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Abstract: The ability to traverse barriers of high-velocity flow limits the distributions of many diadromous and other migratory fish species, yet very few data exist that quantify this ability. We provide a detailed analysis of sprint swimming ability of six migratory fish species (American shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), striped bass (*Morone saxatilis*), walleye (*Stizostedion vitreum*), and white sucker (*Catostomus commersoni*)) against controlled water velocities of 1.5–4.5 m·s⁻¹ in a large, open-channel flume. Performance was strictly voluntary: no coercive incentives were used to motivate fish to sprint. We used these data to generate models of maximum distance traversed, taking into account effects of flow velocity, body length, and temperature. Although the maximum distance traversed decreased with increasing velocity, the magnitude of this effect varied among species. Other covariate effects were likewise variable, with divergent effects of temperature and nonuniform length effects. These effects do not account for all of the variability in performance, however, and behavioral traits may account for observed interspecific differences. We propose the models be used to develop criteria for fish passage structures, culverts, and breached dams.

Résumé : Bien que la capacité de traverser des barrières de débits très rapides limite la répartition de plusieurs poissons diadromes et autres poissons migrateurs, il existe peu de données quantitatives sur le sujet. Nous présentons une analyse détaillée de la capacité de nage en sprint de six espèces de poissons migrateurs (l'alose savoureuse *Alosa sapidissima*, le gaspareau *Alosa pseudoharengus*, l'alose d'été *Alosa aestivalis*, le bar rayé *Morone saxatilis*, le doré *Stizostedion vitreum* et le meunier noir *Catostomus commersoni*) dans des courants de vitesse contrôlée de 1,5–4,5 m·s⁻¹ dans une grande canalisation ouverte. La performance y était totalement volontaire; il n'y avait pas de stimulation coercitive pour pousser les poissons à la nage rapide. Ces données nous ont servi à mettre au point des modèles de la distance maximale traversée, en fonction des effets de la vitesse du courant, de la longueur du corps et de la température. Bien que la distance maximale traversée diminue avec l'augmentation de la vitesse du courant, l'importance de cet effet varie d'une espèce à l'autre. Les autres effets qui sont en covariation avec les premiers, comme les effets de la température et ceux des longueurs non uniformes, sont aussi variables. Ces effets n'expliquent pas, cependant, toute la variabilité de la performance; les caractéristiques comportementales expliquent peut-être les différences observées entre les espèces. Nous suggérons que nos modèles soient utilisés pour mettre au point des critères pour l,aménagement de passes migratoires de poissons, de canaux et de barrages comportant des brèches.

[Traduit par la Rédaction]

Introduction

Zones of high-velocity flow characterize many natural rivers and are often unavoidable, or even intentional, features of fishways, dams, and culverts (Clay 1995; Haro et al. 1998). These zones may constitute velocity barriers that exceed the physiological or behavioral capabilities of fishes and so define the upstream boundaries of their populations. The swimming performance of diadromous and other riverine fishes limits their ability to traverse these velocity barriers and is therefore central to their life history.

Many studies describe swimming endurance at sustained and prolonged speeds (for reviews, see Beamish 1978; Videler 1993), but few provide empirical measures of sprinting performance (throughout this text, we follow Webb's (1975) definition of sprinting as steady-state burst swimming). Of those studies that do measure sprinting performance (Beamish 1978), most are largely anecdotal, based on small sample sizes and collected under poorly controlled conditions. Even less common are studies that allow fish to volitionally ascend large-scale experimental open-channel flumes that more closely approximate natural conditions, allowing fish to express normal upstream migratory behaviors (for examples, see Dow 1962; Weaver 1963; Colavecchia et al. 1998).

Brett et al. (1958), Bainbridge (1958), and Beamish (1978) recognized the relevance of this information to improved fish passage and fishway design, but only Dow (1962) and Weaver (1963, 1965) quantified performance in units of the

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distance that fish were able to negotiate against a velocity challenge, the appropriate units for most applications. Weaver's (1963, 1965) work is exceptional, describing various aspects of swimming performance of thousands of individual salmon (*Oncorhynchus* spp.) and American shad (*Alosa sapidissima*) that entered his structure volitionally, with no handling and minimal human interference. Weaver's (1963, 1965) analyses were limited, however, to describing species-specific performance during fixed-velocity tests and gave only cursory treatment to covariates such as length and temperature. Moreover, hydraulic conditions varied down the length of his flume apparatus, complicating interpretation of his results.

Although the techniques used by Dow (1962) and Weaver (1963, 1965) provide close approximations to conditions fishes encounter in nature, most studies on swimming performance have followed the approach of Brett (1964) in which fishes swim against carefully controlled flow within enclosed chambers. None of these studies has matched the scale of Weaver's (1963, 1965) work, however, and the ability of fish to traverse velocity barriers has remained poorly quantified.

The lack of information on sprinting performance is problematic for the design of structures for passing fish around dams and other obstacles. Most fishway manuals (e.g., Powers et al. 1985; Bell 1991; Clay 1995) use figures presented by Beach (1984) to estimate maximum swimming capacities. Beach's (1984) models were derived from the swimming energetics of sockeye salmon (*Oncorhynchus nerka*) (Brett 1965), in vitro muscle kinematics data (Wardle 1975, 1980), and numerous assumptions, including homogeneity of glycogen stores across populations and taxa. Clearly, these models do not support the breadth of their current application. Moreover, they do not predict traversable distance through velocity barriers, only maximum swim speeds and expected endurance. If maximum sprinting ability is underestimated (and this may often be the case (Videler and Wardle 1991)), then some fish passage designs could be simplified, facilitating mitigation efforts and making available much-needed habitat.

The value of low-cost mitigation efforts is not trivial. A recent inventory identifies more than 77 000 dams greater than 8 m throughout the United States, and smaller structures that also impede passage of anadromous and riverine fishes are even more numerous (US Army Corps of Engineers 2001). Similar densities of riverine obstructions can be found throughout the developed world (e.g., several references in Jungwirth et al. 1998). Of the lower-head structures, many are nonfunctional or in disrepair and could be easily breached to form routes of passage, provided that fishes are capable of traversing the resulting velocity barriers (Odeh 1999).

Because of the lack of detailed information on sprinting performance, however, engineers and managers often are unable to assess whether species of concern will be able to pass such simple structures as breaches, culverts, etc. Existing manuals for fish passage engineers provide scant estimates of instantaneous maximum sprint speeds and no estimates of sprint distances through high-velocity flow (e.g., Bell 1991; Clay 1995). The need for reliable data on volitional fish swimming performance is increasing as fish passage issues and concerns expand to include riverine species that are not anadromous but that may regularly migrate considerable distances throughout a watershed. Relatively little is known about swimming performance of these species.

