

**SPRINTING PERFORMANCE
OF UPSTREAM MIGRATORY FISHES**

Theodore Castro-Santos
University of Massachusetts, Conte Anadromous Fish Research Center
Turners Falls, MA 01376

Alex Haro
USGS-BRD, Conte Anadromous Fish Research Center
Turners Falls, MA 01376

Abstract

Migratory fishes are often confronted with zones of high velocity flow that must be traversed in order to reach spawning habitat. These challenges can be exacerbated by dams and other anthropogenic obstacles with profound implications for spawning success. The extent to which a given velocity challenge will impede migration is difficult to predict, however, because existing data on swimming performance (largely derived from respirometry studies) fail to quantify maximum anaerobic locomotor capacity of free-swimming species. We addressed this issue using a 23-m long open-channel flume that fish enter volitionally and swim against controlled water velocities of 1.5- 4.5 m*s⁻¹. Performance indicators included distance and duration of ascent and maximum swimming speed. Distance of ascent and duration of time spent in the flume varied among species, being determined largely by water velocity and body length. We observed maximum volitional swimming speeds of 10-22 lengths s⁻¹, well in excess of maxima predicted in the literature, and found evidence that sprinting behavior may reflect a tradeoff between speed and distance of ascent.

Introduction

The speed at which fish swim fundamentally affects their ecology and life history. This is particularly true of migratory species, where fish need to cross long distances and, in the case of many anadromous species, zones of high

velocity in order to complete their life cycle. The limits to performance are intrinsically interesting, providing biologists with insights on the constraints on evolution imposed by the environment, and providing engineers with boundaries for hydraulic criteria used in the design of fish passage structures.

Much of fish locomotion research has focused on the energetics of swimming, and on the relationship between swim speed and endurance. Respirometers, based on a prototype developed by Brett 1964), have been used to determine metabolic costs of swimming up to maximum sustainable speeds (U_{crit}). Various studies have shown that morphology affects swimming efficiency and that U_{crit} increases with body length (e.g. Brett 1965a; Graham et al. 1994). The

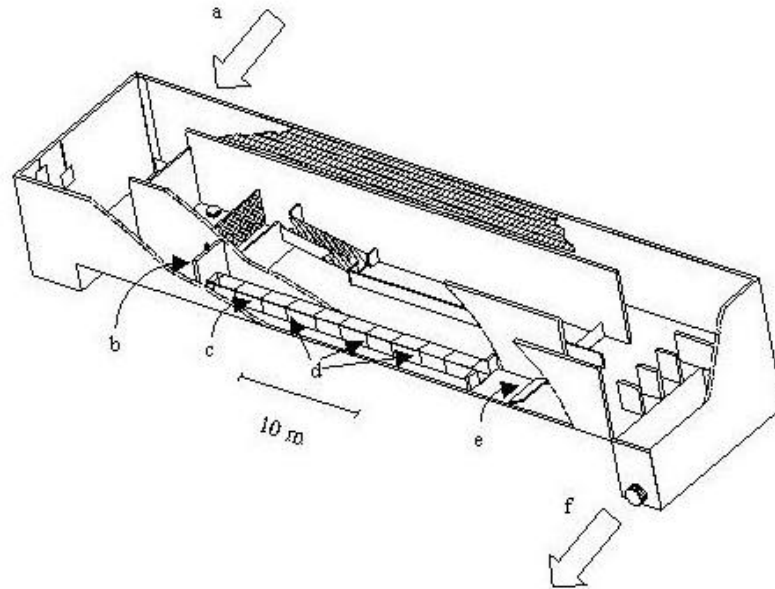


Figure 1. Flume facility at the Conte Anadromous Fish Research Center. Water enters the structure from a power canal (a), and is routed to the near flume, where a headpond is retained by a bulkhead with submerged slide gate (b). Water flows through the gate and into the burst-swimming flume (c), where progress of fish against the velocity challenge is monitored by an array of PIT tag antennas (d). Water depth is controlled by a tailwater gate (e), over which it flows before returning to the river through an outfall pipe (f).

relationship between size, shape, and swimming ability remains elusive, however, in part due to limited availability of data over a range of these values.

Effectively missing from the fish swimming literature are studies quantifying maximum through-water swimming speed (U_{max}) of free-swimming fish, and quantitative assessments of their ability to overcome velocity obstacles. Herein we present results describing sprinting performance of a suite of six migratory species, in terms of both speed attained and distance covered.

