor of $e^{(-0.08\times10)} = 0.44$ over 10 °C, allowing more time for subsequent attempts at higher temperatures. Duration of holding time also influenced attempt times of suckers, with increased holding times

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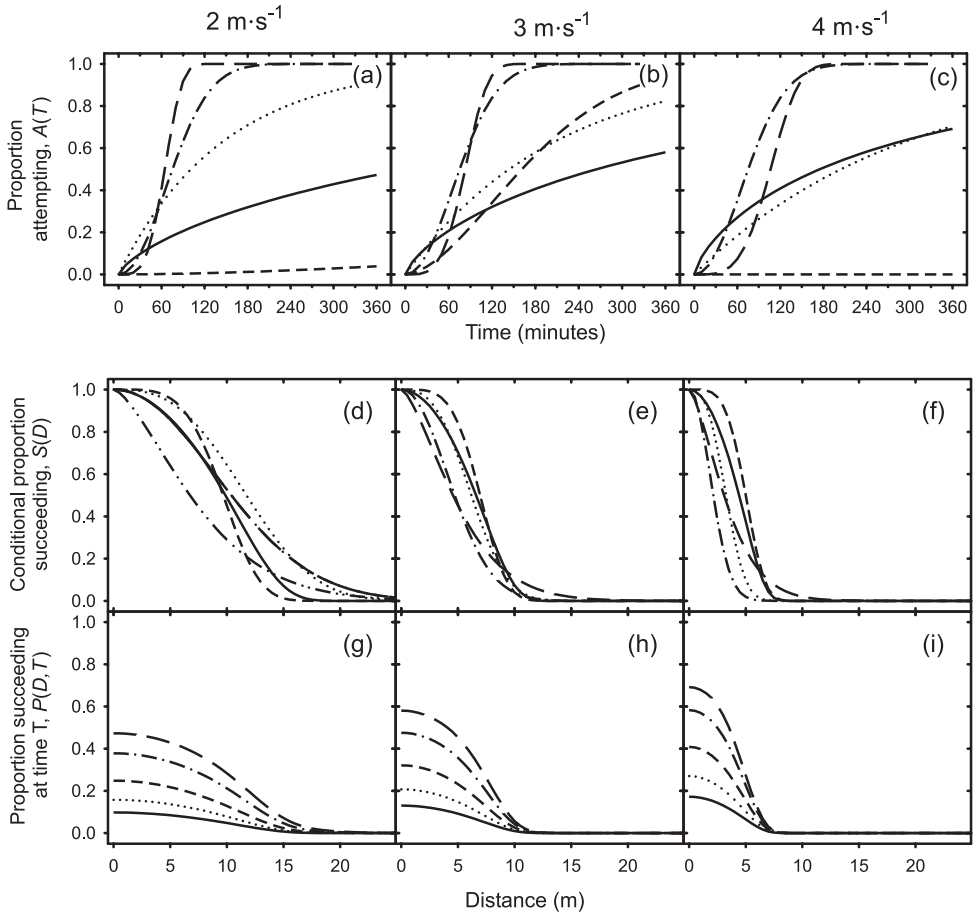
Fig. 4. Model predictions of attempt time (*a–c*), conditional success probability for the first five attempts (*d–f*), and combined probability of passage success over 6 h (*g–i*). Models are for walleye ascending velocities of 2, 3, and 4 m·s^{-1} at 0.5 m depth. Predictions of $A(T)$ and $S(D)$ are for attempts 1 (solid line), 2 (dotted line), 3 (short-dashed line), 4 (dashed–dotted line), and 5 (long-dashed line). Predictions of $P(T,D)$ are for 30 (solid line), 60 (dotted line), 120 (short-dashed line), 240 (dashed–dotted line), and 360 min (long-dashed line).



associated with reduced time to the first and sixth attempts: this means that attempt times of fish held for 7 days were reduced over those that were run on the first day by a factor of 0.52 on these two attempts.