In this study, we provide a detailed description and analysis of high-speed swimming performance (i.e., prolonged and sprint modes) by six species of anadromous, amphidromous, and potamodromous fishes commonly found in rivers of eastern North America. We present species-specific models of maximum ascent distances of fish swimming against steady, open-channel flow velocity conditions ranging from 1.5 to 4.5 $m \cdot s^{-1}$. These data will help identify distributional limits and can also be used to design and evaluate new and existing passage structures or, conversely, to create velocity barriers for nuisance species.
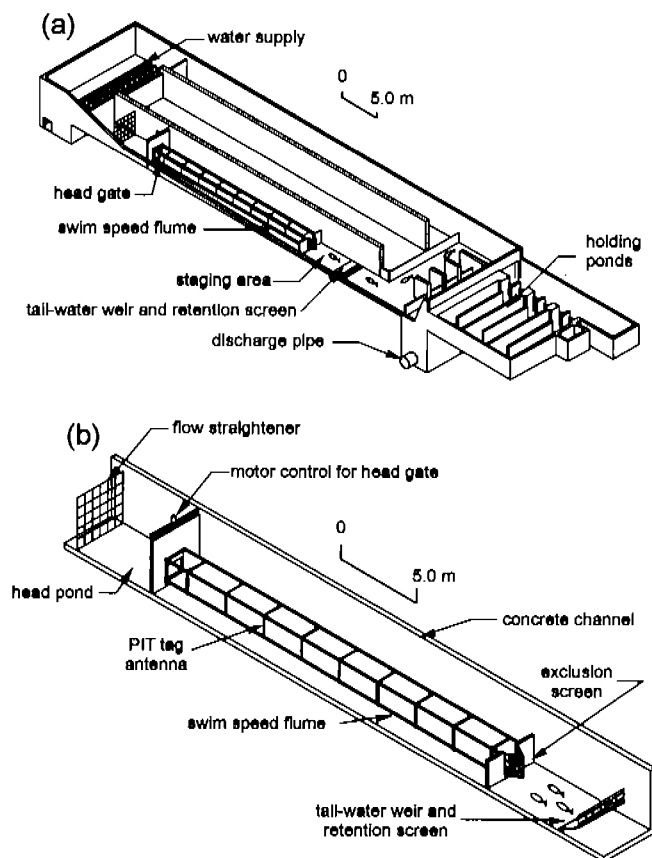
Methods

Flume apparatus

To simulate conditions found at natural and anthropogenic velocity barriers, we built a large open-channel flume (1 m width × 1 m depth × 24 m length, zero slope) in the S.O. Conte Anadromous Fish Research Laboratory fish passage complex (Fig. 1) located at Turners Falls, Massachusetts, next to the Connecticut River. The flume was constructed of a wood and steel frame, with the floor and one wall made of plywood. The opposite wall was made of 2.5-cm-thick clear acrylic sheet. Mirrors installed at a 45° angle to the transparent wall permitted simultaneous side and top views to video cameras arrayed above the flume. The plywood wall and floor were covered with white retroreflective material (3M Corp.) (Scotchlite 6780) on which reference marks (black crosses 10 cm × 10 cm) were painted at 0.5-m (horizontal and vertical) intervals. To prevent the formation of organized eddies (macroturbulence), the floor and walls were made smooth, straight, and level. To ensure uniform lighting and to block sunlight from the skylights of the fish passage complex, a black tarp was laid out on a grating 4.5 m above the flume, covering its full length, and the flume was illuminated with eight 90-W halogen flood lamps.

Ambient river water was supplied to the flume from an adjacent hydroelectric power canal fed by the Connecticut River. Water entered the fish passage complex through a 1.8-m-diameter pipe into an upstream diffusion chamber to the test flume head pond. Water from the head pond entered the test flume through an electronically actuated sliding gate (head gate) and exited the flume into a downstream staging area (8 m long × 3 m wide × 0.60–1.35 m deep). Mean velocities were slower in the staging area because of its greater width and depth, the latter being controlled by a variable-height weir (tail-water weir) at the downstream end. This weir was fitted with a screen to retain fish in the staging area while allowing water to pass through. After passing over the tail-water weir, water was returned to the river downstream of the fish passage complex through a 1.4-m-diameter pipe. Water velocities within the flume were controlled by the head-pond level, the head-gate opening, and the tail-water weir level.

We used a 1:6 scale physical model of the flume to establish experimental hydraulic test conditions. The model was constructed to be geometrically, kinematically, and dynami-

Fig. 1. Fish passage complex at the S.O. Conte Anadromous Fish Research Center. (*a*) Installation of swimming speed flume showing holding ponds and route of introduction for test fish; (*b*) detail of swimming speed flume showing flow control mechanism and arrangement of PIT tag antennas.

At 1.5 m·s^{-1}, flow in the test flume and staging area was subcritical and was set at a depth of 96 cm. At higher velocities, however, this depth of flow created excessive velocity and turbulence in the staging area. Reducing the depth lowered the total flow within the flume, thus maintaining a quiescent staging area. Velocity was sufficient under the 3.5 and 4.5 m·s^{-1} conditions to maintain supercritical flow down the length of the flume at about 45 cm depth. At 2.5 m·s^{-1}, however, flow was unstable and became critical midway down the flume at this depth, so depth was reduced to 26 cm at this velocity to maintain the supercritical condition. For each of these supercritical conditions, tail-water depth was greater than the depth of flow within the flume and was set such that a hydraulic jump was maintained within the flume 0.5–1.0 m from the downstream entrance.

Detailed velocity measurements were made in the model to describe the flow field through which fish would swim. A two-directional electromagnetic velocity meter (Marsh-McBirney model 523) with a 13-mm probe was used to measure model velocities; actual velocities were then measured throughout representative cross sections of the full-scale flume on a 5-cm grid using a propeller meter (Ott model 1-113040). Two-dimensional flow velocity profiles were generated for 1.5, 2.5, and 3.5 m·s^{-1} trial conditions, respectively (Fig. 2). We were unable to collect similar data for the 4.5 m·s^{-1} condition because of excessive forces on the velocity probe; however, hydraulic principles dictate that the velocity profile will be similar to that of the 3.5 m·s^{-1} condition (Chow 1959). To characterize the turbulence of the flow, three-dimensional velocities were measured in the model using a 3D SonTek acoustic doppler anemometer. Measurements were made at mid-depth, both at the center and at distances equivalent to 12.7 cm from the wall of the full-scale flume and 12 m from its downstream end.

cally similar to the full-scale flume, ensuring identical hydraulic characteristics (Chow 1959). The model was used to identify the gate settings and water surface elevations in the head pond, flume, and staging area that characterized four test velocities (U_f; nominally 1.5, 2.5, 3.5, and 4.5 m·s^{-1}) and to quantify the response of flow velocity within the flume to variations in these conditions.

Open-channel flow is characterized as super- or subcritical, depending on whether velocities are dominated by inertial or gravitational forces, respectively. The Froude number, F, which equals the ratio of these two forces, identifies the state of flow:

$$(1) \quad F = \frac{U_f}{\sqrt{gL}}$$

where g is gravitational acceleration and L is the depth of flow in a channel with a rectangular cross section (Chow 1959). Flow is supercritical at $F > 1$ and subcritical at $F < 1$. At $F = 1$, the flow is critical, and a standing gravity wave (or hydraulic jump) may be propagated up the length of the flume (e.g., Weaver 1963). These unsteady flow conditions were unacceptable for this study, so depth of flow was varied to maintain either super- or sub-critical conditions over the full length of the flume.

