Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes

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Summary

Migrating fish traversing velocity barriers are often forced to swim at speeds greater than their maximum sustained speed (U_{ms}). Failure to select an appropriate swim speed under these conditions can prevent fish from successfully negotiating otherwise passable barriers. I propose a new model of a distance-maximizing strategy for fishes traversing velocity barriers, derived from the relationships between swim speed and fatigue time in both prolonged and sprint modes. The model predicts that fish will maximize traversed distance by swimming at a constant groundspeed against a range of flow velocities, and this groundspeed is equal to the negative inverse of the slope of the swim speed–fatigue time relationship for each mode. At a predictable flow velocity, they should switch from the optimal groundspeed for prolonged mode to that for sprint mode. Data from six migratory fish species (anadromous clupeids: American shad *Alosa sapidissima,* alewife *A. pseudoharengus* and blueback herring *A. aestivalis*; amphidromous: striped bass *Morone saxatilis*; and potomodromous species: walleye (previously known as *Stizostedion vitrium*) and white sucker *Catostomus commersonii*) were used to explore the ability of fish to approximate the predicted distance-maximizing behaviors, as well as the consequences of deviating from the optima. Fish volitionally sprinted up an open-channel flume against fixed flow velocities of 1.5–4.5 m s^{-1}, providing data on swim speeds and fatigue times, as well as their groundspeeds. Only anadromous clupeids selected the appropriate distance-maximizing groundspeed at both prolonged and sprint modes. The other three species maintained groundspeeds appropriate to the prolonged mode, even when they should have switched to the sprint optima. Because of this, these species failed to maximize distance of ascent. The observed behavioral variability has important implications both for distributional limits and fishway design.

Key words: burst swimming, anadromy, sprinting, migration, fishway, fish passage.

Introduction

Diadromous and other migratory riverine species often encounter zones of high-velocity flow that impede their migrations. Where these flows exceed maximum sustained swim speed (U_{ms}), successful passage may still be possible, provided that fish select an appropriate swim speed. The focus of this paper is to identify optimal swim speeds for traversing such velocity barriers, to test whether such strategies are employed, and to explore the consequences of failure to optimize, when it occurs.

Because of the fitness consequences of swimming performance, locomotor behavior is a good candidate for optimization. There is disagreement, however, on what constitutes optimal behavior. Most work in this area has applied hydraulic equations to generate predictions of optimizing behaviors (Weihs, 1973, 1977; Webb, 1993; Videler, 1993). These authors used equations based on the combined energetic costs of basal metabolic rate and drag on swimming fish, predicted from hydraulic principles, to create cost-of-transport models that yield predictions of optimal swim speed; Weihs (1974) and Videler and Weihs (1982) further described how burst-and-coast swimming can afford energetic advantages. Trump and Leggett (1980) used a different approach, calculating the metabolic cost of transport directly from empirical equations derived from respirometry data. Both models generated similar predictions, namely that fish could maximize energetic efficiency by swimming at speeds corresponding to about one body length per second (BL s^{-1}). Data supporting these predictions are sparse, due to the difficulties of monitoring swimming fish in their native habitat, and a review of the literature by Bernatchez and Dodson (1987) found that such optimizing behavior is rare, characterizing only certain populations with long migrations.

Both the hydrodynamic and metabolic cost-of-transport models require the assumption of ready availability of energy. While this may be reasonable for aquatic animals swimming at sustained speeds, it does not hold at faster speeds. At these

speeds, contributions of anaerobic metabolism to power production create limits to endurance, with energy supplied increasingly from stores contained within muscle fibers, and insufficient time and circulation to remove metabolic waste products (Brett, 1964).

Because of this, high-speed swimming is not associated with continuous behaviors like filter feeding or migration through lentic environments (e.g. Ware, 1975); instead it is associated with short-term, fitness-critical behaviors, such as capture of mobile prey, predator avoidance, and traversing velocity barriers during migrations. For these behaviors, the trade-off between swim speed and fatigue time may define performance. This relationship has been well studied at prolonged speeds (Beamish, 1978; Videler, 1993; Webb, 1994), and is generally thought to follow a log-linear model:

$$\ln T = a + bU_s , \qquad (1)$$

where T is fatigue time, U_s is relative swim speed (in BL s^{-1}), and a and b are the intercept and slope coefficients, respectively; $b<0$. Given this swim speed–fatigue time relationship, I propose the following new models to predict distance-maximizing behaviors.

The maximum distance a fish can swim (D_s) can be described as $U_s \times T$, or, from Equation 1:

$$D_s = U_s \times e^{a+bU_s}. \qquad (2)$$

This is a nonlinear function, with a clear distance-maximum, dependent on the values of coefficients a and b. Figure 1 is derived from Bainbridge (1960)'s data on rainbow trout (table 10.1 in Videler, 1993; data have been transformed from 10-base logarithms and minutes to natural logarithms and seconds), which predict that distance can be maximized by fish swimming at 2.8 BL s^{-1}. This, however, is below the range of speeds for which the coefficients were developed; at the relevant burst speeds (greater than ~5 BL s^{-1}), a trade-off exists, and distance is maximized by minimizing speed.

This relationship is more complex for diadromous migrants confronted with velocity barriers, such as might be found at rapids, culverts or other constrictions in a river. Because distance through a velocity barrier is often unknown, and because of the sometimes dire fitness consequences of failing to traverse the barrier, fish traversing such barriers should pursue a distance-maximizing strategy. Moreover, the distance that needs to be maximized is not the distance swum, or through-water distance, but rather the distance over ground, as this is what defines the boundaries of the velocity barrier. In the presence of flow, the ground distance (D_g) attained at fatigue time becomes:

$$D_g = U_g \times e^{a+bU_s}, \qquad (3)$$

where U_g is ground speed, or the difference between swim speed and the speed of flow (U_f). Thus,

$$D_g = (U_s - U_f) \times e^{a+bU_s}. \qquad (4)$$

Here, the resulting response surface shows a clear optimum swim speed (U_{opt}), with the maximum distance over ground
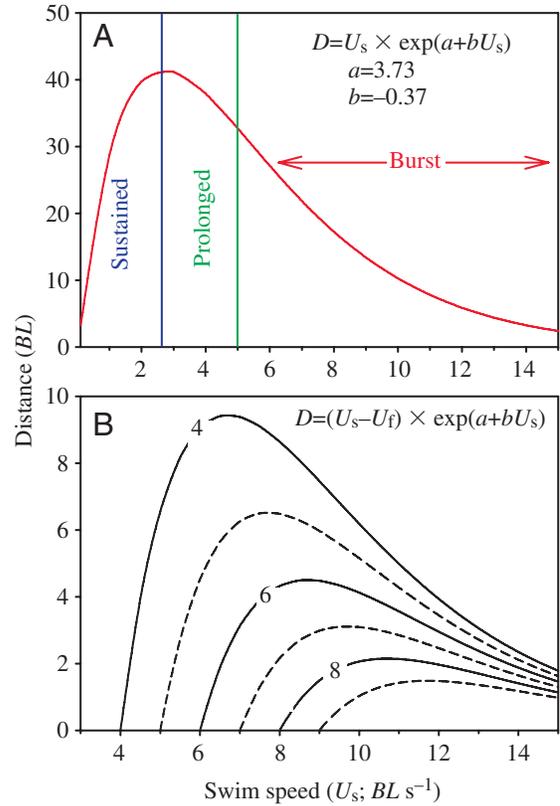

Fig. 1. Predicted distance maxima (in body lengths, BL) based on Equation 1, in still water (A) and in the presence of flow (B; contours indicate flow velocity, U_f). Data are for rainbow trout *Oncorhynchus mykiss* (Bainbridge, 1960).

dependent on both flow and swim speeds (Fig. 1B). By taking the first derivative of D_g with respect to U_s, and solving for zero slope, it can be shown that the optimal swim speed within a given mode is defined by:

$$U_{opt} = U_f - 1/b , \qquad (5)$$

and thus the optimal groundspeed U_{gopt} is:

$$U_{gopt} = -1/b . \qquad (6)$$

In other words, the distance-maximizing strategy for fish swimming against flow velocities equal to or greater than U_{ms} is to swim at a constant groundspeed, regardless of U_f, and equal to the negative inverse of the slope defined in Equation 1.