Covariate effects on attempt time were also variable among walleye (Table 4). On attempts 1 and 3, the models indicate that hydraulic effects caused shortest attempt times under the 4.5 m·s^{-1} condition. The opposite effect is described for the second attempt, and on the fifth attempt, attempt time increased linearly with U_f. The length effect was significant only on the first attempt, with longer fish staging attempts more quickly than shorter ones. Similarly, shorter attempt times were associated with increased temperatures on this attempt. The effect here is much larger than for suckers, with time to the first attempt decreasing by a factor of 0.14 over 5 °C. As with suckers, attempt times were reduced with increasing holding times, affecting the first and third attempts. This indicates that walleye run on the first day after collection took more than six times longer to enter the flume the first time than those that were run on the fourth day (the maximum holding time for this species).

Suckers and walleye differed with respect to the effect of start time (time of attempt initiation) on subsequent attempt rates. This effect was at least marginally significant and consistent among suckers for attempts 2–6. A positive value here indicates that fish that took longer to stage a given attempt had lower rates of successive attempts as well. Specifically, if we assume a mean effect of 0.35, then fish that take 100 min to stage a given attempt will take $e^{0.35}$, or 1.4 times as long to stage their next attempt as fish that entered immediately. This heterogeneity of attempt rate suggests that there may be important covariates that were not included in these models. However, since the objective of this paper is to demonstrate the combined effects of attempt timing and swimming performance on D_{max} over time and not to test hypotheses or fully model the effects that dominate these factors, I will assume that inclusion of start time in the model adequately accounts for this unexplained variability.

Walleye, in contrast, showed no effect of start time on attempt rate except for on the second attempt, where significance was approached. This suggests that the rate of each attempt was effectively independent of the rate of the previous attempt, and no further modifications of the model are indicated. To be conservative, however, I include the start time variable in these models. Although this reduces the parsimony of the model, its inclusion had no substantial effect on the magnitude or significance of the other covariates.

Differences in attempt times of walleye and suckers are apparent in the amount of censoring present on each attempt.

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Table 3. Regression models of white sucker attempt times.

	β ± SE					
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5	Attempt 6
Intercept	5.51±0.37 ($P < 0.001$)	10.52±1.97 ($P < 0.001$)	3.67±0.16 ($P < 0.001$)	3.09±0.21 ($P < 0.001$)	3.62±0.20 ($P < 0.001$)	1.91±0.69 ($P = 0.006$)
U_f (m·s^{-1})	—	–2.48±0.71 ($P < 0.001$)	—	0.14±0.06 ($P = 0.026$)	—	—
Q (m^3·s^{-1})	–0.81±0.18 ($P < 0.001$)	–4.08±1.11 ($P < 0.001$)	—	—	—	0.49±0.16 ($P = 0.003$)
U_fQ (m^4·s^{-2})	—	1.47±0.39 ($P < 0.001$)	—	—	—	—
Length (cm)	—	—	—	—	—	—
Temperature (°C)	–0.08±0.02 ($P < 0.001$)	—	—	—	—	0.06±0.04 ($P = 0.086$)
Holding time (days)	–0.11±0.04 ($P = 0.007$)	—	—	—	—	–0.11±0.04 ($P = 0.005$)
Start time (min × 10^2)	—	0.42±0.14 ($P = 0.002$)	0.24±0.13 ($P = 0.069$)	0.39±0.10 ($P < 0.001$)	0.27±0.11 ($P = 0.015$)	0.49±0.13 ($P < 0.001$)
Scale	1.24±0.14	0.84±0.05	0.99±0.07	0.62±0.05	0.71±0.05	0.67±0.06
Shape	–2.33±0.44	—	0.63±0.18	—	—	—
Distribution	Gamma	Weibull	Gamma	Weibull	Weibull	Weibull
Total	249	166	148	128	112	104
Event	167	149	128	113	104	84
% censored	33	10	14	12	7	19

Note: Coefficients (β) and SEs indicate covariate effects on log attempt time (ln t, min). U_f, flow velocity; Q, discharge.

Table 4. Regression models of walleye attempt times.