Methods

The S.O. Conte Anadromous Fish Research Center (USGS-BRD) houses a large flume facility designed for research and development of new fish passage structures (*i.e.* fish ladders, etc.; Haro et al. 1998; Haro et al. 1999; Figure 1). This facility is situated next to a hydroelectric power canal at Connecticut River km 197, near the Massachusetts-Vermont border (USA). Water is supplied to structures within the flumes through a 1.2-m diameter pipe coming from the power canal (Figure 1a), and outflow is routed to the bypassed reach of the river through a 2-m diameter pipe (Figure 1f). Flow of up to $10 \text{ m}^3 \text{ s}^{-1}$ can be controlled to within $\pm .05 \text{ m}^3 \text{ s}^{-1}$ by gate valves.

An experimental apparatus was constructed at the Conte lab that enabled us to examine and describe burst-swimming performance of a variety of migratory fish species in a controlled laboratory setting (Figure 1). The design consisted of a flume, 1 m^2 in cross section and 23 m long. Water was supplied from a headpond and slide gate designed to allow control of water velocities entering the flume. Depth was controlled by a combination of headpond/gate settings and a tailwater gate. All velocities, depths, etc. were monitored by computer and controlled by the investigators. Downstream of the flume was the tailwater or staging area, a low velocity zone from which fish volitionally entered the flume and attempted to swim against the flow.

Fish were captured at least one day before testing, measured and sexed (where possible). A small (3.8 mm diameter x 32.5 mm long), uniquely encoded transponding telemetry (PIT) tag attached to a fishhook was then attached to the fish through the cartilage at the base of the dorsal fin. Fish were held overnight in flow-through holding ponds connected to the flume building by a system of canals. This arrangement allowed fish to be seined into the test area

immediately before beginning each trial without being handled, an important feature because any handling is likely to affect performance.

Fish were presented with velocity challenges of 1.5, 2.5, 3.5, or 4.5 m s⁻¹. The smaller species (alewife and blueback herring) were not subject to the highest velocity because they were effectively constrained by 3.5 m s⁻¹.

Ascent of fish up the flume was monitored using an array of PIT tag antennas (Castro-Santos et al. 1996), along with standard and high-speed video. Standard

Table 1. Numbers of fish ascending the burst-swimming flume by species and velocity

Species	Fork Length (mm)			N
	Min	Max	Mean	
American shad (<i>Alosa sapidissima</i>)	325	520	417	642
Alewife (<i>A. pseudoharengus</i>)	215	265	239	177
Blueback herring (<i>A. aestivalis</i>)	200	245	220	78
Striped bass (<i>Morone saxatilis</i>)	235	970	486	103
Walleye (<i>Stizostedion vitreum</i>)	225	445	320	94
White sucker (<i>Catostomus comersoni</i>)	285	505	392	177

video was also used to determine the position of fish in three dimensions. One wall of the flume was made of clear acrylic, and an array of mirrors along the length of the flume set at 45° to this wall allowed a single camera to monitor both horizontal and vertical position. Due to the length of the flume, however, four cameras were required to assure complete coverage with a minimum of distortion.

This experimental setup provided a unique opportunity to study volitional burst-

swimming behavior. Because these fish have an innate motivation to move upstream, the jet of water issuing from the flume serves as the only cue necessary to motivate fish to enter and swim against the velocity provided. Thus, this structure simultaneously provides motivation and an enclosed arena, allowing precise measurement of behaviors and kinematics associated with burst-swimming.

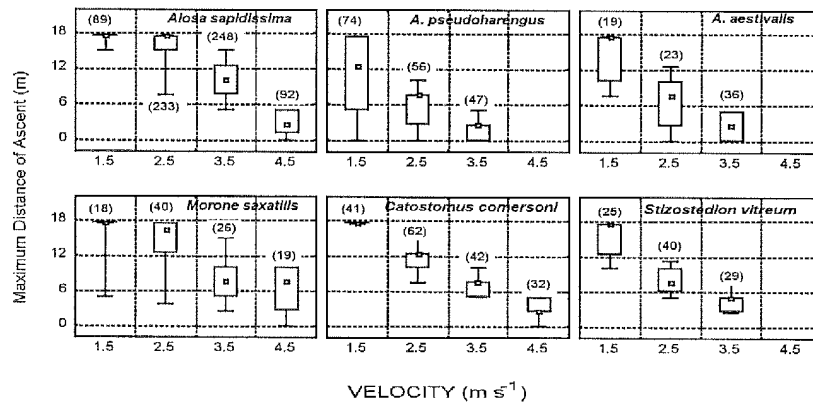
Results

We collected sprinting performance data from 1253 fish of six species between 1997 and 1999 (Table 1). Figure 2 shows maximum distance of ascent achieved by each species against velocity challenges of 1.5 – 4.5 m s⁻¹. Although some species were able to ascend the entire length of the flume at low velocities, none was able to progress beyond 10 m against velocities of 4.5 m s⁻¹.