This relationship, however, is not constant across modes. Brett (1964) first observed, and numerous subsequent studies have confirmed (see tables and figures in Beamish, 1978; Videler, 1993), the existence of two distinct unsustainable modes of steady swimming: prolonged mode, which can be maintained for durations of 20 s to 200 min, and sprint mode, which results in fatigue in less than 20 s. Although a biological explanation for the existence of these two modes has never been definitively established, the change is generally thought to be the result of a shift from mixed contributions of aerobic and anaerobic metabolism and muscle groups in prolonged mode to almost pure anaerobic metabolism and muscle groups in sprint

mode (Brett, 1964; Webb, 1975). Regardless of the underlying cause, the slopes of the swim speed–fatigue time relationships of these two modes vary in ways that are consistent across taxa, namely b is steeper (larger negative magnitude) in prolonged mode than in sprinting, and the transition between modes is discrete. This means that the distance-maximizing swim speed, while still a constant groundspeed within a particular mode, will show a discrete shift to a higher value as fish shift from prolonged to sprint mode.

Because of the parameters describing the swim speed–fatigue time relationship, maximum distance in prolonged mode (D_{maxP}) greatly exceeds that in sprint mode (D_{maxS}) at low U_f. However, as U_f increases, this difference declines, and eventually D_{maxS} exceeds D_{maxP} (Fig. 2A). This suggests that there exists a critical speed of flow U_{fcrit}, at which a mode shift should occur (Fig. 2B). At U_f values less than this, fish should swim at the optimum prolonged speed; at greater values, they should swim at the optimum sprint speed. This critical flow speed can be calculated as the point where the predicted distance maxima are equal, i.e. from Equations 1, 4 and 6, where

$$-b_p^{-1} \times e^{[a_p + b_p(U_f - b_p^{-1})]} = -b_s^{-1} \times e^{[a_s + b_s(U_f - b_s^{-1})]} . \quad (7)$$

Thus,

$$U_{fcrit} = \frac{Ln\left(\dfrac{b_S}{b_P}\right) + a_P - a_S}{b_S - b_P} , \quad (8)$$

and fish should select prolonged or sprint modes, respectively, (along with their optimal groundspeed), depending on whether current velocity is greater or less than U_{fcrit}.

The above leads to the following hypotheses: (1) when confronted with velocity challenges, fish should swim at a constant groundspeed of $-1/b$ BL s^{-1}; (2) selected groundspeed will vary with mode, being lower at prolonged than at burst speeds; (3) The velocity of flow at which the shift to the sprint optimum will occur is described by Equation 8; and (4) to the extent that fish fail to approximate U_{gopt}, the deviation will reduce maximum distance of ascent. This paper describes tests of these hypotheses with data from six species, volitionally swimming up a large scale, open-channel flume.

Materials and methods
The flume

Data for this study come from a series of experiments on sprinting fish using a large-scale hydraulic flume, which is described in detail elsewhere (Castro-Santos, 2002; Haro et al., 2004). The flume apparatus was built at the fish passage facility of the Conte Anadromous Fish Research Center in Turners Falls, MA, USA, which was designed for such studies, and consisted of a bulkhead that retained a headpond, supplied with a maximum of 10 m^3 s^{-1} of water through pipes leading from an adjacent power canal. The flume proper was an open channel, 1 m×1 m in cross-section, and 23 m long. At the interface of this channel and the headpond bulkhead was an
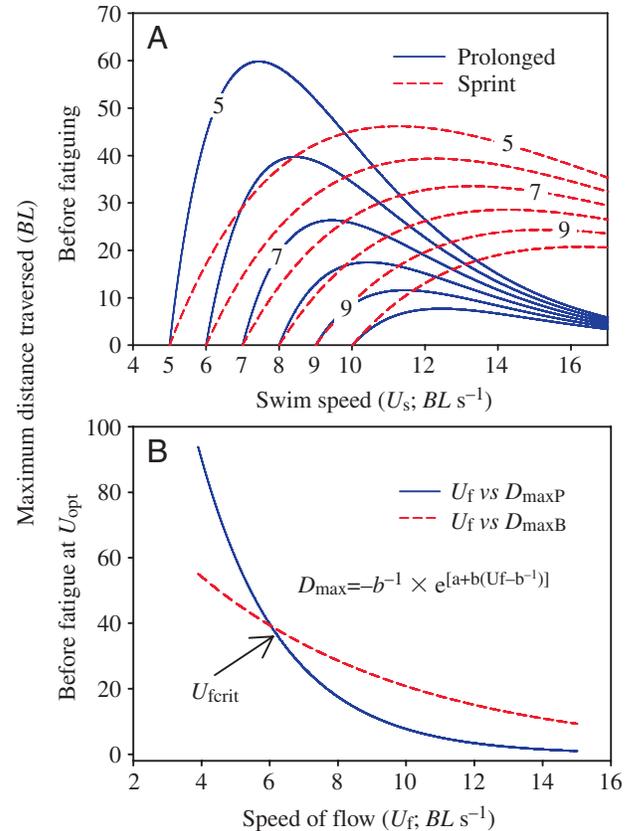

Fig. 2. Ground distance covered before fatigue as predicted from Equation 1 for prolonged and sprint modes of white sucker (this study). (A) The full range of possible distances covered at each mode up to 16 BL s^{-1} against flow velocities of 5–10 BL s^{-1} (contours). (B) Maximum distance attainable at each mode when fish swim at optimum speed against flows ranging up to 15 BL s^{-1}. Fish should switch modes where the two curves intersect (U_{fcrit}). For an explanation of symbols, see List of symbols.

adjustable control gate (headgate). This gate, combined with the headpond level and the level of the water in the flume, served to regulate the flow through the flume. At the downstream end of the channel was a large staging area (0.75–1.5 m×3 m×5 m, depth×width×length) that, with its greater cross-sectional area and length provided fish with a low-velocity zone from which to stage their attempts at swimming up the flume. A variable-crest weir (tailwater weir) fitted with 2.4 cm^2 screening installed at the downstream end served the dual functions of controlling the depth of the water in the staging area and preventing the fish from escaping downstream. At the interface of the staging area and the flume channel was a v-shaped gate (exclusion screen) used to prevent fish from swimming up the flume before beginning a trial, while the velocities were brought to their desired levels.