	β ± SE				
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5
Intercept	15.74±1.75 ($P < 0.001$)	3.88±0.40 ($P < 0.001$)	36.60±10.67 ($P < 0.001$)	4.31±0.34 ($P < 0.001$)	3.71±0.45 ($P < 0.001$)
U_f (m·s^{-1})	—	—	–11.26±3.79 ($P = 0.003$)	—	0.25±0.13 ($P = 0.051$)
Q (m^3·s^{-1})	–0.83±0.40 ($P = 0.04$)	0.71±0.30 ($P = 0.019$)	–20.16±6.74 ($P = 0.003$)	—	—
U_fQ (m^4·s^{-2})	—	—	7.54±2.61 ($P = 0.004$)	—	—
Length (cm)	–0.07±0.03 ($P = 0.014$)	—	—	—	—
Temperature (°C)	–0.39±0.06 ($P < 0.001$)	—	—	—	—
Holding time (days)	–0.63±0.21 ($P = 0.003$)	—	–0.55±0.37 ($P = 0.135$)	—	—
Start time (min × 10^2)	—	0.39±0.21 ($P = 0.061$)	0.09±0.14 ($P = 0.490$)	0.19±0.18 ($P = 0.282$)	0.05±0.12 ($P = 0.650$)
Scale	1.36±0.12	1.01±0.10	0.58±0.069	0.48±0.07	0.26±0.05
Shape	—	—	—	—	—
Distribution	Weibull	Weibull	Weibull	Weibull	Weibull
Total	182	88	65	43	27
Event	88	61	42	27	15
% censored	52	31	35	37	44

Note: Coefficients (β) and SEs indicate covariate effects on log attempt time (ln t, min). U_f, flow velocity; Q, discharge.

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Because censoring was mostly fixed at 6 h on the first attempt, this can be viewed as an indicator of limits to the reliability of the models. Quantile estimates within this time frame are reasonable, especially for suckers, but the 52% censoring of walleye data on this attempt should alert readers to the need for caution in extrapolating far beyond estimates up to median attempt time. Censoring on subsequent attempts was random. The magnitude of censoring was small enough among sucker attempt models to discount any concerns that this may raise. Among walleye, however, censoring continued to be heavy on all attempts, and the results should be viewed with some skepticism, especially where significance is marginal (Allison 1995).

The Weibull and generalized gamma distributions provided a better fit to the data than did the lognormal distribution for all attempt time models. The scale (Weibull and gamma distributions) and shape (gamma distribution only) parameters indicate the shape of the underlying error distributions and hence of the cumulative attempt time functions ($A_a(T)$) for each attempt (Meeker and Escobar 1998; Haro et al. 2004). These are presented for suckers and walleye ascending under hypothetical hydraulic conditions of 2, 3, and 4 m·s^{-1} at 0.5 m depth and with other covariates set to their mean values (Figs. 3*a*–3*c* and 4*a*–4*c*, respectively). Note that predicted attempt times differ between species and among attempts.

Among suckers, the modeled rate of the first attempt is lower than subsequent attempts, which are then fairly consistent. On the first attempt, the rate is greatest under the 4 m·s^{-1} condition; on the second, it is greatest under the 3 m·s^{-1} condition. For both of these attempt models, the rate is least under the 2 m·s^{-1} condition. Attempt times are more consistent across velocities among the other attempt models, with $A(T)$ approaching unity within 3 h.

The attempt time models are much more variable among walleye. Here, strong but variable velocity effects predict greatest attempt rates under the 4 m·s^{-1} condition on the first attempt but lowest rates on the second attempt. On the third attempt, only the 3 m·s^{-1} condition predicts substantial proportions of fish attempting. The velocity effect on the fifth attempt was trivial by comparison with the first three.

Distance of ascent

Covariate effects on swimming capacity indicate that D_{max} was consistent among attempts by suckers, as was the effect of velocity (Table 5; Figs. 3*d*–3*f*). On the first attempt, D_{max} decreased by $e^{-0.70}$, or a factor of 0.50 for each metre per second increase in flow velocity. The coefficients for other attempts estimate the magnitude of this effect to range from 0.44 to 0.53 per metre per second increase. Length appeared to have no effect on D_{max}, and the only indication of a temperature effect was on the fourth attempt. On this attempt, D_{max} decreased by a factor of 0.67 over a 10 °C increase in temperature. Holding time appeared to have little effect on D_{max}, the only exception being on the second attempt, where fish held for 7 days swam only 67% as far as those run on the first day.

