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[Article]

# Modeling the Effect of Varying Swim Speeds on Fish Passage through Velocity Barriers

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*Abstract*.—The distance fish can swim through zones of high-velocity flow is an important factor limiting the distribution and conservation of riverine and diadromous fishes. Often, these barriers are characterized by nonuniform flow conditions, and it is likely that fish will swim at varying speeds to traverse them. Existing models used to predict passage success, however, typically include the unrealistic assumption that fish swim at a constant speed regardless of the speed of flow. This paper demonstrates how the maximum distance of ascent through velocity barriers can be estimated from the swim speed–fatigue time relationship, allowing for variation in both swim speed and water velocity.

The distance fish can swim through zones of high-velocity flow is an important factor limiting distribution and conservation of riverine and diadromous fishes (Weaver 1963, 1965; Winstone et al. 1985; Lucas and Frear 1997; Peake et al. 1997; Warren and Pardew 1998; Cooke et al. 2005). These species often undergo within-stream movements that range from small-scale, daily foraging movements to larger movements associated with range shifts, dispersal, or migrations (Lucas and Batley 1996; Juanes et al. 2000; Bunt et al. 2001; Jellyman and Sykes 2003; Okland et al. 2004). During the upstream phase of these movements, fish may encounter velocity barriers, that is, zones of high-velocity flow that exceed maximum sustainable swim speeds ($U_{ms}$; Beamish 1978, see Table 1 for a complete list of variables). Depending on swimming performance and hydraulic characteristics, these barriers can be impassable. Velocity barriers occur naturally, such as at a falls or rapids, or they may be anthropogenic in origin. Examples of anthropogenic velocity barriers include culverts, some low-head or breached dams, and technical fishways. Poor passage through these barriers is often attributed to limits of swimming capacity, although rigorous tests are lacking. Typically, these barriers are characterized by varying flow velocities, and fish probably swim at varying speeds to traverse them. This paper describes how these varying swim speeds can be incorporated into fatigue time models to produce estimates of maximum distance traversed.

Recent work has shown that when confronted with a velocity barrier, fish can maximize the distance of ascent by swimming at a constant speed relative to the ground, or groundspeed (Castro-Santos 2005). The optimal value of this groundspeed ($U_{gopt}$) can be derived from the effect of swim speed on fatigue time, which follows a well-established relationship:

$$\log_e(T) = a + bU_s \mid b < 0 \qquad (1)$$

(Brett 1964), where fatigue time $T$ is determined by swim speed ($U_s$, in body lengths [BL]/s), which is characterized by intercept ($a$) and slope ($b$) coefficients. Maximum distance of ascent ($D_{max}$) is limited by the swim speed–fatigue time relationship and the speed of flow ($U_f$) as follows:

$$D_{max} = (U_s - U_f) \times e^{a+bU_s}, \qquad (2)$$

and distance is maximized by swimming at the optimal groundspeed: $U_{gopt} = -1/b$ (Castro-Santos 2005). Typically, however, two modes of nonsustainable swim speeds exist: prolonged mode, which is nominally characterized by fatigue times from 20 s to 200 min, and sprint mode, in which fatigue occurs in less than 20 s. Different coefficients exist for these two modes, and the appropriate mode optimum will depend on whether $U_f$ is greater or less than a critical speed of flow ($U_{fcrit}$), which is determined as

$$U_{fcrit} = \frac{\log_e\left(\frac{b_S}{b_P}\right) + a_P - a_S}{b_S - b_P}. \qquad (3)$$

Coefficients are the same as in equation (1), subscripted $P$ or $S$ to indicate prolonged or sprint mode, respectively (Castro-Santos 2005).

It is important to recognize that fish do not always select the distance-maximizing swim speed, and the extent to which the optimum is approached appears to be under the influence of both individual variability and life history or phylogenetic constraints. Where fish fail to select the appropriate swim speed, $D_{max}$ is reduced in accordance with equation (2). Variation in

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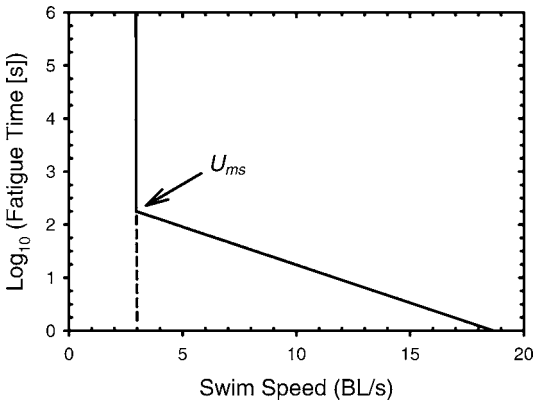


FIGURE 1.—Swim speed–fatigue time relationship for a hypothetical fish with only sustained and sprint modes. Data are from Castro-Santos (2005) and represent values for American shad swimming in sustained and sprint modes. The intercept $a_S$ is 6.16, the slope $b_S$ is −0.33, and the maximum sustainable swim speed $U_{ms}$ is set at 3.0 BL/s. The fatigue time axis is scaled to base-10 exponents for simplicity.