Data collection

We used an automated passive integrated transponder (PIT) system to record the position of fish swimming up the length of the flume. Fish were externally tagged without anaesthesia by bonding PIT tags (32 mm in length, 3.9 mm in diameter) to a small fishhook, which was inserted into the cartilage at the base of the dorsal fin (second dorsal in the case of percomorphs; see Castro-Santos et al. (1996) for a description of the PIT system, tagging method, and its application). Ten PIT antennas were mounted along the length of the flume at 2.5-m intervals (from 0.5 to 23.0 m); of these, eight were in place for the first half of the study, and two more were added in May 1998. Tags were detected within 0.5 m of the plane of each antenna loop. A control computer logged tag detection data (tag code, date, time to the nearest 0.1 s, and antenna location) from PIT readers.

Fish were collected and tested during the period from April through July 1997–1999. Six species of migratory fishes were captured from traps at nearby fishways (American shad (*Alosa sapidissima*), striped bass (*Morone saxatilis*), and white sucker (*Catostomus commersoni*)) and coastal streams (alewife (*Alosa pseudoharengus*) from the Herring River, Bourne, Massachusetts, and blueback herring (*Alosa aestivalis*) from the Charles River, Watertown, Massachusetts) or electrofished (blueback herring, striped bass, walleye (*Stizostedion vitreum*), and white sucker from the

Fig. 2. Cross-sectional velocity profiles ($m \cdot s^{-1}$) of swimming speed flume under nominal (*a*) 1.5 $m \cdot s^{-1}$, (*b*) 2.5 $m \cdot s^{-1}$, (*c*) and 3.5 $m \cdot s^{-1}$ mean water velocity conditions 2 m upstream of the flume entrance.
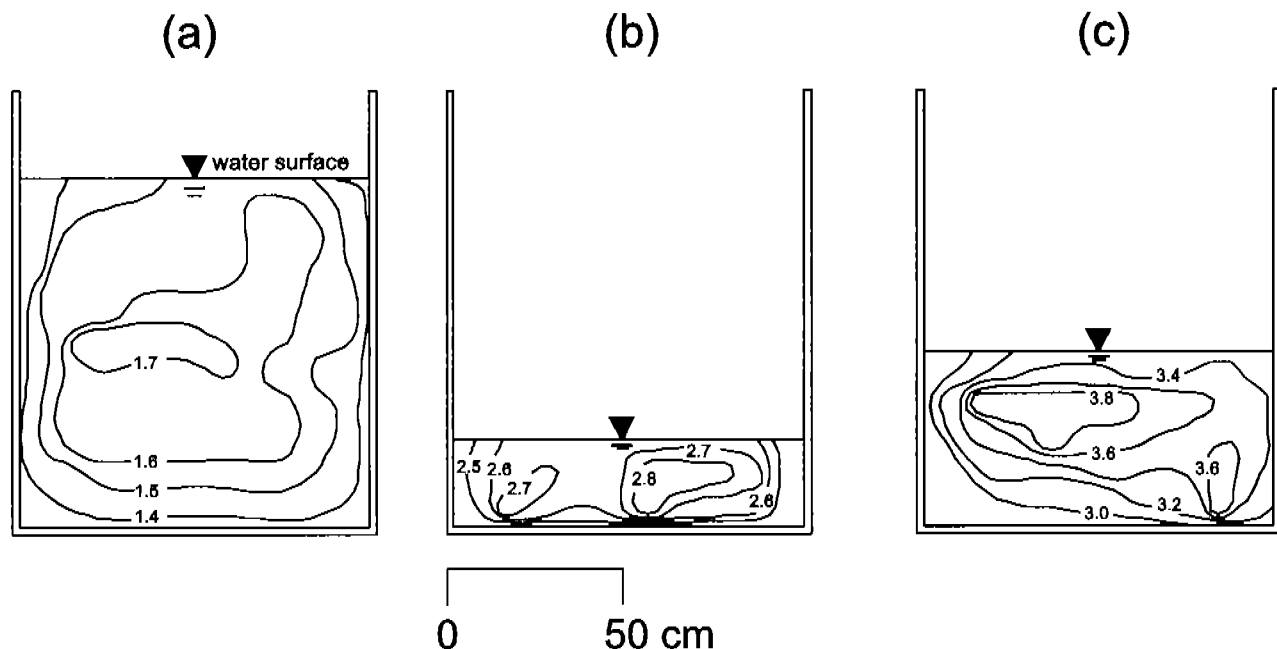
Connecticut River) on dates corresponding to the periods of upstream migration for each species. Fish were transported to the flume facility in one of two truck-mounted tanks (1000 and 4000 L capacity). After transport, fish were measured (fork length), sexed, and fitted with a PIT tag (Castro-Santos et al. 1996); we assume that this very small tag had no substantial effect on swimming performance. Fish were transferred into open, flow-through holding ponds (Burrows and Chenoweth 1970) that were hydraulically continuous with the fish passage complex and held 24 h before testing. Fish were usually tested within 24 h of capture and were released after each trial. In some cases, fish were held longer before testing, but never for more than 7 days.

At the start of a trial, groups of 20–30 fish were seined from the holding ponds into the staging area, and the tailwater weir and screen were raised to confine the fish to this area. Fish were initially prevented from entering the flume by an exclusion screen. Once the water velocity in the flume was brought to the desired level, the exclusion screen was opened and fish were allowed to ascend the flume of their own volition. Only those fish that entered the flume during a given trial were included in our analyses. Although duration of runs ranged from 1 to 6 h, we use only the first hour's data from each trial to maintain consistency in our analyses.

Light level in the flume was 2.5 $\mu W \cdot m^{-2}$ for all species except walleye and white sucker. To encourage attempts by these species, which typically migrate at night, we darkened the flume to 0.03 $\mu W \cdot m^{-2}$. Mean hourly water temperatures were logged using a data logger (Licor LI-1000) and thermocouple probe (Omega T-type). Average temperatures for times corresponding to each trial were included as a covariate in the analyses.

Data analysis

Because the PIT antennas effectively graduated the flume into 2.5-m intervals, we were able to estimate maximum dis-

tance of ascent (D_{max}) by selecting the location farthest upstream that was logged for each fish during the trial. This is an incremental measure and provides a conservative bias to the D_{max} estimate: the reader might detect a fish as far as 0.5 m below an antenna, but the same fish could also be as much as 2 m above that antenna without being logged at the next location.