Model predictions for D_{max} of suckers swimming against hypothetical velocities of 2, 3, and 4 m·s^{-1} are presented for each attempt in Figs. 3*d*–3*f*. Proportion succeeding ($S(D)$) decreased almost linearly with distance down to the 50th

Table 5. Distance of ascent models of white sucker by attempt.

	β ± SE					
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5	Attempt 6
Intercept	4.10±0.25 ($P < 0.001$)	4.37±0.28 ($P < 0.001$)	4.17±0.13 ($P < 0.001$)	4.66±0.29 ($P < 0.001$)	4.35±0.27 ($P < 0.001$)	4.12±0.25 ($P < 0.001$)
U_f (m·s^{-1})	–0.70±0.08 ($P < 0.001$)	–0.78±0.11 ($P < 0.001$)	–0.65±0.05 ($P < 0.001$)	–0.64±0.07 ($P < 0.001$)	–0.82±0.09 ($P < 0.001$)	–0.76±0.08 ($P < 0.001$)
Length (cm)	—	—	—	—	—	—
Temperature (°C)	—	—	—	–0.04±0.02 ($P = 0.036$)	—	—
Holding time (days)	—	–0.07±0.04 ($P = 0.084$)	—	—	—	—
Scale	0.87±0.06	0.91±.07	0.35±0.05	0.37±0.09	0.76±0.07	0.71±0.08
Shape	—	—	2.77±0.45	2.91±0.72	—	—
Distribution	Weibull	Weibull	Gamma	Gamma	Weibull	Weibull
Total	167	149	128	113	104	84
Fatigued	148	132	112	94	89	72
% censored	11	11	13	17	14	14

Note: Coefficients (β) and SEs indicate covariate effects on the log distance of ascent (ln D_{max}, m). Scale and shape parameters refer to disturbance terms of the accelerated failure time models of each distribution type. U_f, flow velocity.

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percentile with no noticeable difference among attempts and diverged only slightly thereafter.

Values for the walleye models were less consistent than those for the sucker models (Table 6). Coefficients for the intercept were uneven, and the velocity coefficient varied by a factor of 2.4. On the first three attempts, longer fish traversed greater distances, with no length effect thereafter. A significant temperature effect was present only on the third and fourth attempts. This effect differed in sign and was small on the third attempt (D_{max} decreased by 26% with a 5 °C increase in temperature) but more substantial on the fourth attempt (a 182% increase over the same temperature range). As with attempt time, walleye were more sensitive to holding time than suckers, except here, D_{max} decreased with increased holding time on attempts 1–3.

As with the attempt time models, the generalized gamma and Weibull distributions provided better fits to the data than the lognormal distribution. The finite length of the flume resulted in some censoring, particularly at low velocities. Overall, however, the proportion of censored observations was small (≤17% on all attempts), so these models can be considered reliable, at least up to 23 m, the length of the flume. The two notable exceptions are the fourth and fifth attempts by walleye, particularly the latter, where small sample size, not censoring, led to questionable estimates.

Model predictions of D_{max} for walleye swimming against hypothetical velocities of 2, 3, and 4 $m \cdot s^{-1}$ highlight the variability of capacity among attempts (Figs. 4*d*–4*f*). The shape of the survivorship curves ($S(D)$) took on more of a sigmoid shape than those of the suckers (Figs. 3*d*–3*f*). Despite these differences, the predicted D_{max} was similar between the two species at each of the velocities modeled.

To allow for comparison of effects of length, temperature, and holding time with the results presented by Haro et al. (2004), the above analyses were run on only the data of the 1st hour. The results differed from those found over the full 6 h. Among suckers, only length had a significant effect on attempt time (with time decreasing with increased length), and none of the three variables substantially influenced distance of ascent. Among walleye, the patterns were more similar to the 6-h data: the only effect of temperature was to increase attempt rate, and increased length was correlated with both increased attempt rates and increased distance of ascent. Holding time also affected performance of walleye, but in competing ways: attempt rate increased with increased holding time on the first three attempts, but distance of ascent decreased.