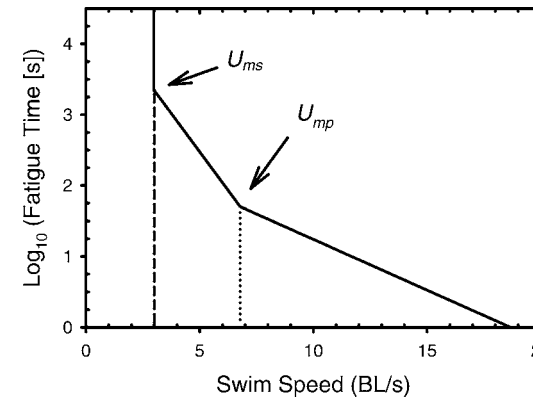


FIGURE 2.—Swim speed–fatigue time relationship for a realistic fish (American shad; from Castro-Santos 2005). Maximum swimming speeds for the sustained ($U_{ms}$) and prolonged ($U_{mp}$) modes are indicated by arrows. Hypothetical coefficients are those required for equation (6) (prolonged mode: intercept $a_P = 10.7$; slope $b_P$ −1.0) (note that the figure scales to base-10 logarithms).

both the extent to which individual fish approximate $U_{gopt}$ and in endurance leads to a reduction and variation in $D_{max}$, consistent with the findings of Haro et al. (2004) and Castro-Santos (2002, 2004).

Although the studies described above were conducted in uniform, axial-flow conditions (Chow 1959), the same principles apply when fish are confronted with varying flow: fish will maximize $D_{max}$ by swimming at the mode-appropriate $U_{gopt}$. Where $U_f$ crosses the $U_{fcrit}$ threshold, fish should switch between prolonged and burst mode, otherwise $U_{gopt}$ will be a constant. Regardless of whether fish approximate $U_{gopt}$, available data indicate that $U_s$ changes with $U_f$ (Castro-Santos 2005). This negates Beach's (1984) assertion that fish will choose a constant swim speed when confronted with velocity barriers, an assertion that forms the basis of swimming performance estimates currently used in most fishway design guidelines (Bell 1991; Clay 1995; Larinier 2002). The following model of passage success is derived directly from the swim speed–fatigue time relationship and allows for variation in both swim speed and flow velocity.

## The Model

Consider a hypothetical fish whose swim speed–fatigue time relationship consists of only two modes (Figure 1). Fish fatigue only when swimming at speeds greater than $U_{ms}$ (set here at 3.0 BL/s; $a_S = 6.16$; $b_S = 0.33$; from Castro-Santos 2005). From equation (1), a fish swimming at 4.0 BL/s would fatigue after $e^{4.84}$, or 126 s. Thus, every second the fish spends swimming at 4.0 BL/s will consume 1/126th of the remaining available time to fatigue ($T$). If this fish were to swim at 10 BL/s, then the expected fatigue time is $e^{2.86}$, or 17.5 s, and each second of effort would consume 1/17.5th of the remaining $T$. At 18.5 BL/s, the fish would fatigue in a single second. To summarize, each time interval (dt) in which $U_s$ exceeds $U_{ms}$ consumes a proportion of the initial $T$ (call this $\Delta T$) equal to the inverse of the swim speed–fatigue time relationship. Thus, from equation (1),

$$\Delta T = e^{-(a+bU_s)}dt \mid U_s > U_{ms}. \tag{4}$$

Percent fatigue ($F\%$) is the cumulative value of the $\Delta T$s failure occurs when the sum of all the $\Delta T$s equals 1.0:

$$F\% = 100 \times \int_{t=0}^{T*} e^{-(a+bU_s)}dt, \tag{5}$$

where $T*$ is the final fatigue time, which is conditional on the actual speeds swum by the fish. This implies that (1) the passage of time at any given $U_s$ greater than $U_{ms}$ acts to increase $F\%$ and (2) this percentage, rather than the total amount of time left, is independent of subsequent swim speeds. Note that no accounting is made for recovery from fatigue that may occur if sprinting bouts are interspersed with bouts of sustained swimming or rest.