The configuration of the PIT antennas imposed restrictions on the methods used to develop predictive models. Since PIT antennas were installed only for the first 18 m of the flume during the first half of the study, and the first 23 m thereafter, D_{max} values do not reflect the true maximum ability of the fish, but rather the maximum that our apparatus was able to measure — the actual performance capacities may have been higher. This condition, in which the magnitude of a measured variable exceeds the ability of an instrument to measure it, constitutes censoring (Lee 1992). Ordinary least-squares regression techniques are unable to accommodate censoring, so we applied the maximum likelihood regression techniques commonly used in survival analysis (Allison 1995; Castro-Santos 2002; Castro-Santos and Haro 2003) to develop our predictive models. For the reasons just described, as well as to negate any effect of fish avoiding the upstream end of the flume, fish attaining D_{max} values of 18 m or greater were included in the analyses as censored observations.

The regression models used here follow the form

$$(2) \qquad (\ln D_{max})_p = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k + w_p$$

where $(\ln D_{max})_p$ is the *p*th quantile of the natural log of D_{max}, βs are coefficients, x_is are the *k*-covariates, and w_p is the *p*th quantile of the baseline distribution. One advantage of this regression approach is that it does not require the error term to be normally distributed. For this reason, it takes on a more complex structure than that of ordinary least-

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squares regression, with scale (σ) and shape (δ) parameters that influence the value of w_p.

We determined which distribution best described our data by first including all three covariates: velocity, temperature, and body length. We then generated separate models based on exponential, lognormal, Weibull, log-logistic, and generalized gamma distributions (Lawless 1982) as well as their nonlogged counterparts. Next, we ranked these models using Akaike's information criterion and selected the one with the best fit (Allison 1995; Burnham and Anderson 1998). Finally, we refined the models by removing covariates in a stepwise fashion, retaining only those with P values less than 0.15.

Results

Flume hydraulics and tolerances

Mean velocities differed consistently from the projected nominal velocities (Table 1). Test velocities varied little, with most standard deviations less than 0.1 m·s^{-1}. This variability arose primarily as a result of fluctuating head-pond levels in the power canal.

Flow is either laminar or turbulent depending on its Reynolds number, R. This is the ratio of inertial to viscous forces:

$$(3) \qquad R = \frac{U_f d}{v}$$

where d is a characteristic length (in this case, the cross-sectional area divided by the length of its wetted perimeter) and v is the kinematic viscosity of the working fluid. Open-channel flow becomes turbulent at $R > 2500$ (Chow 1959). Under all of the velocity and depth conditions used here (Table 1), $R > 300\,000$, well within the turbulent regime.

Turbulence is typically quantified by the standard deviation of the velocity vector (u') or alternatively by its coefficient of variation (CV) or relative turbulence intensity:

$$(4) \qquad CV = u'/\overline{U_f}$$

where $\overline{U_f}$ is the mean channel velocity. In geometrically similar channels, turbulence scales directly with velocity, regardless of Froude and Reynolds numbers, and so its CV is constant (Nezu and Nakagawa 1993). The acoustic doppler anemometer data indicated that turbulence intensity within the flume was 0.11–0.17, which is characteristic of open-channel flow over smooth surfaces. The turbulence was disorganized, however, consisting of random fluctuations and microeddies with no evident periodicity (Fig. 3) (Nezu and Nakagawa 1993). The measured level of turbulence in our flume was representative of flows through long open channels (i.e., culverts, dam notches) but less than that within technical pool and weir and Denil-type fishways.

Velocities were lowest near the walls and floor of the flume (Fig. 2) and were within 10% of the mean cross-sectional velocity throughout its length. However, assertions that fish will consistently seek out zones of lowest velocity (e.g., Beamish 1978; Pavlov et al. 2000) were not borne out by our observations. Although some species (most notably white suckers) actively selected these low-velocity zones at the 1.5 and 2.5 m·s^{-1} conditions, all species swam near the cross-sectional center of the flume at the higher velocities (Castro-Santos 2002).

The presence of the hydraulic jump 0.5–1.0 m from the flume entrance under the supercritical flow conditions may have provided some advantage to the fish, particularly at higher velocity flow, allowing them to ascend the first half metre with greater ease than they would have had the jump been outside the flume. The jump was kept within the flume to reduce the strength of the jet issuing into the staging area and to help encourage fish to enter the flume. Researchers seeking to replicate our results should maintain similar conditions; those seeking to predict ascent distances at field sites should measure from 1.0 m below the hydraulic jump in conducting their calculations.

Swimming capacity

Because impingement of smaller species (alewife, blueback herring, and walleye) on the tail-water weir screen occurred in initial 4.5 m·s^{-1} trials, and because performance was poor under the 3.5 m·s^{-1} condition (Fig. 4), these smaller species were not run at 4.5 m·s^{-1}. Percentages of fish entering the flume varied both among species and among velocities within species (Table 1).

Increasing water velocity consistently reduced D_{max} for each species (negative β, Table 2). Coefficients indicate the relative effect of each covariate on log distance of ascent, i.e., each unit increase in covariate results in an increase in distance of $100 \times [1 - \exp(\beta)]$ percent. Thus, although all species showed the expected negative effect of water velocity on D_{max}, the degree of this effect varied widely among species (e.g., 49% decrease in distance per metre per second for walleye versus a 69% decrease for blueback herring).

Body lengths and temperatures (Table 1) represent values typical for active migrants of these species in our region (northeastern United States). Blueback herring and alewife had the smallest size ranges (45 and 55 mm, respectively) followed by American shad and walleye (195 mm each) and white sucker (220 mm). Our walleye sample, however, did not include the largest individuals present in the adult migratory spawning population (this was to accommodate concerns of local fisheries managers). Striped bass, in contrast, showed the greatest size variability of all (735 mm). This is because upstream migration of striped bass includes both juvenile and spawning individuals, so the tested fish of this species are not necessarily mature adults.

Performance improved significantly with length for American shad, blueback herring, striped bass, and walleye. This effect varied over an order of magnitude, being least for American shad and greatest for blueback herring. However, over the range of lengths represented by ±1 SD, the predicted effect on D_{max} was greatest for striped bass (277% increase in D_{max} from small to large individuals) and least for American shad (16% increase), with 60% and 36% increases among blueback herring and walleye, respectively. Note that the narrow scope of sizes of blueback herring means that these data should be viewed with caution.

Trial temperatures reflected ambient river conditions. Alewife experienced the narrowest temperature range (4.7 °C) and white sucker and striped bass the largest (12.4 and 13.6 °C, respectively). Trials of the remaining species had similar temperature ranges (8.3–8.5 °C). These temperature

Table 1. Species characteristics, sample sizes, and hydraulic conditions of tests performed in the swimming flume by nominal water velocity, all years pooled.