Also, to test for the possibility that the 1-h duration of the trials presented in Haro et al. (2004) selected for more motivated, and hence better-performing, individuals, I added attempt time to the first attempt D_{max} models (Tables 5 and 6). Time of entry was not correlated with D_{max} among suckers (P = 0.776). Among walleye, significance was approached (P = 0.055), but the effect was very weak (β = –0.09 per 100 min), suggesting that walleye entering after 100 min went 91% as far as those that entered immediately.

Combined effects of attempt rate and distance of ascent

The combined effects of attempt timing and swimming capacity are shown by the estimated overall proportion passing ($P(D, T)$, Figs. 3*g*–3*i* and 4*g*–4*i*). Here, separate curves

Table 6. Distance of ascent models of walleye by attempt.

	β ± SE				
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5
Intercept	2.61±0.39 (P < 0.001)	3.43±0.56 (P < 0.001)	4.89±0.62 (P < 0.001)	2.36±0.82 (P = 0.004)	2.94±1.81 (P = 0.104)
U_f	–0.40±0.08 (P < 0.001)	–0.64±0.11 (P < 0.001)	–0.33±0.11 (P = 0.002)	–0.79±0.18 (P < 0.001)	–0.39±0.65 (P = 0.546)
Length (cm)	0.04±0.01 (P < 0.001)	0.03±0.01 (P = 0.046)	0.02±0.01 (P = 0.030)	—	—
Temperature (°C)	—	—	–0.06±0.02 (P = 0.004)	0.12±0.03 (P < 0.001)	—
Holding time (days)	–0.17±0.10 (P = 0.091)	–0.20±0.09 (P = 0.037)	–0.70±0.11 (P < 0.001)	—	—
Scale	0.28±0.05	0.35±0.04	0.23±0.03	0.49±0.09	0.68±0.16
Shape	1.86±0.46	—	—	—	—
Distribution	Gamma	Weibull	Weibull	Weibull	Weibull
Total	88	61	40	27	13
Fatigued	81	52	35	25	13
% censored	8	15	13	7	0

Note: Coefficients (β) and SEs indicate covariate effects on the log distance of ascent (ln D_{max}, m). Scale and shape parameters refer to disturbance terms of the accelerated failure time models of each distribution type. U_f, flow velocity.

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are drawn for predicted passage at five time intervals from 30 to 360 min. The importance of attraction is apparent: for both species, the greatest passage rates over short distances are predicted at each time step against 4 $m \cdot s^{-1}$ flow, succeeded with increasing distance by 3 $m \cdot s^{-1}$ flow. For both species, 2 $m \cdot s^{-1}$ flow yields the greatest passage success only over distances >4–6 m, even after 6 h. Just the opposite effect would be predicted from swimming capacity alone ($S(D)$, Figs. 3*d*–3*f* and 4*d*–4*f*). Indeed, at 6 h, the proportion of suckers expected to successfully pass the obstacle exceeds the maximum distance of ascent on any single attempt at distances >13 m, >5 m, and from 2.5 to 9 m (against 2, 3, and 4 $m \cdot s^{-1}$, respectively). This is surprising, given that <80% of the fish are expected to even stage attempts under these conditions. Thus, the benefit of staging multiple attempts helped to mitigate for those fish that failed to stage any attempts.

Because of their lower entry and repeat rates, passage success of walleye did not accrue the same benefits as for suckers, rarely exceeding $S_a(D)$. This was particularly true under the 2 and 4 $m \cdot s^{-1}$ conditions, where very few walleye were predicted to stage more than two attempts. This is reflected in the censoring data as well (Tables 3 and 4): more than half of the available suckers staged at least three attempts, whereas only 23% of walleye did. Thus, hydraulic conditions clearly do limit passage success, with attraction serving a role fully as important as swimming performance in determining the outcome.

Discussion

This study quantifies the effects of both attempt rate and swimming capacity on passage success. This represents a departure from most current practices, which have focused exclusively on capacity (Bainbridge 1960; Peake et al. 1997, 2000). Recognizing the limitations of current practices, Bunt (2001) and Bunt et al. (1999), reported percentages of both attraction and capacity. This study differs from their approach, however, in three important ways: attraction is measured as a function of time, swimming performance is quantified as a function of ascent distance on successive attempts, and the combined effect of attraction and swimming capacity on overall passage success is explained. Elsewhere (Castro-Santos and Haro 2003), we have pointed out the limitations of recording event endpoints as percentages, when they in fact represent an instantaneous measure of a continuous, time-dependent process. This study further illustrates this point.