Water levels were monitored and recorded every 60 s in the headpond, at three locations within the flume, and in the staging area. Settings for the headgate and tailwater weir were likewise monitored. Instantaneous velocity estimates were generated for each point of a 10 cm grid over the full cross-

Table 1. *Species characteristics and flume velocities*

Species	N	FL (mm)	U_{nom} (m s^{-1})	U_f (m s^{-1})	U_{fa} (m s^{-1})	CF
American shad	80	420±35	1.5	1.75±0.06	1.72	0.98
	220	418±32	2.5	2.68±0.09	2.71	1.01
	215	417±35	3.5	3.41±0.08	3.35	0.98
	69	416±35	4.5	4.52±0.04	4.40	0.97
Alewife	107	236±12	1.5	1.60±0.15	1.49	0.93
	73	239±11	2.5	2.59±0.06	2.58	1.00
	25	237±10	3.5	3.40±0.03	3.28	0.97
Blueback herring	20	225±11	1.5	1.63±0.09	1.58	0.97
	25	218±11	2.5	2.66±0.09	2.67	1.00
	31	217±11	3.5	3.38±0.11	3.31	0.98
Striped bass	7	574±312	1.5	1.49±0.20	1.73	1.16
	86	421±114	2.5	2.63±0.08	2.67	1.01
	70	489±110	3.5	3.41±0.07	3.37	0.99
	33	580±147	4.5	4.52±0.03	4.51	1.00
Walleye	40	326±57	1.5	1.68±0.07	1.68	1.00
	61	316±44	2.5	2.67±0.10	3.04	0.97
	49	315±49	3.5	3.37±0.05	3.31	0.99
White sucker	50	391±40	1.5	1.72±0.05	1.55	1.00
	68	389±30	2.5	2.63±0.04	2.62	1.14
	89	399±35	3.5	3.40±0.05	3.29	0.98
	36	393±30	4.5	4.52±0.04	4.47	0.90

N, sample size; FL, mean fork length (± 1 S.D.); U_{nom}, nominal velocity; U_f, mean actual velocity of flow (± 1 S.D.); U_{fa}, mean U_f adjusted for species- and U_{nom}-specific ascent routes; CF, correction factor used to calculate U_{fa}.

section of the flume using a combination of physical modeling and hydraulic equations, confirmed with direct measurements in the flume (Fig. 3; Castro-Santos, 2002; Haro et al., 2004). Mean cross-sectional velocities were then controlled to within ±5% of their average values within each nominal velocity, corresponding to 1.5, 2.5, 3.5 and 4.5 m s^{-1}, the variability arising from fluctuating water levels, both in the power canal and within the facility (Table 1).

Data collection

To avoid using coercive measures to motivate fish to swim, we relied instead on the innate rheotactic behaviors of six fish species that migrate annually through rivers of Northeast USA. Collections and testing were performed between the months of April and July, 1997–1999, on dates corresponding with periods of upstream migration for each species. Test fish were captured from traps at nearby fishways (American shad *Alosa sapidissima* Wilson 1811, striped bass *Morone saxatilis* Walbaum 1792, and white suckers *Catostomus commersonii* Lacepède 1803), coastal streams (alewife *A. pseudoharengus* Wilson 1811) from the Herring River, Bourne MA, and blueback herring *A. aestivalis* Mitchill 1814 from the Charles River, Watertown, MA), or electrofished [blueback herring, striped bass, walleye *Sander vitreus* Mitchill 1818 (formerly *Stizostedion vitreum* Mitchill 1818) and white sucker] from the Connecticut River.

Fish were transported to the flume facility in one of two truck-mounted tanks containing either 1000 or 4000 liters.

There they were measured (fork length, *FL*), sexed, and each was fitted with an externally attached passive integrated transponder (PIT) tag. This consisted of a glass-encapsulated, cylindrical tag measuring 32 mm×3 mm, length×diameter, fastened to a fishhook, which was inserted through the cartilage at the base of the dorsal fin (second dorsal, in the case of the percomorphs; see Castro-Santos et al., 1996, for a complete description of the PIT tag system). Tagged fish were released into open, flow-through holding ponds (Burrows and Chenoweth, 1970), connected hydraulically to the fish passage complex and held for 24 h before testing. The linkage between the holding ponds and the flume facility precluded the need to handle fish the day they were tested. Instead, groups of 20–30 fish were crowded from the holding ponds into the facility at the start of each trial, and the tailwater weir was raised to confine the fish to the staging area. Once the velocity of flow was brought to the desired level, the exclusion screen was opened, and fish were allowed to ascend the flume of their own volition. Duration of trials ranged from 1 to 6 h.

Progress of individual fish up the flume was monitored both electronically and visually. The flume was electronically graduated with PIT detection antennas wired around the outside every 2.5 m, beginning at 0.5 m from the entrance. Antennas were driven by controllers that charged and read tags as they moved through, and sent the identifying codes back to a central computer at a rate of 14 Hz. The computer logged these codes, recording position to within ± 50 cm and time to the nearest 0.01 s (Castro-Santos et al., 1996; Castro-Santos, 2002).

The flume was also graduated visually, in part to verify the accuracy of the PIT tag data. Four video cameras (NTSC i.e. a standard video format) were positioned 5 m above the flume; high-speed video (250–500 frames s^{-1}) provided additional detailed information on swimming mechanics during 16 trials. The floor and one wall of the flume were covered with a retroreflective surface (Scotchlite 6780, 3-M Corp., St Paul, MN, USA) that was graduated into 50 cm intervals with black crosshatch marks. The other wall of the flume was made of clear acrylic, 2.5 cm thick. Mirrors, the full height of the flume and situated at a 45° angle to it, allowed each camera to monitor dorsal and lateral views of the swimming fish simultaneously, thus positioning the fish in three dimensions.

The speed at which fish moved up the flume (groundspeed, U_g) was measured by calculating the difference in mean times between pairs of antennas. Maximum distance of ascent (D_{max}) corresponded to the highest recorded reader. Mean groundspeed was the time between detections at the first antenna and the D_{max} antenna, divided by D_{max}. Swim speed (U_s) was measured by adding the measured water velocity (U_f) to U_g.

Video was also used to determine if fish were actively seeking out low velocity zones. At least 10 individuals were tracked swimming up the flume from each species-nominal velocity combination. The proportion of time (to the nearest 5%) that each fish spent in each of 15 cross-sectional quadrants was measured using the dual perspectives provided by the camera arrangement. A correction factor (CF) was calculated for each fish by summing the proportion of time spent in each quadrant multiplied by the ratio of the water velocity in that quadrant to the mean cross-sectional velocity (Fig. 3). The resulting values were used to calculate an overall correction factor by which to multiply the mean cross-sectional flume velocity for each species-velocity combination.

Analysis

The above data were used to calculate swim speed–fatigue time relationships for each species and mode, as described below. The associated equations were then used to evaluate whether the models described in Equations 1–8 can be used to predict distance-maximizing behavior, whether these species exhibited such behaviors, and if not, how that affected distance of ascent.