Species	N	%	Fork length (mm)	Temperature (°C)	Hydraulics Nominal velocity (m·s⁻¹)	Measured velocity (m·s⁻¹)	Water depth (m)	Q (m³·s⁻¹)
American shad	92	86	421±34 (355–495)	16.8±1.5 (15.3–19.1)	1.5	1.74±0.07	0.96	1.67
	233	68	417±33 (355–495)	18.9±2.1 (13.4–21.6)	2.5	2.69±0.09	0.26	0.70
	285	71	415±36 (325–520)	18.4±2.0 (13.4–21.5)	3.5	3.43±0.09	0.45	1.54
	92	33	416±35 (350–510)	18.2±2.4 (13.3–21.5)	4.5	4.53±0.04	0.46	2.08
Alewife	122	55	235±12 (210–265)	10.2±1.4 (8.5–13.2)	1.5	1.60±0.15	0.96	1.54
	60	30	238±11 (215–265)	10.4±1.4 (8.9–13.0)	2.5	2.60±0.06	0.26	0.68
	40	37	235±11 (215–260)	11.2±1.4 (9.1–13.0)	3.5	3.40±0.03	0.45	1.53
Blueback herring	19	17	229±11 (210–245)	16.7±2.3 (13.2–18.2)	1.5	1.61±0.09	0.96	1.55
	24	18	219±11 (205–245)	16.7±3.4 (13.0–21.4)	2.5	2.69±0.07	0.26	0.70
	38	34	216±11 (200–240)	17.1±2.4 (13.0–20.6)	3.5	3.40±0.13	0.45	1.53
Striped bass	10	33	558±270 (290–970)	18.6±0.0 (18.6)	1.5	1.58±0.05	0.96	1.52
	57	38	430±118 (235–780)	19.9±2.7 (16.3–23.6)	2.5	2.64±0.07	0.26	0.69
	62	33	478±120 (280–760)	19.3±2.8 (10.7–24.3)	3.5	3.40±0.06	0.45	1.53
	48	70	554±162 (285–835)	17.2±1.3 (16.2–21.9)	4.5	4.55±0.09	0.46	2.09
Walleye	13	24	314±45 (240–395)	12.6±2.5 (9.3–14.4)	1.5	1.74±0.11	0.96	1.67
	24	30	315±41 (270–410)	15.7±3.4 (10.0–17.8)	2.5	2.73±0.11	0.26	0.71
	12	22	317±53 (225–415)	10.3±0.7 (9.7–11.1)	3.5	3.34±0.01	0.45	1.50
White sucker	35	65	385±41 (285–505)	11.8±0.9 (10.9–14.4)	1.5	1.75±0.05	0.96	1.68
	35	41	384±29 (305–430)	14.9±3.6 (11.0–18.4)	2.5	2.62±0.05	0.26	0.68
	31	36	392±30 (340–450)	17.6±5.6 (10.7–22.8)	3.5	3.36±0.03	0.45	1.51
	31	49	398±26 (340–450)	15.0±3.6 (10.4–21.5)	4.5	4.51±0.04	0.46	2.07

Note: Sample size (N) is presented as total number of fish entering the flume followed by the percentage that this represents of the total number of fish introduced into the staging area. Lengths, temperatures, and measured velocities are given as means ±1 SD; length and temperature ranges are in parentheses. Q is the total flow within the flume.

ranges should have been sufficient to detect any effect of temperature on performance. This effect, however, was ambiguous. Performance increased with temperature for blueback herring, walleye, alewife, and striped bass (although the effect was nonsignificant for the latter two species) but decreased with temperature among American shad.

Duration of holding times before testing varied because the timing of trials was contingent on availability of fish. Although 89% of fish were tested within 48 h of capture, some collections, most notably among white sucker, were held for as long as 7 days before testing. Inclusion of this factor in the regression models (Table 2) indicated that holding time had no significant effect on D_{max} for any of the species tested ($P > 0.07$ among walleye, $P > 0.42$ for all others). Likewise, collection point and method did not substantially affect D_{max} ($P > 0.19$).

The distributions that best describe the performance data differed among species (Table 2). The gamma distribution provided the best fit to the data for American shad, alewife, striped bass, and walleye; the Weibull distribution best described the blueback herring and white sucker data. The scale (σ) and shape (δ) parameters of the regression models describe the shape of the underlying error distribution. Evaluation of probability plots (SAS Institute Inc. 1999) and Cox–Snell residuals (Allison 1995) suggests that these models provide a reasonable fit to the data.

The purpose of the regression models (Table 2) is not only to identify significant factors influencing swimming perfor-

mance but also to quantify these effects in a way that enables managers and engineers to apply our data to similar hydraulic environments. By setting covariate values to levels representative of specific situations, managers can use these models to predict proportions of populations able to pass barriers under various velocity conditions (Fig. 5). Proportions can be estimated for each model as Weibull

$$(5) \qquad S(D) = \exp\left[-\exp\left(\frac{\omega - \mu}{\sigma}\right)\right]$$

and gamma

$$(6) \qquad S(D) = \frac{\Gamma\left\{\delta^{-2}, \delta^{-2} \exp\left[\delta\left(\frac{\omega - \mu}{\sigma}\right)\right]\right\}}{\Gamma(\delta^{-2})}$$

where the survivorship function $S(D)$ is the proportion of fish successfully passing a velocity barrier of distance D, $\omega = \ln(D)$, σ is the the scale parameter, δ is the the shape parameter, $\Gamma(a)$ and $\Gamma(a,b)$ are the complete

$$(7) \qquad \Gamma(a) = \int_0^\infty D^{a-1} \exp(-D) dD$$

and incomplete

Fig. 3. Time series of three-dimensional water velocity within the flume apparatus at 1.5 m·s⁻¹ nominal velocity 12 m upstream from the flume entrance and 50 cm from the floor at positions (a) near the side wall and (b) at the flume midline. Dashed line, X velocity; solid line, Y velocity; dotted line, Z velocity.
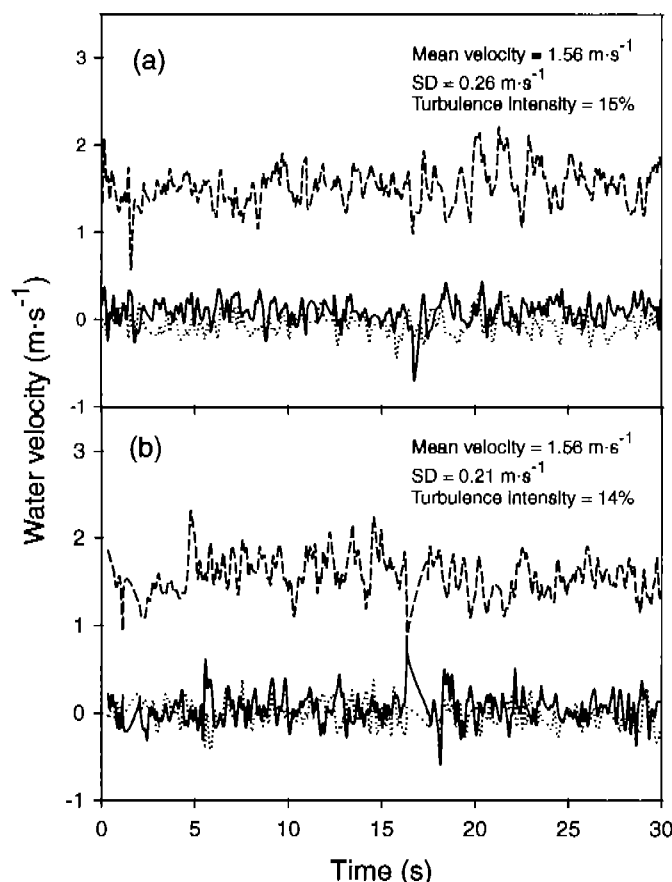
$$(8) \quad \Gamma(a, b) \int_0^\infty D^{a-1} \exp(-D) \mathrm{d}D$$

gamma functions, respectively (Lawless 1982), and $\mu = X\beta$, the vector product of covariate values and their coefficients.