Effects of temperature, length, and holding time

Because the intent of this paper is to demonstrate the effects of repeat attempts on passage success, I have omitted many variables (e.g., sex, date, effort expended on previous attempts, recovery times, etc.) that might influence swimming performance and motivation. While trying to keep these models as parsimonious as possible, effects of temperature and length on swimming performance are so well established in the literature (Beamish 1978; Videler 1993) that I felt compelled to include them as potential covariates. Likewise, the potential effects of holding times on performance justified the inclusion of this effect. Comparison of the first hour's results here with those of Haro et al. (2004) helps to illustrate the interplay between attempt time and swimming capacity on passage success.

Among suckers, temperature, length, and holding time had little effect on attempt rate or distance of ascent during the first hour, consistent with the findings of Haro et al. (2004). Effects of these variables were present among walleye, however. Greater lengths were associated with both increased attempt rate and distance of ascent. Both of these factors should lead to increased D_{max}, which was the case (Haro et al. 2004). The only effect of temperature, however, was to increase the rate of the second attempt, with no affect on D_{max} on any single attempt. Still, D_{max} was positively correlated with temperature over this time period, suggesting that the increased attempt rate was responsible rather than any increase in capacity. Similarly, walleye that were held for longer periods had reduced D_{max} on each of the first three attempts. One might reasonably have expected this to produce a strong and significant effect on the combined data, but it did not. This follows directly from the increased attempt rate among walleye that were held for longer periods, counteracting the D_{max} effect.

Concerns raised by Haro et al. (2004) that our 1-h trials may have selected for more motivated, and therefore better-performing, individuals were not borne out in this study. Distance of ascent on the first attempt was similar among fish, whether they entered immediately or after several hours. No effect was present among suckers, and although significance was approached among walleye, the magnitude of the effect was trivial. Such an effect may have been present among the other species, but data were available for these tests only among suckers and walleye. It is interesting to note that although we ran all of our trials during the daytime, suckers and walleye typically migrate at night; it may be that the low rates of entry observed for these species had more to do with behavioral proclivities than physiological capacity. The relationship between motivation, behavior, and capacity is an interesting and potentially very important subject, one deserving of further study.

The results of this study also support the observations by Haro et al. (2004) and Castro-Santos et al. (2000) that these fish did not appear to be swimming to physiological exhaustion. Attempt rates increased after the initial attempt; just the opposite would be expected from fatigued fish. Similarly, the consistent D_{max} values among sucker suggests no cumulative effects from having staged previous attempts.

The inconsistent effects of length and temperature described in this study were surprising, given the wealth of data describing correlations between swimming performance and both of these variables. This is particularly true of the D_{max} models, where only the positive length effect among walleye matched expectations. Reproductive stage and status may explain the weakness of both effects. Females of both species are longer than males (Eschmeyer 1950; Quinn 1982): if males are more motivated swimmers than females, or if the egg burden limits swimming performance of females (Reidy et al. 2000), then this could confound the length effect among suckers. Among walleye, the largest individuals were excluded from our collections. Assuming that we had fewer females as a result (we were unable to consistently determine the sex of walleye), the presence of a length effect

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among walleye would be consistent with this pattern. Alternatively, anaerobic physiology may act to limit the performance benefits generally associated with large size. Goolish (1991) found that, owing to the scaling of power requirements and the allometry of anaerobic metabolism, burst-swimming capacity may actually decrease with size in some cases.

The only important effect of temperature for either species was to increase the rate at which fish staged their first attempts. This suggests some increase in motivation associated with greater temperatures. The effect was absent in later attempts, however. This is consistent with findings that suggest that the rate of recovery from anaerobic activity is largely independent of temperature (Brett 1964; Franklin et al. 1996; Schreer et al. 2001). Nevertheless, it is unclear why the increased motivation observed on the first attempt was not perpetuated in later attempts. Perhaps the initial delay reflected an ephemeral reluctance to enter an unfamiliar, high-velocity environment that was mitigated for by increasing temperatures. Once this reluctance was overcome, attempt rates increased, and temperature may have become unimportant.