The presence of two nonsustainable modes that characterize swimming of actual fish further complicates this relationship (Figure 2). Here, the magnitude of $\Delta T$ is governed by distinct slope and intercept

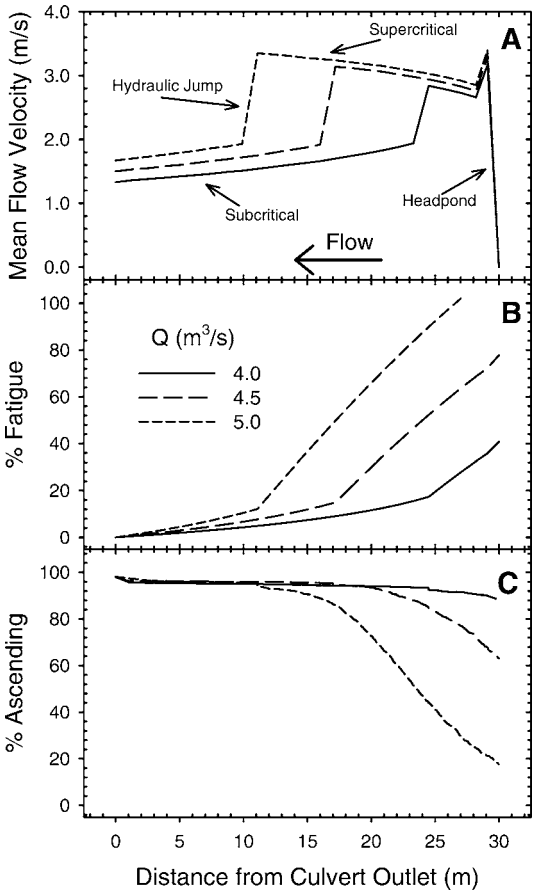


FIGURE 3.—Application of equations (6) and (7). Panel **(A)** shows the mean velocity profile of a 30-m-long box culvert at 1% slope. At each of three discharge levels ($Q$; $m^3/s$), flow is initially supercritical (shallower and faster) and then becomes subcritical (slower and deeper); these phases are separated by a hydraulic jump. Panel **(B)** shows the expected percent fatigue for a 41.8-cm American shad ascending the culvert at distance-maximizing swim speeds. At 4.0- and 4.5-$m^3/s$ flows, the fish successfully exits the culvert without fatiguing; at 5.0-$m^3/s$ flow, the fish fatigues at 27 m. In panel **(C)**, the results from a stochastic model illustrate the expected $D_{max}$ distributions when the selected swim speed and fish size are allowed to vary. Note that some fish failed very early in the culvert and that some failure occurred under all three conditions.

coefficients that characterize each mode. Assuming that $\Delta T$ (i.e., the reduction in available endurance time) remains proportional across modes, this effect can be represented as follows:

$$F\% = 100 \times \int_{t=0}^{T*} \left[e^{-(a_S+b_S U_s)}\right]^{\delta_t} \times \left[e^{-(a_P+b_P U_s)}\right]^{1-\delta_t} dt \quad \left| \begin{array}{l} \delta_t=1 \text{ for } U_s>U_{mp} \\ \delta_t=0 \text{ for } U_{ms}<U_s\leq U_{mp} \end{array}\right., \tag{6}$$

where $U_{mp}$ is the maximum prolonged speed. As above, fatigue occurs when $F\%$ reaches 100%. Having identified the fatigue time $T*$, conditional on the variable swim speeds, it is now possible to calculate $D_{max}$ based on those swim speeds and times:

$$D_{max} = \int_{t=0}^{T*} (U_s - U_f)dt. \tag{7}$$

## Results

Suppose an engineer wants to install a new culvert that must allow passage of American shad *Alosa sapidissima*. The culvert is a square concrete box (30 m long × 3 m wide × 3 m high) set at a 1% slope. The approach flow velocity in the culvert inlet is negligible, and the tailwater depth is 1 m. No roughening elements are to be added, giving a roughness value for smooth concrete of 0.013 (Manning's $n$; Chow 1959). The stream that is to pass through the culvert has a median flow of 4 $m^3/s$ during the migratory period. Flows can be much higher though, and the 90th percentile of discharge (10% exceedance flow) is 5 $m^3/s$.