Discussion

Current criteria for the design of fishways and velocity barriers are based on biological data collected under very artificial conditions. Often, these conditions are a necessary feature of controlled laboratory studies. For example, respirometry studies require a uniform flow profile to prevent fish from taking advantage of low-velocity zones. Also, fish are typically required to swim within enclosed tubes, and it is not known how representative the resulting data are of natural situations. Our data represent a departure from and improvement over these methods: fish swam volitionally in open-channel flow, and D_{max} values represent behavioral rather than explicitly physiological fatigue.

Our results can be readily compared with published direct measures of sprint swimming and distance ascended. Weaver (1965) measured a median distance of ascent of 9.4 m for American shad at a flow velocity (U_f) of 3.47 m·s⁻¹ and of 5.94 m at a U_f of 4.02 m·s⁻¹ (temperature 20.8 °C, fish lengths not given). For comparable U_f values, temperatures, and a mean fork length of 417 mm, our model predicts 50% passage at 10.1 and 5.9 m (respectively) for American shad. It is also interesting to note that Weaver's (1965) estimates of sprint swimming performance of adult Pacific salmonids greatly exceeded that of any of our test species. Thus, our data do not conflict with previous observations of swimming performance of salmonids; rather, they point to superior swimming performance measured in open-channel flow. Dow (1962) and Stringham (1924) observed alewives swimming in open-channel flows against velocities of 3–4.5 m·s⁻¹, but their data were poorly quantified. Because we did not directly measure relationships between swimming speed and fatigue time, our data do not readily compare with most published information on these metrics. However, we did observe that many fish swam at speeds of 10–20 body lengths·s⁻¹ (Castro-Santos 2002), which are well above those measured by earlier investigators employing forced swimming techniques (Beamish 1978; Videler 1993).

There are, however, limits to the application of our data. Natural rivers, fishways, and culverts often have roughness elements, weirs, or objects in the flow that impart structure to the turbulence (macroeddies). In some situations, fish are able to use this structure to assist their forward movement (Hinch and Rand 2000; Pavlov et al. 2000) or station holding abilities (Webb 1998; Liao et al. 2003a, 2003b). In other situations, turbulence structures can hinder these same behaviors (Hinch and Rand 1998; Webb 1998). Because our flume was an open channel, with smooth walls and floor, the turbulence was characterized by microeddies (much smaller than the length of a fish), which can be expected to increase the cost of swimming (Enders et al. 2003). Thus, the models presented here should be applied only to those situations that are hydraulically similar to our laboratory conditions. Examples include box culverts, breached dams (with minimal structure in the flow), and zones of supercritical flow within fishways. The models may reasonably provide guidance for situations that deviate moderately from those presented here, such as culverts with corrugated roughening elements. Also, some fishway types (e.g., Alaska steeppass) are characterized by zones of axial flow surrounded by zones that are more turbulent (Odeh 2003). If fish ascend these fishways using the less turbulent zones, then the models presented here may have some relevance. Application to any such situation should be viewed with skepticism, unless information on the behaviors of the fish is available to justify it. Future work should focus on providing detailed descriptions of the behaviors of fish traversing zones of turbulent flow, characterizing the turbulence, and identifying those conditions that act to increase or decrease D_{max}. The methods described here can serve as a model for this work.

Because we constructed the flume to be of such a length as to provide realistic estimates of passage ability past obstacles of relatively short length (e.g., breached low-head dams), some individuals could successfully negotiate the full length of the flume, particularly at the lowest velocities. Other places where high velocities exist, such as culverts, natural obstructions, etc., may extend well beyond the length of our structure, and our data may have limited relevance to such situations. Using the survival analysis approach, our data al-

Fig. 4. Maximum distance of ascent (D_{max}) by species and nominal water velocity (U_f). (*a*) American shad; (*b*) alewife; (*c*) blueback herring; (*d*) striped bass; (*e*) walleye; (*f*) white sucker. Data are presented as median (■), 25–75 percentiles (boxes), and 5–95 percentiles (whiskers). Note that actual water velocities deviated from nominal velocities. Smaller species (alewife, blueback herring, and walleye) were not run against the 4.5 m·s⁻¹ condition. Data are truncated to 18 m for consistency.
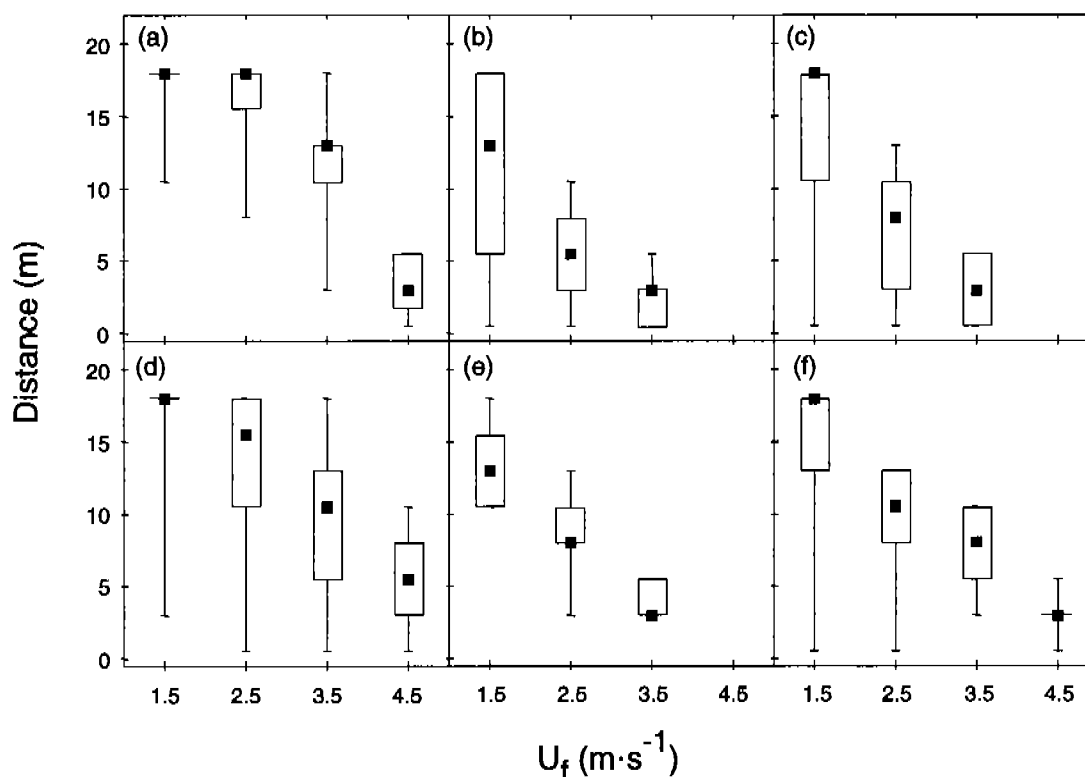
low for modest extrapolation beyond the actual length of the flume and for interpolation between and extrapolation beyond the experimental test velocities (Hosmer and Lemeshow 1999). We recommend limiting such extrapolations to velocities of 0.5 m·s⁻¹ greater or less than the test velocities and total distances of 25 m. These values are similar to those required for interpolation between test conditions and antenna locations; extrapolation beyond these limits is not justified. It should be noted, however, that at lower speeds, fish might shift to prolonged, or even sustained, mode (Webb 1975). These modes are characterized by different swim speed – fatigue time relationships, and estimates of D_{max} based on sprint data can be expected to be low (Castro-Santos 2002).