The swim speed–fatigue time relationship was calculated by regressing speed at which the fish swam against the natural log of the time it took for fish to reach their maximum distance of ascent. Data for this relationship were pooled across velocities. Often, fish ascended the full length of the flume; in this case the observation is not of fatigue, but of the failure of the fish to fatigue. This constitutes censored data, some of the implications of which are discussed elsewhere (Hosmer and Lemeshow, 1999; Castro-Santos and Haro, 2003; Castro-Santos, 2004): using methods of survival analysis, the observed data are included, coded for censoring, and the likelihood of the regression model is maximized with respect to the probability density function $f(T)$ for complete observations, and to the survivorship function $S(T)$ for
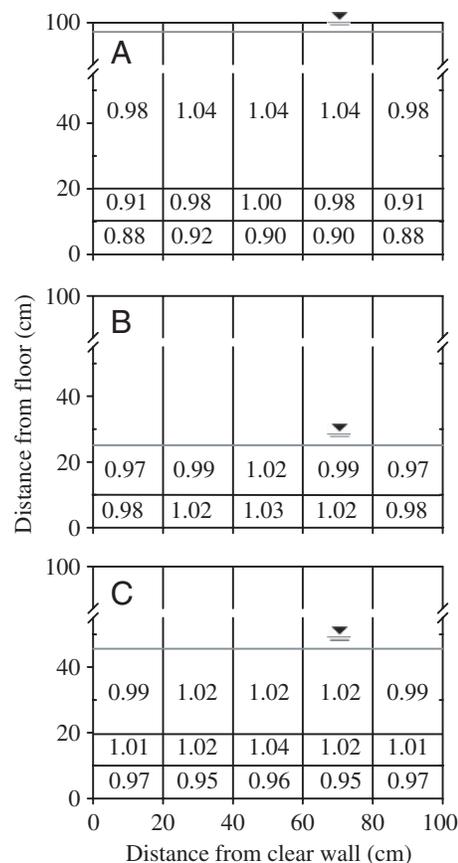

Fig. 3. Cross-sectional profiles of the relative velocities in each zone of the flume, by nominal velocity. Data are for flow rates of 1.5 m s^{-1} (A), 2.5 m s^{-1} (B) and 3.5 and 4.5 m s^{-1} (C), and were used to calculate the correction factors in Table 1 (see text for details). Arrowheads, location of the water surface.

censored observations. This method generates sufficient and consistent least-biased estimates of the swim speed–fatigue time relationship (Neter et al., 1985; Hosmer and Lemeshow, 1999).

The model was then modified to test for evidence of a mode shift between prolonged and sprint modes (maximum prolonged speed: U_{mp}). A dummy variable and an interaction term were included:

$$\text{Ln}T = \beta_0 + \beta_1 U_s + \beta_2 x_1 + \beta_3 x_1 U_s, \qquad (9)$$

such that $x_1=0$ for values of U_s less than a nominal U_{mp} value, and 1 at greater values (β_i are regression coefficients, analogous to a and b terms in Equation 1). This model was run iteratively, incrementing U_{mp} by 0.01 BL s^{-1}; the log-likelihood values from each iteration were used to calculate a χ-square likelihood ratio statistic (2 d.f.; Allison, 1995; Hosmer and Lemeshow, 1999) to define a confidence band around the maximum calculated value. I used this approach to fit exponential, lognormal, Weibull and generalized gamma distributions, and used likelihood ratios or Akaike's Information Criterion (AIC), where appropriate, to select the most parsimonious model (Burnham and Anderson, 1998;

Allison, 1995). The model that provided the best fit also defined U_{mp}. Where significant shifts in slope were observed ($P<0.05$), data were then divided into observations greater and less than the estimated U_{mp}, and separate coefficients of Equation 1 were generated for each mode (a_P, b_P, a_S, b_S for prolonged and sprint modes, respectively); the predicted U_{gopt} from Equation 6 equals the negative inverse of the slope term, i.e. $-b_P^{-1}$ or $-b_S^{-1}$.

Evidence for optimizing behavior was assessed by comparing observed groundspeed with predicted values; U_{fcrit} was calculated from Equation 8 and the regression models described above. If the optimization model is correct, then there should be costs associated with deviating from U_{opt}; specifically, fish that swim faster or slower than U_{gopt} should swim less far. Alternatively, if fish select swim speeds that differ from the predicted optimum, but that in fact represent true distance-maximizing optima that this model fails to predict, then deviation from the mean ('true optimum') will likewise yield reduced distance of ascent. I tested for each of these conflicting hypotheses by regressing the expected cost of deviating from the optimum groundspeed, measured as the difference in distance of ascent predicted at the optimum minus the observed groundspeed (values are always positive), against D_{max}, censoring where fish arrived at the uppermost reader. These residuals are denoted R_P and R_S for prolonged and sprint predictions, respectively. To test for optimizing behavior not predicted from the model, I regressed the absolute value of the residual groundspeed, $|U_g-\overline{U_g}|$, against D_{max}, censoring as above. Significant positive slopes indicate greater distances achieved by deviating from U_{gopt} and $\overline{U_g}$; significant negative slopes indicate costs of deviation. Either significant positive slopes or non-significance support the null hypothesis against the model; only a significant negative slope supports the alternative hypothesis suggested by the model, and significance tests are correspondingly one-tailed.

Results

The results of these experiments suggest that the models are good descriptors of distance-maximizing behavior. Actual behaviors were variable, however, both within and among species. Only the anadromous clupeids approximated the appropriate distance-maximizing behavior in both prolonged and sprint modes. Nonclupeids selected appropriate speeds for prolonged mode, even where $U_f>U_{fcrit}$; the data indicate that this represents a failure to optimize, rather than an alternative distance-maximizing strategy.

Flume tolerances and behavior

Water velocities (U_f) deviated from the target velocities both in time and over the cross-section of the flume. These deviations are described elsewhere (Castro-Santos, 2002; Haro et al., 2004), and are summarized in Fig. 3 and Table 1. Although flow was turbulent at all velocities (Reynold's number >300,000) the turbulence was disorganized, consisting of random fluctuations and microeddies with no evident periodicity (Haro et al., 2004). This means that, with the exception of slightly lower velocities in the corners (Fig. 3), opportunities for fish to take advantage of hydraulic structure were minimal. Preferred zones of ascent within the flume varied among individuals and species, with the following general trends: (1) most fish tended to swim within 20 cm of the bottom, this effect being least at the 1.5 and 4.5 m s^{-1} conditions; (2) most fish avoided the walls, generally swimming more than 20 cm from either wall; and (3) white sucker consistently swam in the corners at 1.5 and 2.5 m s^{-1}, presumably taking advantage of the lower velocities there, but at higher velocities they swam closer to the middle of the flume. Correction factors and adjusted mean velocities are presented in Table 1.

The PIT detection antenna array provided a nearly continuous record of the position of fish within the flume. Read range of the antennas extended 50 cm up- and downstream of each antenna. By taking the mean value of time for each antenna, fish were located in time and space with an accuracy of ±18 cm, i.e. 95% of fish were within 18 cm of the antenna at the time their presence was logged, with no apparent bias in the error.