This information is used to determine hydraulic characteristics of the culvert. FishXing 3.0 software (Furniss et al. 2006) provided the hydraulic data in Figure 3a, which described the longitudinal velocity profile in the culvert under three hypothetical flows of 4.0, 4.5, and 5.0 $m^3/s$. These data, coupled with equations (6) and (7) and the endurance relationships (Castro-Santos 2005), provide estimates of $F\%$ for a single American shad swimming up the culvert (Figure 3b).

In this example, an average-sized American shad (from the Connecticut River: BL = 41.8 cm; Castro-Santos 2005 and personal observation) swimming at optimal groundspeeds of 1.00 and 3.03 BL/s in prolonged and sprint mode, respectively, will ascend the full length of the culvert without fatiguing at each of the lower discharge rates but will fail against 5 $m^3/s$. Thus, if we assume that fish always swim at distance-maximizing groundspeeds ($U_{gopt}$), then these models suggest that the culvert should not be a velocity barrier except under the highest modeled flows.

In fact, however, fish do not always swim at these optimal speeds (Castro-Santos 2005). Moreover, the model assumes an average-sized American shad. What about larger or smaller fish that vary in their swimming ability and their ability to approximate the distance-maximizing swim speeds? Using data from Castro-Santos (2005) and unpublished data, I incorporated both of these sources of variability into a stochastic model and simulated 1,000 American shad entering under each level of discharge. Fork lengths were

TABLE 1.—Variables and coefficients used to model the effect of swimming speed on passage through velocity barriers.

| | |
|---|---|
| $a$, $b$ | Coefficients (intercept, slope) of the swim speed–fatigue time relationship |
| $T$ | Fatigue time, assuming a fixed swim speed |
| $T^*$ | Fatigue time, conditional on actual swim speed and duration |
| BL | Body lengths |
| $U_s$ | Swim speed (BL/s) |
| $U_{ms}$ | Maximum sustainable swim speed |
| $U_{mp}$ | Maximum prolonged swim speed |
| $U_{crit}$ | An estimate of $U_{ms}$, derived from ramped-velocity tests |
| $U_f$ | Flow velocity (BL/s) |
| $D_{max}$ | Maximum distance of ascent |
| $U_{gopt}$ | Distance-maximizing groundspeed |
| $U_{fcrit}$ | Critical flow velocity, where fish should switch between $U_{gopt}$ for prolonged and sprint modes in order to maximize $D_{max}$ |
| $\Delta T$ | The proportional reduction in fatigue time incurred by swimming at a given speed for a fixed amount of time |
| $dt$ | Time interval (s) during which a fish swims at a fixed speed |
| $F\%$ | Percent fatigue, the cumulative value of $\Delta T$ over time |
| $S(D)$ | Survivorship function, or the proportion of fish expected to successfully traverse a given distance without fatiguing |

41.8 ± 3.49 cm, and groundspeeds were 0.93 ± 0.53 BL/s in prolonged mode and 2.66 ± 1.14 BL/s in sprint mode; all distributions were approximately normal and are presented here as means ± SDs.

This yielded the models presented in Figure 3c. These are survivorship models (Kaplan and Meier 1958; Hosmer and Lemeshow 1999) similar to those reported by Castro-Santos (2002) and Haro et al. (2004); they model the proportion of the population that successfully reaches a given distance ($S[D]$).

In each of the three models, a small but significant proportion fails to ascend the culvert without even entering. This is because the model randomly allows a small proportion of the population to swim at speeds less than or barely greater than the speed of water flow. In these models, the fish were not allowed to adjust their groundspeed strategy, and so they never got past the culvert entrance.

Similar failures can be seen as fish encounter flow transitioning from subcritical to supercritical (Figure 3a; Chow 1959). The accompanying increase in flow velocity ($U_f$) caused the simulated American shad to cross the $U_{fcrit}$ threshold and to switch swim speeds to approximate groundspeeds characteristic of sprint mode. This was allowed to vary independently from the approximation of the prolonged optimum. Because the characteristic mean groundspeed was greater for sprint mode than for prolonged mode, American shad rarely swam at speeds less than $U_f$ once they crossed the $U_{fcrit}$ threshold into sprint mode. Some fish, however, did not have sufficient groundspeeds to make adequate forward progress and so fatigued themselves, or they swam too fast without passing the culvert. This happened even under the 4-$m^3$/s condition. In contrast, some fish did pass the full length of the culvert even under the 5-$m^3$/s condition. These represent stronger-swimming, larger fish that sufficiently approximated the distance-maximizing groundspeed ($U_{gopt}$) to be successful.