Keeping in mind that caution should be used when applying these equations to situations much different from our experiments, the following example might help elucidate their application. To estimate the proportion of 50-cm striped bass passing a 10-m-long velocity barrier of 3.0 m·s⁻¹ flow at 18 °C, values from Table 2 are entered into eq. 6 to generate an estimate of 65.9% passage through this barrier. A similar process could be used to describe a population with a range of sizes by breaking it down into more meaningful ranges (e.g., by age class).

Few studies of unsustained (i.e., prolonged and sprint) swimming performance have been conducted on this scale, and this is the first to quantify performance in terms of distance traversed against controlled open-channel velocity barriers with such resolution and large sample sizes and on such a range of taxa. Weaver (1963, 1965) provided empirical

quantile curves for American shad, steelhead (*Oncorhynchus mykiss*), chinook salmon (*Oncorhynchus tshawytscha*), and coho salmon (*Oncorhynchus kisutch*) but did not rigorously evaluate effects of temperature, fish length, or flume hydraulics. Other efforts have focused on timing the movements or recording the success of individuals ascending fishways (Dow 1962) or on angled fish running out a line attached to a tachometer (Gero 1952). All of these approaches have been done under poorly controlled conditions or failed to gather detailed individual information.

As a result of the large sample sizes and individual information that we were able to collect, we could construct models that accurately describe the shapes of probability functions, thus permitting realistic estimates of percentiles of populations capable of passing barriers of specific velocities. This allows for the ability to target for passage of a particular proportion of the population, which is an improvement over use of means and medians that only describe midpoints for proportion of fish passed and do not account for variability (Venditti et al. 2000; Castro-Santos and Haro 2003).

One caveat to consider when applying these data is that we do not include all fish in our analyses, only those that initiated attempts within 1 h. This was done to eliminate the effect of motivation or attraction (quantified in this study by the percentage of fish entering the flume from the staging area), which differed nonlinearly between velocities (Castro-Santos 2002). Thus, our models are conditional on the fish staging attempts and may not be representative of those achievable by fish that made no attempts to ascend the

Table 2. Regression models of covariate effects on log maximum distance of ascent (ln (D_{max})).

Species*	Intercept	Velocity ($m \cdot s^{-1}$)	Temperature (°C)	Fork length (mm)	Scale (σ)	Shape (δ)
American shad (702, 263,–569,gamma)						
β	5.706	–0.983	–0.029	0.0022	0.316	2.070
SE	0.291	0.032	0.010	0.0005	0.022	0.173
$P > \chi^2$	<0.001	<0.001	0.003	<0.001		
Alewife (222, 39, –319, gamma)						
β	4.571	–0.920	—	—	0.513	2.431
SE	0.169	0.074	—	—	0.075	0.412
$P > \chi^2$	<0.001	<0.001	<0.15	>0.15		
Blueback herring (81, 12, –94.9, Weibull)						
β	–0.435	–1.165	0.079	0.0196	0.665	
SE	1.991	0.149	0.029	0.0079	0.070	
$P > \chi^2$	0.827	<0.001	0.006	0.0131		
Striped bass (177, 36, –159, gamma)						
β	3.309	–0.854	0.024	0.0035	0.324	2.175
SE	0.440	0.050	0.015	0.0003	0.039	0.331
$P > \chi^2$	<0.001	<0.001	0.106	<0.001		
Walleye (49, 3, –15.3, Weibull)						
β	2.304	–0.679	0.039	0.0035	0.250	
SE	0.370	0.067	0.010	0.0009	0.031	
$P > \chi^2$	<0.001	<0.001	<0.001	<0.001		
White sucker (136, 24, –155, Weibull)						
β	4.399	–0.720	—	—	0.574	
SE	0.197	0.058	—	—	0.050	
$P > \chi^2$	<0.001	<0.001	>0.15	>0.15		

*Numbers in parentheses represent total N, censored N, log-likelihood, and distribution, respectively.

flume. Among those fish that did stage attempts, these models are conservative because they do not take into account the additional attempts that might have been staged had trial duration been extended for more than 1 h. In contrast, if fish that stage attempts quickly also swim farther (e.g., owing to superior condition or motivation), then the results shown here may be greater than expected for the population as a whole. This issue, as well as the effects of trial duration and attempt rate on estimates of swimming performance, is explored extensively elsewhere (Castro-Santos 2004).

Similarly, managers intending to apply these models should consider the potential effect of fatigue: the rate and distance of successive attempts may be affected by the extent to which fish exhaust their glycogen stores or other metabolic resources. Once depleted, these stores can take hours or even days to recover (Black et al. 1962) and, in some cases, can lead to postexercise mortality (Brobbel et al. 1996; Wilkie et al. 1997; Brick and Cech 2002).

This did not appear to be a concern here: fish showed no obvious signs of fatigue at the end of the trials, and no significant mortality occurred within 24 h after each trial. Moreover, biochemical analyses of blood and white muscle of American shad suggested that these fish did not swim to physiological exhaustion (Castro-Santos et al. 2000 and unpublished data). American shad did take longer to stage second attempts than their first attempt, and D_{max} tended to decrease with attempt number (Castro-Santos 2002). Later attempts occurred at greater rates, however, suggesting that the cause of the reduced distance may not have been physio-

logical fatigue. By contrast, walleye and white sucker showed no evidence of reduced attempt rate on successive attempts (if anything, it increased), and distance of ascent was consistent across attempts (Castro-Santos 2004). Taken together, these data suggest that these species do not volitionally swim to physiological exhaustion when attempting to traverse velocity barriers.