The lack of a strong temperature effect on D_{max} (even negative in some cases) may reflect the presence of an underlying thermal optimum. Trials run later in the season (when temperatures were warmer) may have occurred near or past the end of the spawning period (Quinn 1982; Hamel et al. 1997), when motivation, and perhaps even swimming capacity, may have been declining.

Both of these factors underscore the importance of ecological and life history considerations when conducting performance studies. Studies should be done during periods and under conditions that are relevant to the animals in their native habitat, and temperature effects on metabolic processes and critical swim speeds (e.g., Brett and Glass 1973) may not be the most important determinants of swimming capacity, particularly at high speeds.

Hydraulic effects

Owing to the intrinsic properties of open-channel flow, we were unable to achieve the desired flow velocities using a constant depth of water in the flume. This means that flow velocity and discharge, while not perfectly orthogonal, were not directly correlated. Because both parameters can reasonably be expected to influence attempt rate (velocity because of its implications for performance and discharge because of its effects on the hydraulics of the staging area), both were included as potential factors in determining the adjusted Akaike's information criterion best model. The fact that each velocity was run at only one depth remains a weakness in our design, and the resulting predictions of hydraulic effects on attraction should be viewed as preliminary and subject to verification; further testing will be required to establish a rigorous relationship.

Within the confines of our design, the data do suggest separate but related roles of flow velocity and discharge. For both species, time to the first attempt was greatest under the 2.5 $m \cdot s^{-1}$ condition. Discharge was least under this condition, but it cannot be determined from our data whether the low attempt rates resulted from the low discharge or the shallow depth of flow (Haro et al. 2004).

Hydraulic effects were uneven in subsequent attempts, however. This was most noticeable among walleye, where a substantial proportion of the population was expected to stage a third attempt only under the 3 $m \cdot s^{-1}$ condition. Among suckers, the 3 $m \cdot s^{-1}$ condition was also most conducive to multiple attempts, owing to the greater rate of the second attempt. Variation in predicted attempt times as a result of the hydraulic conditions caused the models to predict superior passage through short distances against higher velocities, especially among walleye.

Readers should bear in mind that, although the models presented here have obvious potential for field applications, managers should use caution when interpreting these data. The hydraulic conditions in our flume mimicked only a small portion of the conditions that fish actually find in nature (Haro et al. 2004), and the staging area was entirely artificial. Thus, even where the D_{max} data may have broader applicability, the attempt rates observed here might not be representative of what one might expect to find in a field situation. Nevertheless, the effect of the various hydraulic conditions on attempt rate may serve as the basis for further study.

Effect of multiple attempts

The approach to calculation of D_{max} applied here differs from that used in Haro et al. (2004): here, I calculate separate models for each attempt, whereas in the previous paper, we calculated the overall D_{max} for each individual, regardless of how many attempts they staged. For this reason, readers comparing fig. 5 in Haro et al. (2004) and Figs. 3 and 4 here will note that on no single attempt do we expect fish to travel as far as they do when compared with the total data, even after only 1 h. This, in fact, is the premise for the model in eq. 10 and is the direct result of staging multiple attempts.

The methods used by Haro et al. (2004) do have some advantages, however. Their approach uses direct observation to estimate the likelihood of successful passage over a given distance by those fish that stage attempts. This requires fewer assumptions and many fewer parameters and modeling steps than the methods described here. As such, the models are likely to be more robust within the bounds of the modeled trial duration, but estimates of D_{max} will be conservative relative to what might be expected when these bounds are removed. Future studies that use trials of meaningful duration could use their method with minimal risk; but managers should bear in mind that the models may not realistically reflect changes in performance over time and, of course, must adjust for the proportion of the population that is expected to stage attempts.