Table 2. *Endurance variables in prolonged and sprint modes*

Species	Distribution	Prolonged					Sprint			
		U_{mp} (BL s^{-1})	a_P	b_P	U_{goptP} (BL s^{-1})	N	a_S	b_S	U_{goptS} (BL s^{-1})	N
American shad	Weibull	7.2	10.70	−1.00	1.00	86 (67)	6.16	−0.33	3.03	497 (162)
Alewife	Gamma	–	–	–	–		5.12	−0.20	5.00	205 (29)
Blueback herring	Lognormal	–	–	–	–		5.39	−0.20	5.00	76 (10)
Striped bass	Gamma	10.4	5.99	−0.39	2.56	126 (32)	4.38	−0.19	5.26	61 (4)
Walleye	Weibull	10.6	6.65	−0.41	2.44	53 (19)	4.02	−0.13	7.69	97 (0)
White sucker	Weibull	10.4	6.32	−0.42	2.38	124 (44)	3.72	−0.15	6.67	119 (0)

U_{mp}, maximum prolonged swim speed; a_P, b_P, a_S, b_S, coefficient estimates of the swim speed–fatigue time relationship (Equation 1); U_{gopt}, predicted optimal ground speed.

Coefficients are subscripted with a P or S to indicate sprint or prolonged mode, accordingly.

N, sample size, presented as fatigued (censored). See text for details.

Once within the flume, fish tended to move steadily up the channel until they reached D_{max}. Swimming behavior was mostly steady, with burst–coast behavior observed only rarely, and then among large individuals swimming against the lower velocity flows. Subsequent behavior also varied with speed of flow. At the fastest flows, fish tended to fall back passively, oriented either up- or downstream or even lateral to the flow, maintaining at most enough velocity relative to flow to maintain equilibrium. At intermediate water velocities, they tended to maintain greater velocity relative to the flow (again, oriented either up- or downstream), but usually returning rapidly to the staging area. At the slowest flows, some fish proceeded to exit the top of the flume, or lingered near the upstream end (see Fig. 2.5 in Castro-Santos, 2002). Some individuals made multiple ascents; in this case I used the first ascent where a fish attained its D_{max} value in my analyses. This usually occurred on the first attempt (65–95% of individuals, by species).
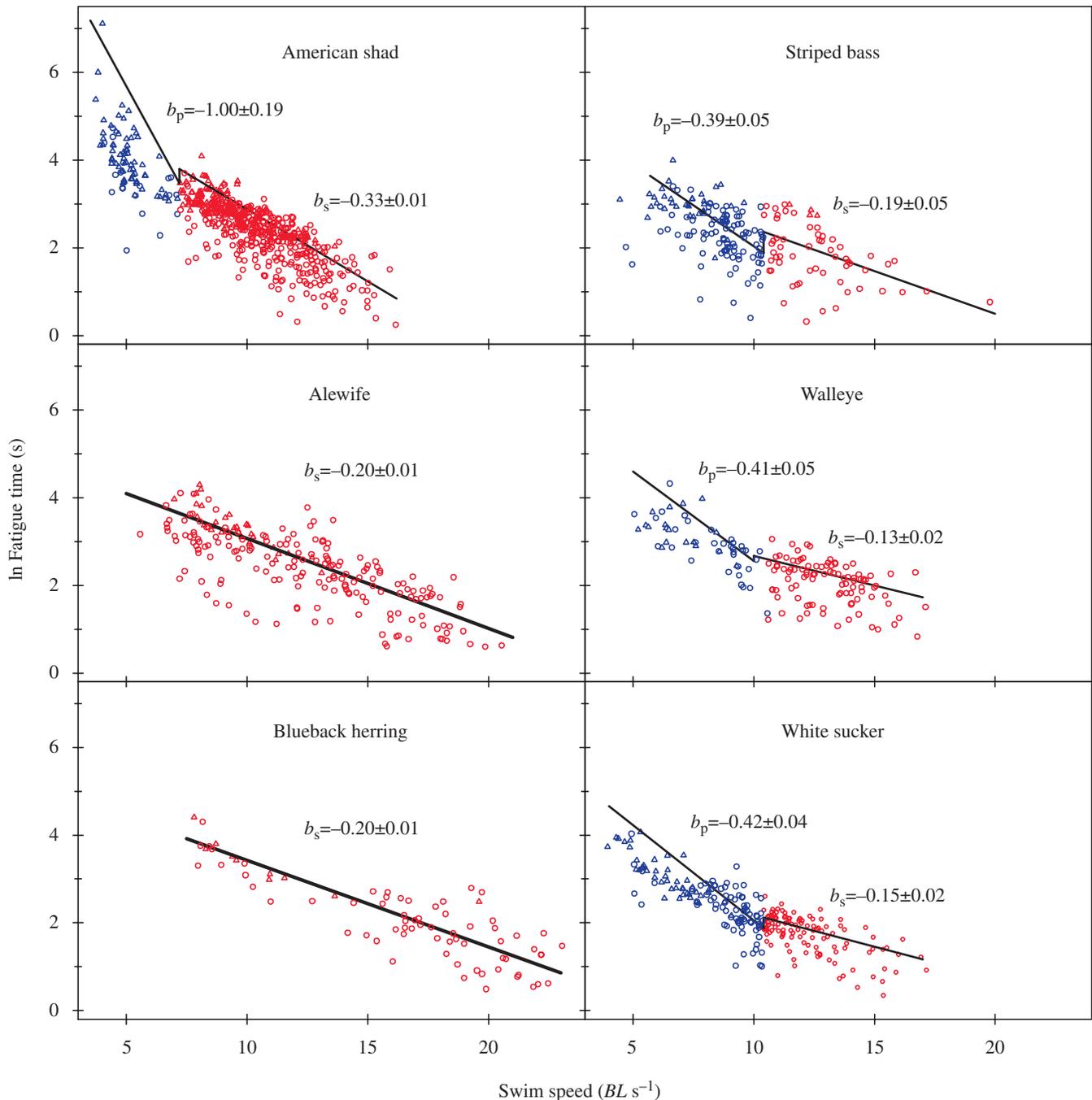

Fig. 4. Swim speed–fatigue time relationship by species. Data are color-coded to indicate prolonged (blue) and sprint (red) modes; censored data are indicated by triangles, and complete data by circles. Coefficients indicate the slope ± 1 S.E.M. of the relationship for prolonged (b_P) and sprint (b_S) modes.

Swim speed–fatigue time curves

The relationship between swim speed and fatigue time is presented in Fig. 4 and Table 2. Whenever fish ascended to 18 m or above, observations were included as censored, i.e. the fish did not fatigue as of the last observation. This means that the ability to measure fatigue was limited by the constraints of the apparatus. The regression techniques used here, however, account for censored data and generate sufficient and consistent least-biased estimates of the swim speed–fatigue time relationship; uncertainty arising from all sources, including censoring, is reflected in the standard error of the estimates. Since censoring constitutes incomplete observation, and was more prevalent among lower swim speeds (Fig. 4), variance of the estimates are correspondingly greater at prolonged than at burst speeds. The presence of censored data also explains why regression lines in Fig. 4 do not fall in the middle of the data; they are instead adjusted upward to account for those fish that did not fatigue (Allison, 1995; Hosmer and Lemeshow, 1999; Castro-Santos and Haro, 2003).