## Discussion

Although fisheries managers, engineers, and scientists have long been interested in the ability of fish to traverse velocity barriers (Stringham 1924; Bainbridge 1964; Brett 1964; Beamish 1978), predictive models have been notoriously unreliable. This has prompted some researchers (Weaver 1963, 1965; Castro-Santos 2002; Haro et al. 2004) to develop empirical models of swimming performance based on actual distance traversed over the ground. A common factor of all these models, however, is the assumption that the modeled barriers are of steady uniform velocity. This condition is rare in the wild, which undermines model validity. The models described here provide a partial solution to this problem, releasing managers from the restrictions of these unrealistic assumptions.

However, the improved verisimilitude of these models places a greater burden on managers, who will now have to include explicit assumptions about the speed at which fish actually swim when confronted with velocity barriers. This is a marked change from Beach (1984) and others (Powers et al. 1985; Bell 1991; Clay 1995) who based their models on the assumption that fish would approach velocity barriers by swimming at near-maximal speeds. Those models include other unrealistic assumptions as well: (1) that fish will all have similar levels of glycogen in their white muscle; (2) that fish will volitionally swim to physiological fatigue; and (3) that interspecific and intraspecific variation in swimming performance is negligible (Nelson et al. 2002, 2003; Castro-Santos and Haro 2006). Castro-Santos (2005) showed that although average swim speeds can be predictable, they are not necessarily those that maximize distance and considerable variability exists among both individuals and species. Thus, researchers that use predictive tools such as FishXing (Furniss et al. 2006) and Katopodis (1994) must take this variability into account if they wish to avoid serious inaccuracies.

The example provided here both illustrates and addresses these issues. Under the deterministic models, we would expect all American shad to pass the culvert under the 4.0- and 4.5-$m^3$/s conditions and none to pass under the 5.0-$m^3$/s condition. The stochastic models showed how inaccurate those predictions can be. These

models predicted about 12% failure even at the 4.0-$m^3/s$ condition, where at distance-maximizing swim speeds an average American shad would generally not exceed an $F\%$ value of 40%. Although the behaviors that led to this failure, primarily swimming at negative or near-zero groundspeeds, may seem intuitively unrealistic, experience suggests otherwise. American shad are known to take several days to ascend a single fishway (Sullivan 2004), and during the studies described in Castro-Santos (2002, 2005) fish were often seen spending considerable time at the entrance of a culvert-like channel but making little progress up the flume (author's unpublished data).

Clearly, however, the model could be improved. For example, modeled fish were not allowed to stage more than one attempt to ascend the flume. Repeated ascent efforts can have a dramatic effect on success rate, in part because in each attempt fish have another opportunity to improve their approximation of $U_{gopt}$ (Castro-Santos 2002, 2004). Fish that selected negative groundspeeds never had an opportunity to fatigue; this means they should have been able to immediately re-enter for a second attempt. Those that did fatigue should be allowed to re-enter after a period of recovery, and subsequent performance could be linked to the extent of recovery. Data supporting recovery rates and volitional sprinting behavior are rare, however, and more work needs to be done before these aspects can be reliably estimated.

A further criticism of these models may be that they rely on swim speeds standardized to BL per second. This implicitly assumes that swimming performance scales isometrically with BL, whereas it is well known that the relationship is allometric and varies by species (Goolish 1991; Packard and Boardman 1999). Inaccuracies arising from this practice can be significant, especially when a large range of sizes are to be modeled or when the modeled populations deviate substantially from the original data. However, standardized endurance relationships were used here and in Castro-Santos (2005) because (1) the preponderance of data available to managers is reported in this way and (2) the primary purpose of these models is to help develop engineering specifications. Furthermore, when applied to a relatively small range of body sizes that approximate the data from which the swim speed–fatigue time models are derived (as was done here), the error associated with standardization to BL should be inconsequential.