Another measure of performance is maximum attained speed (U_{max}). Figure 3 shows preliminary U_{max} data for all six species. Maximum speed varied between species and increased with water velocity. The highest average speeds ranged from 10 L s⁻¹ (striped bass) to 23 L s⁻¹ (blueback herring).

Maximum speed also varied within species. For example, male American shad had higher U_{max} values than females, an effect that is even more pronounced when adjusted for body size (Figure 4).

Figure 2. Maximum distance of ascent against controlled velocity by species. Data are median, quartiles, and upper and lower 10th percentiles, with sample sizes in parentheses.



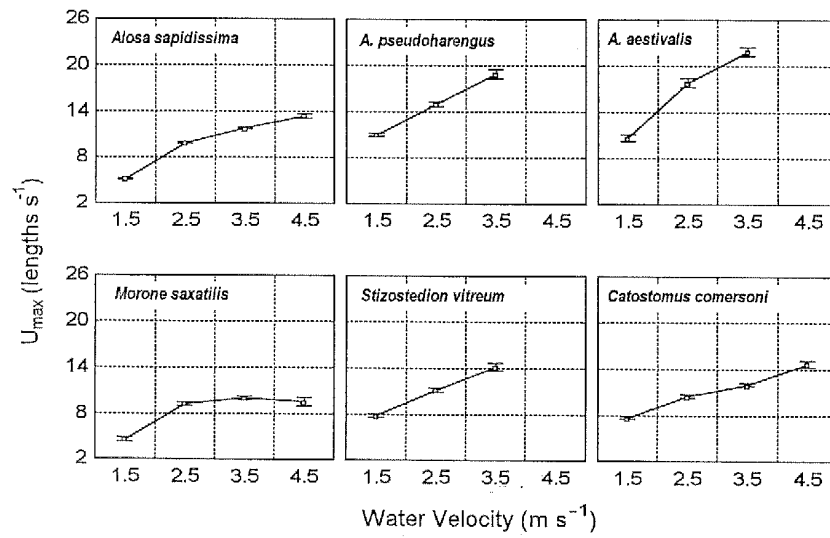
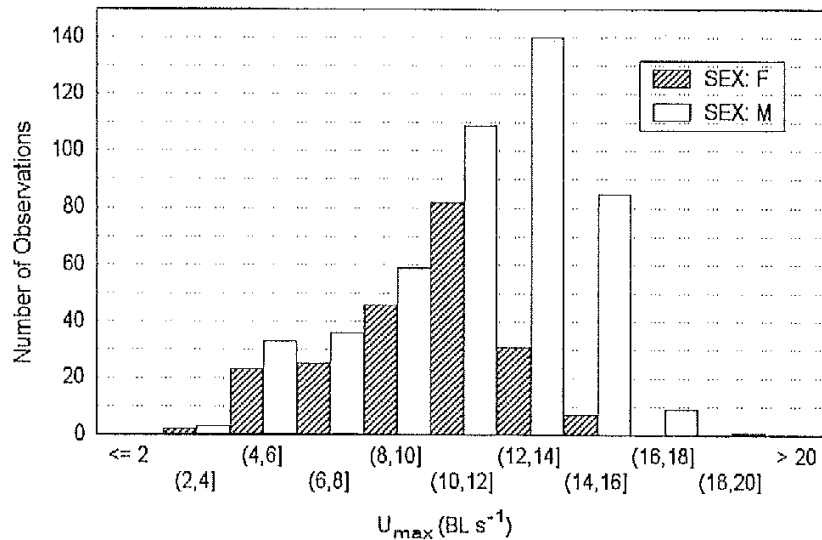


Figure 3. Maximum swim speed (U_{max}) by species and velocity. Data are mean \pm 2 SE.