Discrete prolonged and sprint modes were found with corresponding slopes and intercepts for American shad, striped bass, walleye and white sucker, but not for alewife or blueback herring. The locations of these mode shifts represent the models with the best fit. A 95% confidence interval (based on the likelihood statistic) around the models with the selected breakpoints indicates that actual values may fall within about ± 1 BL s^{-1} of the best model. Over this range of potential models, parameter estimates varied little: standard deviations (S.D.) of model b_P values ranged from 0.01–0.05, except for American shad, for which the S.D.=0.23; values of model b_S standard deviations were even more stable, ranging from <0.01 to 0.04 BL s^{-1} for all species. Note that the variance in b_P S.D. values among models matches the proportionately larger standard error value for this estimate in the best models (Fig. 4).

Among blueback herring, a small sample size resulted in poor power to detect a mode shift that was probably present (P=0.08). A further mode shift may have been present for striped bass: when data greater than the observed breakpoint of 10.4 BL s^{-1} were excluded, an additional shift was detected at 5.7 BL s^{-1}. To avoid potential bias introduced by including an additional mode, data less than 5.7 BL s^{-1} were excluded from the regression analyses. Interestingly, when swim speeds below U_{mp} were excluded from the American shad analysis, an additional mode shift became apparent here also at 10.2 BL S^{-1}.

Slopes and intercepts for each species are presented in Table 2, along with the predicted groundspeed optima (U_{gopt}) within each mode and the estimated maximum prolonged speed (U_{mp}). Where no mode shift was observed, these parameters are assumed to correspond to their values for sprinting – otherwise they are subscripted with P or S to refer to prolonged and sprint modes, respectively. A separate regression for striped bass swimming at speeds <5.7 BL s^{-1} resulted in coefficients of a=6.6 and b=–0.98.

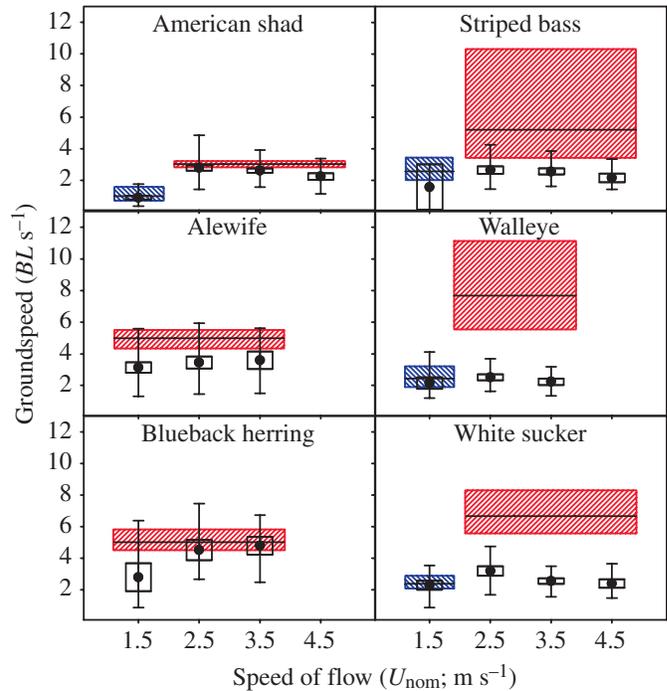The groundspeed at which the various species of fish

Fig. 5. Observed and predicted groundspeeds. Points and boxes are observed mean and 95% confidence intervals of mean groundspeed by species and nominal velocity; whiskers are 10th and 90th percentiles. Horizontal lines indicate predicted optimum groundspeeds for prolonged (blue) and sprint (red) modes; hatching reflects 95% confidence interval of the prediction.

actually swam is shown for each nominal velocity in Fig. 5, with the predicted optima overlaid for reference. Variance in estimates of slope lead directly to variance in predicted optimal swim speeds. Since $|b_P|$ was always of greater magnitude than $|b_S|$, the inverse predicts a lower optimal swim speed at prolonged than at sprinting modes. However, the inverse of the variance also increases proportionally, thus two estimates with similar variance, such as in striped bass, yield predictions with ranges of substantially different magnitude.

Where data from two modes were available, values of U_{fcrit} ranged from 4.28 to 5.92 BL s^{-1}, or between the relative speeds for the 1.5 and 2.5 m s^{-1} nominal velocities (from Tables 1, 2; Equation 8). Thus, of all species that exhibited a mode shift, most individuals should select the optimal groundspeed for the prolonged mode at the 1.5 m s^{-1} condition and that for the sprint mode at the higher velocities. American shad did precisely this, and the other clupeids also appeared to follow a distance-maximizing strategy (Fig. 5). Although most alewife swam at groundspeeds slightly slower than the predicted optima, this is because several outliers – fish that had unusually short fatigue time at low swim speeds (Fig. 4) – acted to reduce the slope of the swim speed–fatigue time curve. When these observations are removed, the mean groundspeeds coincide with the predicted optima. Among the nonclupeids, the actual behavior was quite different. Instead, these three species selected a constant groundspeed that corresponded with the

Table 3. *Effect of deviating from the predicted optimal groundspeeds for prolonged (R_P) and sprint modes (R_S), and of deviating from the mean observed groundspeed within each nominal velocity (R_U)*

	R_P			R_S			R_U		
Species	Coefficient	P	Distribution	Coefficient	P	Distribution	Coefficient	P	Distribution
American shad	0.0022	0.337	Weibull	**−0.0326**	**<0.001**	Gamma	−0.0223	0.546	Weibull
Alewife	–	–	–	**−0.0081**	**0.033**	Weibull	−0.0336	0.358	Weibull
Blueback herring	–	–	–	**−0.0155**	**0.005**	Lognormal	−0.041	0.5336	Lognormal
Striped bass	−0.0031	0.694	Lognormal	**−0.0194**	**0.013**	Lognormal	0.1479	0.083	Lognormal
Walleye	−0.005	0.551	Weibull	**−0.0204**	**<0.001**	Gamma	0.056	0.406	Weibull
White sucker	0.0309	0.002	Weibull	**−0.0329**	**<0.001**	Weibull	0.1284	0.001	Weibull

Data are from nominal velocities where >10% of fish swam within the modeled mode. Significant negative coefficients (based on one-tailed tests and highlighted in bold) indicate that deviating from the predicted optimum swim speed resulted in reduced distance of ascent and support the optimization hypothesis; positive coefficients indicate increased distance of ascent.

optimum for the prolonged mode, regardless of U_f (with the possible exception of striped bass at 1.5 m s^{-1}), even though most of these fish were swimming at speeds corresponding with the sprinting mode. This consistency was remarkable: among white suckers, for example, a 7.1 BL s^{-1} range of U_f produced a U_g range of only 0.88 BL s^{-1}.

Among species that exhibited mode shifts, >90% of all individuals swam at speeds corresponding with the prolonged mode when swimming against 1.5 m s^{-1}. Although 100% of clupeids swam at sprint modes at nominal velocities ≥2.5 m s^{-1}, behavior of non-clupeids was more variable. Here, 10–69% swam within prolonged mode at each of the higher velocities, except for white sucker, where all fish swimming against the 4.5 m s^{-1} condition swam in sprint mode (Table 3).