The results of the regression models highlight some important differences among these species. Although all six species exhibited the expected decline in D_{max} with increasing velocity, variation among species in the magnitude of this effect differed from our expectations. For example, because American shad are by far the largest of the three alosine species, we expected the velocity effect to be smaller than among blueback herring and alewife. Instead, the effect was similar among the three species, with alewife showing the smallest and blueback herring the greatest response to increasing velocity. The contrast between blueback herring and alewife is interesting because of the morphological and ecological similarity of these two species. This difference occurred primarily because several alewife abandoned their efforts at short distances against the lowest velocity, resulting in a smaller overall velocity effect compared with the blueback herring. Despite this difference, blueback herring had greater overall D_{max} values, which is consistent with the fact that they often have greater migration distances and spawn in more lotic habitat (Loesch 1987).

Numerous studies have shown that temperature is positively correlated with endurance, especially at sustained

Fig. 5. Model predictions of percentages of (a) American shad, (b) alewife, (c) blueback herring, (d) striped bass, (e) walleye, and (f) white sucker successfully traversing velocity barriers. Velocities: solid line, 1 m·s⁻¹; long-dashed line, 2 m·s⁻¹; dashed-dotted line, 3 m·s⁻¹; short-dashed cline, 4 m·s⁻¹; dotted line, 5 m·s⁻¹. All other covariates are set to their mean values. To keep extrapolations on the same order as the interpolations, modeled velocities extend only to 4 m·s⁻¹ for alewife, blueback herring, and walleye. Note that these predictions apply only to those fish that stage attempts within the first hour (see Castro-Santos (2002, 2004) for appropriate adjustments to account for attempt rates).
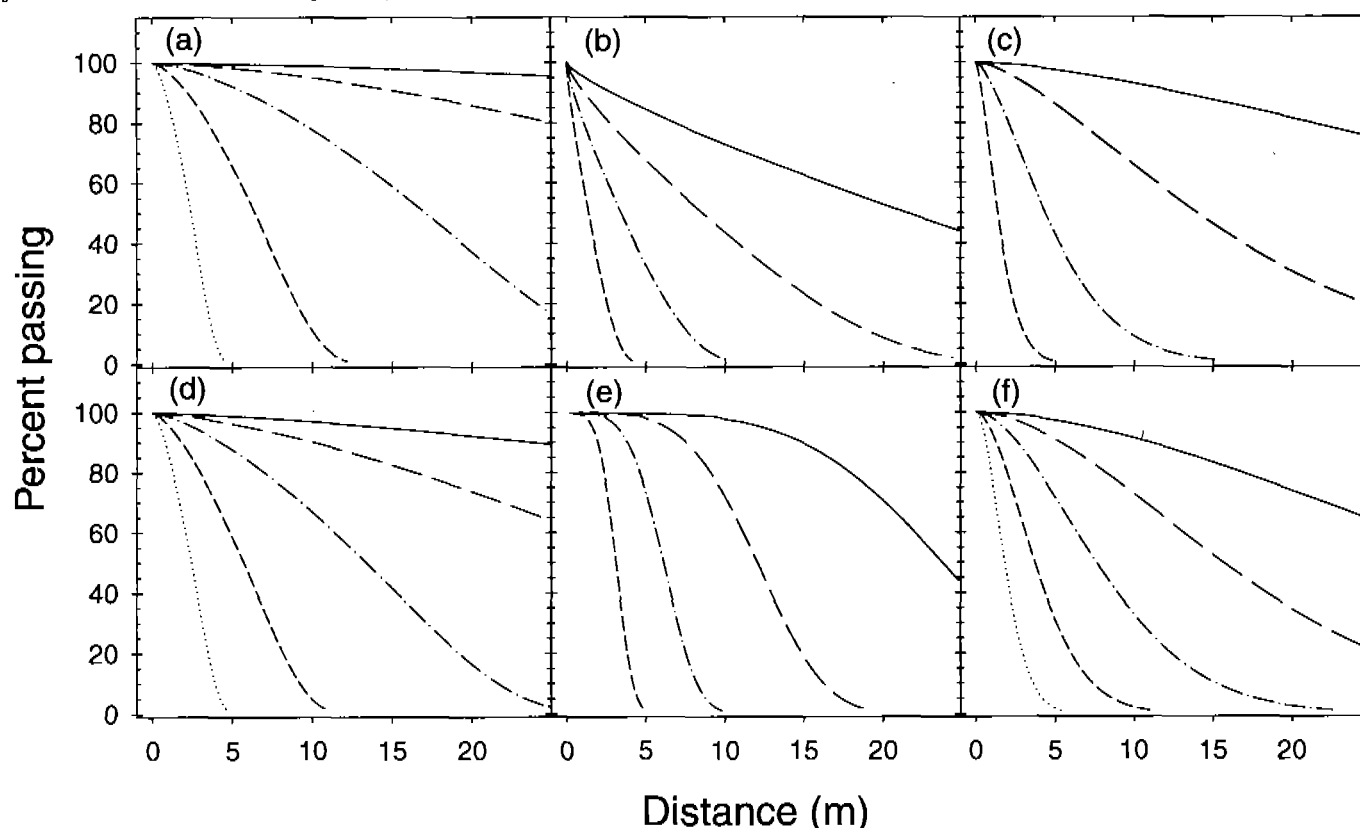
speeds (Brett 1964; Videler and Wardle 1991). Few studies quantify this effect on sprinting performance, however, and there is disagreement over its importance (Beamish 1978). We observed a positive correlation between temperature and D_{max} for blueback herring and walleye, but the opposite was true of American shad, and the effect among other species was not significant. Lack of significance should not be confused in this case with absence of effect: the range of temperatures at which species were run was variable and, because it corresponds to periods of fitness-crucial activity, may reflect a performance optimum for these species (Castro-Santos 2002). Thus, the signs of these coefficients may owe as much to nonlinear effects of migratory motivation as to physiological capacity. Also, because sprinting is largely powered by anaerobic processes, the temperature effects on sustained swimming may not be relevant. Temperature does not seem to be correlated with performance or recovery times during sprinting (Brett 1964; Schreer et al. 2001; Castro-Santos 2004).

As with temperature, many studies have shown length to be correlated with swimming performance, so much so that performance data are usually normalized for length, particularly when there is substantial variation in the lengths of the study animals (Bainbridge 1960; Brett 1965; Brett and Glass 1973). We, too, found significant correlations between length and D_{max}, but the effect was not universal and was much stronger among striped bass than among other species. Sex-

ual dimorphism can obscure the effect of length on performance. In the case of American shad, females are larger than males, but much of their mass is devoted to eggs rather than to propulsive musculature. The small magnitude of the length effect in this species may be due to differences in performance between the sexes (see Castro-Santos (2002) for a detailed discussion of the effects of sex and length). The absence of a significant length effect among alewife and white sucker may be due to the relatively small variance in length for these species; similarly, and for the same reason, the strong length effect among blueback herring should be viewed with skepticism.

The information gained in this study defines performance of upstream migrant fishes swimming through velocity barriers in a novel way and at a realistic scale. The distance that fish are able to ascend high-velocity flow is a useful parameter for defining swimming performance and identifying potential distributional limits. Thus, the technical and numerical approaches that we have described have broad applicability both to site-specific fish passage problems and to understanding implications of velocity barriers for population ecology of migratory riverine species.