The passage predictions ($P(D,T)$) presented here are superior to those of Haro et al. (2004) in that they expressly account for the proportion of fish that stage attempts as well as the number of attempts staged. To the extent that the staging area and flume entrance conditions differ from those found in natural or field environments, however, the broader applicability of these predictions is limited. Instead, these predictions should serve as an illustration of the importance of attraction and motivation to passage success, and the models should serve as templates for quantifying this effect in both field and laboratory situations.

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These methods are more likely to be useful where it is not feasible to run trials for extended periods or where delay is a concern. Using this approach, managers can estimate rates of successive attempts, even (modestly) extrapolating beyond the observed attempt number and trial duration. Because attraction is explicitly quantified as a time-based function, effects of varying rates of entry and reentry are readily incorporated into the models, and population-level effects of delay could be more accurately predicted. Also, because attraction and capacity are treated separately, identification of measures to improve either component is possible, and the effects of these improvements on passage performance can be estimated.

The results presented here demonstrate the importance of this approach over 6 h (the limits of our experimental protocol), but the technique has much broader application and relevance for field situations and for future studies where fish can be monitored for even longer periods of time. Such studies should select time periods that are appropriate for the population, species, and situation in question. Among fish with brief migratory periods or with strong diurnal constraints, 6 h may be an appropriate measure of acceptable delay. For fish that spend longer periods in fresh water, the period may be extended for days or weeks. Energetic constraints should also be considered: velocity barriers that require fish to swim in prolonged or sprint mode (powered by anaerobic metabolism) will be more costly than those that can be traversed in sustained mode (powered by aerobic metabolism; Webb 1975). The energetic costs of staging multiple attempts will therefore scale very differently depending on the swimming capacities of the individual fish. In each case, the expected costs and consequences of delay should be a factor in determining the biologically relevant scope of time allowed for fish to stage attempts through the velocity barrier.

In field applications, these methods must be modified to account for the fact that not all fish arrive at the staging area simultaneously. Thus, eqs. 6 and 7 can be generalized to all attempts, removing the restriction $a \geq 2$ and replacing the condition $f_1^*(i) = f_1(i)$ with $f_0^*(i)$ = the probability density function of the arrival times of fish to the staging area. If appropriate data are available, e.g., from radiotelemetry, fish that leave the staging area without passing can be included in the data set, with censoring time set to their time of departure.

The idea that fish are capable of staging multiple attempts, indeed required to do so in many instances, has been broadly overlooked in the fish passage literature (Farrell et al. 1998). Instead, predictions of passage success have focused on a deterministic view, derived from swimming speed – fatigue time models that identify theoretical maxima (e.g., Peake et al. 1997). These models ignore the fact of behavioral plasticity; the time at which fish abandon swimming efforts (generally assumed to indicate fatigue when the fish are coerced into swimming) is assumed to be a fixed function of swimming speed. This assumption is not always justified, and fish may elect to abandon attempts before fatiguing to maintain energy reserves for future attempts (Castro-Santos et al. 2000). Further, such models tacitly assume that fish swim at their optimal speeds and ignore the costs associated with deviating from these optima (Castro-Santos 2002).

These data demonstrate the importance of attempt rate and hence the importance of providing conditions that maximize attraction. Thus, passage must be thought of as a joint probability based on both attraction and capacity. Further, this probability will increase over time as fish stage multiple attempts. Conversely, fishways comprising multiple pools or chutes *require* fish to stage multiple attempts, and passage likelihood declines exponentially as $P(T,D)^w$, where w is the number of weirs, or steps, and consequently the minimum number of attempts required to pass.

Currents that challenge fishes' swimming capacity and those that fail to motivate passage attempts have important implications with regard to fitness and recruitment. Even subtle differences in the underlying performance structure of a population may affect passage success, ultimately leading to fragmentation of populations, with the associated loss of genetic diversity. Such loss is not necessarily harmful to populations: these are the very processes that lead to anadromous migrations in the first place, and the decision whether to expend energy on multiple efforts or to choose alternative spawning sites represents a trade-off that helps define a species' life history (Loesch 1987).

Still, fish passage structures that are constructed in such a way as to stimulate entry but that deny passage to large proportions of a population constitute artificial filters that have little relevance to the natural history and ecology of their target species. Passage may mimic natural selective processes but should do so in a way that is consistent with the stewardship objectives of conservation and mitigation.

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