I used the same distinction described above to test for the costs of deviating from predicted optima: tests include data from only those velocities where >10% of individuals swam within the designated mode. The results of these tests, as well as tests of the cost of deviating from the observed mean swim speed within each velocity, are presented in Table 3. These tests indicate that the distance-maximization models are correct in sprint mode, but results for prolonged mode were equivocal. Significant reductions in D_{max} were associated with deviation from U_{goptS} among all species, but there was no correlation between D_{max} and deviation from U_{goptP}, except among white sucker, where deviation was associated with greater distances of ascent. This is not surprising, because most of these individuals should, under the model, have made the switch to the sprint optimum. Similarly, there was no significant effect of deviating from the mean groundspeed, except for striped bass and white sucker, where greater deviation was associated with greater distance of ascent.

In addition, I separately tested for the possibility that U_{goptP} was the optimizing speed at the 1.5 m s^{-1} condition as well as at the faster nominal velocities. Only walleye showed a significant cost of deviation under the 1.5 m s^{-1} condition (negative correlation; $P=0.004$). Heavy censoring under the 1.5 m s^{-1} condition resulted in poor power to detect a cost here: only among walleye did fewer than 50% of individuals successfully reach the upper end of the flume under this

condition (Haro et al., 2004). Thus, failure to identify a cost of deviating from the predicted optimum probably reflects the constraints of the experimental apparatus, rather than any flaw in the model. At the higher velocities, where all species should have been swimming at the sprint optimum, only white sucker showed any effect, with greater distance of ascent associated with deviation from U_{goptP}. This concurs with the model hypotheses, and indicates that fish swimming at U_{goptP} were not selecting a distance-maximizing strategy at these speeds.

Discussion

The results of this study indicate that, although distance-maximizing behaviors can be predicted from the swim speed–fatigue time relationship, species differ in the extent to which they approximate these optima. Further, the consistent failure by the nonclupeids to switch to the distance-maximizing groundspeed for sprint mode means that these species are less likely to successfully traverse velocity barriers, even though such success is within their physiological capacity.

Assumptions and parameters

The approach to quantifying the swim speed–fatigue time relationship presented here differs substantially from the standardized approach developed by Brett (1964). Where others have produced fatigue using coercive methods such as electrified screens, prodding, or impingement avoidance to induce fish to swim against sequentially increased water velocities, we have presented fish that are innately motivated to swim upstream with an opportunity to do so volitionally, measuring fatigue as a behavioral choice to abandon the effort.

This approach is not without assumptions, however, and the following are implicit in this analyses: (1) a linear relationship adequately describes the effect of swim speed on the log of fatigue time; (2) the methods and data presented here were sufficient to identify any mode shifts; (3) the apparatus provided a realistic estimate of the slope(s) of this relationship; and (4) fish are either unaware of the length of the velocity barrier, or such knowledge does not affect their behavior. Substantial empirical evidence exists to support the first

assumption, both in this study and elsewhere (numerous references in Beamish, 1978; Videler, 1993). The second assumption is more suspect, however. Although clear mode shifts were identified for American shad, white sucker and walleye, the phenomenon was less clear for the other species. Because of their smaller size, alewife and blueback herring swam at faster relative speeds against a given flow than did the larger fish, and the absence of slow swimming speed data precluded identification of mode shifts for both species. Conversely, the large size of some striped bass allowed them to swim at a slower mode against the 1.5 m s⁻¹ flow condition. In both cases, these limitations may have precluded accurate prediction of U_{gopt}, particularly against low velocity flow.

The third assumption is also suspect: because fish were able to abandon their effort at will, estimates of fatigue time at a given speed will inevitably be low. This is true for two reasons: (1) fish probably do not voluntarily swim to exhaustion; and (2) some individuals may exert less effort than others, i.e. abandon their effort at a reduced level of fatigue. Both behavioral characteristics can be expected to reduce the intercept value of the swim speed–fatigue time relationship. The slope, in contrast, may have remained unaffected if fish abandoned their ascent at a similar level of fatigue. However, at faster flows (U_f) and swim speeds (U_s), the range of times at which fish could abandon their effort was reduced, i.e. skewness was constrained at zero time. Greater skewness at smaller values of U_s led to reduced magnitude of the slope, as well as greater variance of the estimate. For these reasons, estimates of both slope and intercept values are conservative, and one can expect estimates of U_{gopt} to be correspondingly high. The presence of outliers had this effect on the alewife models; among other species, the magnitude of this error appears to be relatively small.

A further limitation of this approach that calls into question the validity of assumptions 2 and 3 is the absence of the cross-sectional uniformity of flow and consistency of velocity that characterizes most controlled laboratory studies. Future modifications to the flume apparatus may address this limitation; however, such nonuniformity of flow is a feature of natural rivers, culverts and fishways, and may provide a realistic context for fish behavior (Haro et al., 2004). In any case, the disorganized, microturbulent character of the flow in this flume can be expected to have acted to decrease performance (Enders et al., 2003); opportunities for fish to take advantage of eddies (e.g. Hinch and Rand, 2000; Liao et al., 2003) were minimal or nonexistent here. By continuously monitoring hydraulic parameters, changes in water velocity were accounted for; combining this with the correction factors (Table 1) removed any bias from values of water velocity assigned to each ascending fish. In this way, performance measures described here can be considered accurate, but conservative relative to actual performance in a natural setting.

The adequacy of the methods for identifying mode shifts and slopes was also limited by the finite length of the flume and the resulting censored observations, particularly at low water velocities. The statistical methods applied here, though novel in this application, are well-known to be robust in the presence of censoring. Any uncertainty arising from the censored data is adequately accounted for by and included in the standard error estimates; the large sample sizes presented here should be more than sufficient to eliminate any systematic bias introduced using these methods (Allison, 1995; Hosmer and Lemeshow, 1999). Heavy censoring at the lowest water velocities did limit the power of these estimates, however, especially among American shad swimming in prolonged mode.

The fourth assumption is more reasonable. Since all fish were naïve, they clearly had no previous knowledge of the length of the barrier. They were, however, able to stage multiple attempts, and it is possible that some knowledge was acquired in this way (Castro-Santos, 2004). With knowledge of the length of the barrier, fish could select either a time-minimizing (i.e. speed-maximizing) strategy (swim faster than U_{gopt}, and thus minimize, for example, exposure to predators), or a time-maximizing strategy (swim slower than U_{gopt}, and thus reduce instantaneous energetic costs). By matching fatigue time and swim speed to barrier length (Figs 1, 2A), fish could potentially reduce energetic costs or other risks associated with the distance-maximizing swim speeds. While these strategies may make sense in some circumstances, they are unlikely in this context. Moreover, because most individuals achieved the greatest distance on the first attempt, there is no reason to expect the fish to adopt any strategy other than distance-maximization, i.e. by swimming at the appropriate U_{gopt}.

Although this approach will probably tend to underestimate the physiological limits to performance, it may provide a more realistic measure of the behaviors that fish actually exhibit in the wild, and may therefore be more meaningful from ecological and evolutionary perspectives. Moreover, because of the limitations of the coercive approach, along with those of the machines within which fish are usually swum, few studies exist that describe swimming performance at such high speeds. Indeed, many of the observed swim speeds far exceeded predicted maxima for fish of this size and morphology (Videler and Wardle, 1991).