Discussion

Meaningful estimates of swimming performance have been difficult to obtain, and our results demonstrate the dramatic effect experimental apparatus and design can have. Previous work (Brett 1965b; Wardle 1975; Webb 1975; Videler and Wardle 1991; Videler 1993) has consistently predicted lower maximum sprint speeds from those we observed. For example, Wardle (1975) predicted maximum sprint speeds of about 10 L s^{-1} for subcarangiform swimmers the size of American shad, walleye, and white suckers, and of about 15 L s^{-1} for alewife and blueback herring. By contrast, we observed fish outperforming these values by 50%, and the fact that maximum speed increased linearly with water velocity suggests that even greater speeds are possible. The only species that did not show this trend of increased speed at higher water velocities was the striped bass. This may reflect the large size range in this species relative to the others. Smaller bass tended not to enter the flume at higher velocities, and thus our data may reflect velocity based size selection, rather than actual decreased performance at higher velocities.

These discrepancies in maximum speed estimates are probably due to the limitations of the techniques used by previous researchers. Because of the scale of our apparatus, we were able to observe volitional sprinting behavior, without resorting to the coercive techniques typical of other experiments (*e.g.*, electric shock, closed respirometers). It is reasonable to assume that such coercion can induce stress, thereby limiting performance.

Previous work has also failed to predict intraspecific differences in performance such as those we observed between male and female American shad. The greater U_{max} values attained by males may be due in part to their smaller size ($\bar{x} = 40.0$ cm) relative to females ($\bar{x} = 45.1$ cm). However, although Wardle (1975) predicts greater values for smaller fish, the observed differences in U_{max} are far greater than predicted. This suggests underlying differences between sexes in either ability or motivation to perform; the former could result from greater investment in gonads characteristic of the females of this species, the latter could reflect some as-yet undescribed life-history characteristic.

The observed differences in performance of similarly sized but morphologically distinct species (*i.e.* American shad, walleye, white sucker) suggests that interspecific differences in morphology or behavior could influence performance. Little information is available describing differences in performance among subcarangiform swimmers, and further investigation is needed to describe the relationship between morphology and kinematics of this mode of swimming.

Acknowledgments

This work would not have been possible without the support of the Engineering section of the Conte Anadromous Fish Research Center. Specifically, the flume structure was designed and modeled by Mufeed Odeh and John Noreika, Phil Rocasah directed its construction, and Steve Walk oversaw the hydraulic instrumentation. Phil Herzig (U.S. Fish and Wildlife Service) was instrumental in the collection of striped bass, and Ken Sprankle (New Hampshire Fish and Game) provided walleye and white suckers.

References

- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Canada* 21:1183-1226.
- Brett, J.R. 1965a. The relations of size to the rate of oxygen consumption and sustained swimming speeds of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Canada* 22:1491-1501.
- Brett, J.R. 1965b. The swimming energetics of salmon. *Sci. Am.* 213:80-85.
- Castro-Santos, T., Haro, A., and Walk, S. 1996. A passive integrated transponder (PIT) tagging system for monitoring fishways. *Fisheries Research* 28:253-261.
- Graham, J.B., Dewar, H., Lai, N.C., Korsemyer, K.E., Fields, P.A., Knowler, T., Shadwick, R.E., Shabetai, R., and Brill, R.W. 1994. Swimming physiology of pelagic fishes. *In* *Mechanics and Physiology of Animal Swimming*. Edited by L. Maddock, Q. Bone, and J.M.V. Rayner. Cambridge University Press, Cambridge.
- Haro, A., Odeh, M., Castro-Santos, T., and Noreika, J. 1999. Effect of slope and headpond on passage of American shad and blueback herring through simple Denil and deepened Alaska steep pass fishways. *N. Am. J. Fish. Mgt.* 19:51-58.
- Haro, A., Odeh, M., Noreika, J., and Castro-Santos, T. 1998. Effect of water acceleration on downstream migratory behavior and passage of Atlantic

salmon smolts and juvenile American shad at surface bypasses. *Trans. Am. Fish. Soc.* 127:118-127.

Videler, J.J. 1993. *Fish Swimming*. Chapman & Hall, London.

Videler, J.J. and Wardle, C.S. 1991. Fish swimming stride by stride: speed limits and endurance. *Rev. Fish Biol. Fisheries* 1:23-40.

Wardle, C.S. 1975. Limit of fish swimming speed. *Nature* 255:725-727.

Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Canada* 190:1-158.