The models described in this paper raise additional questions regarding the response of fish to critical flow velocities ($U_{fcrit}$). Previously, I suggested that fish should choose optimal groundspeeds for sprint or prolonged mode depending on whether the critical speed of flow was greater or less than $U_{fcrit}$ (Castro-Santos 2005). In environments of rapidly varying velocities, however, this might require fish to switch repeatedly between prolonged and sprint optima, particularly if the median velocity is near $U_{fcrit}$. This would entail frequent accelerations that may incur greater energetic costs, thereby resulting in a lower $D_{max}$ than might be achieved by swimming at speeds that would be suboptimal in steady flows. The relative costs and benefits of mode switching could potentially be calculated but would require information on (1) the effect of acceleration rates and durations on the swim speed–fatigue time relationship; (2) the rates at which fish actually accelerate when confronted with $U_f$ that switches above and below $U_{fcrit}$; (3) the relative benefit, in terms of $D_{max}$, of swimming at the faster mode; and (4) the expected duration of exposure to the faster flows. Of these, item (3) can be estimated from the swim speed–fatigue time relationship and item (4) is a measurable combination of hydraulic and behavioral characteristics. Items (1) and (2) would require experimentation and direct observation, although the former might be estimated from known relationships (Weihs 1974; Videler and Weihs 1982).

Although the costs of acceleration can be estimated from purely mechanical principles, these estimates may overlook biological processes that cause actual costs and performance to differ from their expected values (Driedzic and Hochachka 1978; Jones and Randall 1978). A more-accurate approach would be to directly measure the effect of acceleration on the swim speed–fatigue time relationship.

Such data would have additional benefits. For example, they would help predict the extent to which perched culverts (a common condition where culverts are raised above the streambed) pose barriers to fish movements (e.g., Gibson et al. 2005). This condition requires fish to leap into the culvert, where they may then be confronted with a velocity challenge. Thus, it would be of some interest to know the extent to which the acceleration required in the leap phase (perhaps entailing multiple leaps) affects subsequent endurance.

An obvious flaw in the foregoing models is they provide no opportunity for fish to recover from fatigue by swimming at speeds less than $U_{ms}$. Although some data describe recovery rates as a function of swim speed or expended effort (Hochachka 1961; Black et al. 1962; Driedzic and Kiceniuk 1976; Franklin et al. 1996; Farrell et al. 1998; Jain et al. 1998; Castro-Santos 2002), most of these measure physiological recovery, or the time required for metabolites and substrates to return to pre-exercise conditions. A more-relevant measure of recovery would be performance based. Jain et al. (1998) quantified the effect of

repeated swimming bouts on recovery of $U_{crit}$ (an estimate of $U_{ms}$), while others have evaluated the effect of fatigue on recovery rates after volitional sprinting performance (Castro-Santos 2002, 2004; Peake and Farrell 2005). A similar approach could be applied using these models, where the quantified variable is the rate of recovery of $F\%$. When such data do become available, they can be readily incorporated into equation (6) to provide estimates that apply more broadly to passage models and may be used to develop improved fishway designs that include resting pools.

These questions of the physiological basis of fatigue and recovery also bear on the mechanisms underlying the swim speed–fatigue time relationship, and the models presented here provide a framework for testing several assumptions. These include: (1) that the limiting factor in both sprint and prolonged mode is governed by common substrates and byproducts of anaerobic metabolism (Hochachka 1961; Moyes and West 1995) and (2) that the swim speed–fatigue time relationship in sprint mode derives from the costs of steady swimming and continuous use of anaerobic processes, whereas the greater slope and intercept of the prolonged relationship represent some proportional reduction in these costs. Such a reduction may be derived, for example, from unsteady (burst-and-coast) swimming or some other means of mixed recruitment of aerobic and anaerobic metabolism (Brett 1964; Peake and Farrell 2004). If these assumptions are valid, then the logic applied above can be directly applied to the two nonsustainable modes. In other words, the proportion of available resources consumed ($F\%$) applies equally to both modes, a hypothesis that can be tested using equation (6). Such tests may also help explain the widely observed phenomenon of discrete transition zones between sustained, prolonged, and sprint modes (Brett 1964; Webb 1975; Videler 1993).

In this paper, I have laid out several models and hypotheses based on accepted models of swim speed and fatigue time. It is intended that these will help both fisheries managers and bioengineers to better predict the ability of fish to pass obstacles, whether they are natural stream settings, culverts, or technical fishways. It must be acknowledged, however, that the underlying models, though widely accepted, have yet to be adequately explained on a physiological or biomechanical basis. Moreover, recent work suggests that estimates of swim speed and fatigue time generated using enclosed swim chambers may underestimate actual performance (Nelson et al. 2002; Peake 2004; Peake and Farrell 2004; Castro-Santos 2005). As our understanding of the physiological and behavioral mechanisms driving the swim speed–fatigue time relationship improves, the models presented here may have to be modified to accommodate new data. In the meantime, however, these models provide a basis for testing the accuracy of existing data along with various hypotheses that are of interest to both basic and applied researchers.

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