Swim speed optimization

Of the six species tested, only the anadromous clupeids fully adopted the predicted distance-maximizing behavior. This was most evident with American shad, which switched from U_{goptP} to U_{goptS} at the predicted flow velocities, and maintained a relatively constant groundspeed in sprint mode against a U_f range >4 BL S⁻¹.

The nonclupeids also adopted constant groundspeeds, but these were appropriate only for prolonged mode (U_{goptP}), and no apparent benefit accrued to any species for swimming at U_{goptP} at $U_f > U_{fcrit}$. This is evident from the general absence of significant negative correlations with the R_U and R_P residuals, and is consistent with the hypothesis that this was not a distance-maximizing strategy. On the contrary, positive coefficient values for white sucker and striped bass suggest that there was a cost associated with the observed speed, and fish that deviated from the mean swam greater distances.

Conversely, fish did maximize distance by swimming at U_{goptS} at flows $>U_{fcrit}$, as indicated by the strongly significant negative values of coefficients of the R_S statistic.

These results, while supporting the hypotheses indicated by the model, may instead be an artifact of varying condition of individual fish: fish in better condition may swim faster and farther than the others (Brett et al., 1958; Hochachka, 1961). Furthermore, inaccuracies arising from the scaling of swim and flow speeds to body lengths may cause spurious results (Drucker, 1996; see also Packard and Boardman, 1999 for a more mathematical treatment of this issue). This is a concern primarily for the striped bass models, owing to the large size range; scaling errors should be minimal among the other species (Table 1). Nevertheless, these data do support the idea that an optimum groundspeed exists for each mode, and that failure to swim at the correct speed results in reduced distance of ascent.

The same logic used above can be applied to mode shifts in the absence of flow. The distance-maximizing critical swim speed at which fish should switch from prolonged to sprint modes (U_{scrit}) occurs when

$$U_{scrit} = \frac{a_P - a_B}{b_B - b_P} \quad .$$ (10)

Thus, if the switch between modes is a facultative behavioral response (Drucker, 1996; Peake and Farrell, 2004), it should always be a discrete effect, whether in still or moving water. This may help explain why Brett (1964) and others have described modes as categorical shifts, with transition zones characterized by few data.

Trump and Leggett (1980) explored the effect of currents on optimal swim speeds, and produced predictions that are superficially similar to those presented here. Where a velocity challenge is encountered that is constant in time but finite in space, their model predicts an optimal groundspeed of m^{-1}, where m is the exponent of the energy equation $E_s = ae^{mU_s}$ [J kg^{-1} s^{-1}] (Brett, 1965; Webb, 1975), much like the model presented here. However, because the slope of the metabolism–swim speed relationship should increase as fish recruit anaerobic processes, the optimal groundspeed should decrease as fish switch from prolonged to burst modes – exactly the opposite of what my model predicts, and what these data suggest.

Likewise, the predictions of models generated by Weihs (1973) and Videler (1993) are not supported by these data. When Weihs' equations 7 and 8 (Weihs, 1973), and Videler's equations 9.1 and 9.2 (Videler, 1993) are adjusted for flow (similar to Equations 2–4 here), both sets of models predict distance-maximizing groundspeeds that accelerate with increasing flow. Again, this is not in accordance with the observed behaviors. None of these other models was developed for fish swimming in nonsustainable modes, however, and recruitment of anaerobic metabolism, alternative gaits, etc., may alter the relationship between cost of transport and swim speed on which they are based.

Other strategies may optimize for conditions unlike those present in this study. For example, fish may approach velocity barriers by swimming at maximum possible speed. This could be appropriate for leaping species like salmon that may want to maximize the likelihood of traversing a falls of unknown height. None of the species tested here employs leaping behavior in migration, so it is not surprising that maximum speed was not employed. Another strategy might be to employ alternate gait patterns, thereby improving energetic efficiency (Weihs, 1974; Videler and Weihs, 1982), or to capitalize on low-velocity zones, as white sucker did against the lower velocities here. Any such kinematic or behavioral strategy will still have an associated swim speed–fatigue time relationship, however, and so will be intrinsically included in the models presented here. As such, these models may be considered robust in the presence of behavioral, kinematic, and physiological diversity.

One optimizing strategy that these models may not adequately account for is the staging of repeated attempts. By increasing the rate at which they stage successive attempts fish can increase the likelihood of passage (Castro-Santos 2002, 2004). Fish may reduce recovery time by swimming at slower speeds, thereby increasing attempt rate and possibly offsetting the costs incurred by deviating from U_{gopt}. This strategy still does not account for the consistency in groundspeed observed here, particularly among the non-clupeids, nor for the fact that most individuals reached their maximum distance of ascent on the first attempt. It seems likely that some other factor is at work.

The apparent presence of distance-maximizing behavior among the anadromous clupeids, and its partial absence among the potomodromous non-clupeids, suggests the presence of underlying selective processes. Webb (1994) points out that the range of gaits available to fishes can have profound evolutionary consequences; perhaps the relationship between swim speed and fatigue time is shaped in part by the hydraulic conditions fish need to traverse in order to maximize fitness. Anadromous clupeids need to ascend rivers during spring freshets to spawn, when high flows and cold temperatures place strong demands on swimming capacity. Thus sprinting among these fish constitutes a fitness-critical migratory mode. Potomodromous species, in contrast, have greater choice in where they spawn, and the striped bass used here are amphidromous, entering the river to feed. The fastest modes for these species may therefore not be associated with migration, but rather with other fitness-crucial behaviors, like predation and predator avoidance. By selecting the appropriate groundspeed for the prolonged mode, these species may be optimizing for different habitats, a behavior that could help explain observed limits to their distributions.

In addition to their ecological context, these results also have important implications with respect to the design of fish passage structures. To maintain such consistent groundspeeds, fish must use some means of detecting their progress relative to the ground (presumably vision). This may help explain why anadromous fish often follow structure when migrating up rivers, and also points to the potential harmful effect of entrained bubbles and turbulence on passage success, and even on willingness to attempt to traverse zones of difficult passage.

Bainbridge (1960) observed that maximum distance of ascent through fishways is governed by the swim speed–fatigue

time relationship, and such data have been used extensively to determine the location and size of resting pools within fishways (Beamish, 1978). The distance of ascent predicted from this relationship, however, assumes that fish swim at their optimum speed which, as in this study, may often not be the case. Any recommendations for fishway designs based on the swim speed–fatigue time relationship should therefore take into account the expected variability around the optimum, and the costs of such variability in terms of distance of ascent when predicting passage success.

List of symbols

a,b	coefficients
BL	body length
CF	correction factor
D_g	ground distance
D_{max}	maximum distance
D_{maxP}	maximum distance in prolonged mode
D_{maxS}	maximum distance in sprint mode
D_s	maximum distance a fish can swim
$f(T)$	probability density function
FL	fork length
R	residual
$S(T)$	survivorship function
T	fatigue time
U_f	speed of flow
U_{fa}	mean U_f adjusted for species- and U_{nom}-specific ascent routes
U_{fcrit}	critical speed of flow
U_g	ground speed
U_{gopt}	optimal ground speed
U_{mp}	maximum prolonged speed
U_{ms}	maximum sustained speed
U_{nom}	nominal velocity
U_{opt}	optimum swim speed
U_s	relative swim speed

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