Determining swim speed performance characteristics for fish passage of burbot using an experimental flume and nature-like fishway

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November 2009

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Acknowledgments– This project was funded by the Connecticut Department of Environmental Protection through the State Wildlife Grants Program. Extensive collaboration with Theodore Castro-Santos, Alex Haro and others at the USGS S.O. Conte Anadromous Fish Research Center was critical for completion of this work. University of Connecticut students who assisted with burbot collection included Yoichiro Kanno, Benjamin Gahagan, Elise Benoit, and George Maynard.

Please Reference:

Vokoun, J. C, and D. Watrous. 2009. Determining swim speed performance characteristics for fish passage of burbot using an experimental flume and nature-like fishway. Completion Report *submitted to* Connecticut Department of Environmental Protection. University of Connecticut, Storrs. 27pp.

Abstract

Burbot are listed as state-endangered in Connecticut and are a species of Greatest Conservation Need (GCN) identified in the state Comprehensive Wildlife Conservation Strategy. In both state occurrences, in the Hollenbeck River and Blackberry River, burbot are apparently excluded from suitable habitats by mainstem dams that fragment the watersheds. The quantitative swimming performance information necessary to determine a suitable fishway design to pass burbot is lacking. We used an experimental smooth flume equipped with a passive integrated transponder (PIT) system to record the swimming speeds and distances of burbot as they volitionally attempted to ascend the flume. Forty-two burbot matching the size range of the Connecticut populations were collected in Vermont, brought to the flume location at the USGS S.O. Conte Anadromous Fish Research Center in Turner Falls, MA and were surgically implanted with PIT tags and randomly split into two trial groups. Trials were conducted overnight at nominal flume velocities of 1.05ms^{-1}, 0.75ms^{-1}, 0.90ms^{-1}, and 1.25ms^{-1}, presented here in chronological order. Burbot readily entered the flume of their own volition, often staging multiple attempts during a trial. Distance of ascent in the flume decreased with increasing water velocity, noticeably above 0.90ms^{-1}. Burbot were found to switch from prolonged to sprint swimming modes near 4.72 BLs^{-1}. A survival regression analysis was used to quantify the swim speed to fatigue time relationship for both prolonged and sprint swimming modes. In general, compared to other tested species, burbot were less capable swimmers. Burbot switched to sprint swimming at slower swimming speeds, abandoned ascent attempts at lower nominal velocities than species commonly targeted in fish passage projects. Succesful fish passage designs for burbot will need to carefully consider maximum velocities and distances.

Introduction

Burbot, *Lota lota*, are listed as state-endangered in Connecticut and are a species of Greatest Conservation Need (GCN) identified in the state Comprehensive Wildlife Conservation Strategy. Near the southern extent of their natural range, burbot are of conservation concern primarily because there is only one known viable population in Connecticut located in the Hollenbeck River watershed in Northwest Connecticut (Whitworth 1996), making the species more susceptible to extirpation (Angermeier 1995). Other records are sporadic from the state, but burbot have been documented in the Blackberry River watershed (immediately north of the Hollenbeck River) and the Connecticut River (Vokoun and Dixon 2007). The Hollenbeck River burbot population itself is somewhat atypical. The population is comprised of young fish (2-5yrs old) that mature early (around 2 yrs old) at a smaller size than other reported burbot populations, and complete their life cycle in relatively shallow lotic habitats (Vokoun and Dixon 2007). The native status of the Hollenbeck River population is a continued subject of speculation. Burbot are considered native to Connecticut because of the historical records in the Connecticut River, which is connected to (at least was prior to dam construction) burbot populations north in Vermont and New Hampshire. However, the Hollenbeck population could be either a glacial relict or attributed to accidental stocking along with trout, which have been stocked in Connecticut for hundreds of years (Gherardi et al. 2008).

In both the Hollenbeck and Blackberry River watersheds burbot are excluded from apparently suitable habitats by mainstem dams that dissect the watershed (Vokoun and Dixon 2007). Dam removal as a management option is a proven method of restoring lotic species to native reaches (Paragamian 2005; Catalano et al. 2007). Dam removal in the Blackberry River is unlikely as the dam is associated with an iron smelting furnace and is a state historical site. Similarly, dam removal would be complicated for the Hollenbeck dam because it is sited directly upstream of important summer stream reaches and dam removal could place a large portion of the population at risk from excessive sedimentation (Lorang and Aggett 2005; Thomson et al. 2005). Fish passage solutions in these systems are more likely to be applied in the near future to expand the range of burbot and hopefully increase population sizes.

The quantitative swimming performance information necessary to determine a suitable fishway design to pass burbot is lacking. Few studies in the scientific literature have described fishways used by burbot (Slavik and Bartoš 2002; Calles and Greenberg 2007). A single study has published laboratory-based swimming performance values using swim chamber exercise experiments (Jones et al. 1974).

The confined swim chamber techniques used by Jones et al. (1974) can result in limited applicability by not accounting for the behavioral constraints and hence often underestimate swimming ability (Peake 2004; Peake and Farrell 2006; Holthe et al. 2009). In contrast, Haro and Castro-Santos (2004) established an open channel volitional swimming method for predicting fish passage through velocity barriers. In addition, Castro-Santos (2006) established a new model relating swim speed and fatigue time for both sprint and sustained swimming modes. Thus, studies in open channel flumes that feature volitional attempts by fishes represent a new approach that takes into account behavioral and physiological aspects of fish swimming performance.

This project was designed to characterize burbot swimming performance by identifying velocities that would challenge burbot and subsequently identify the distance of maximum ascent at said velocities. This study was also designed to document the swim-speed fatigue-time relationship for burbot and describe the shift from prolonged to sprint swimming modes, if present. The project incorporated the utilization of volitional swimming trials in both an experimental flume and a scale-model nature-like fishway. The scale-model nature-like fishway was included in this study due to high passage efficiencies documented (Calles and Greenberg 2005) and increased interest in the concept in southern New England. Scale model fishways and open channel flume studies such as these are considered to be better representations of the realized swimming capabilities of fish species (Haro et al. 2004; Peake and Farrell 2006; Pon et al. 2009).

Methods

Fish collection—The state-endangered status of burbot in Connecticut necessitated that collections take place elsewhere. The East Branch of the Passumpsic River in Lyndonville, Vermont is a tributary of the Connecticut River and was identified as a collection site because burbot are not endangered in Vermont, were known to be present through previous sampling, and the Passumpsic River is within the Connecticut River drainage which was a criteria for the targeted fish holding facilities at the USGS S.O. Conte Anadromous Fish Research Center in Turner Falls, Massachusetts (hereafter Conte). Collections were conducted during the daylight hours in early June 2008 with a push-barge electrofisher (Smith-Root Inc.; controlled by a Coffelt VPP-15 electrofisher powered by a 3600 watt generator, pulsed-DC). Burbot were captured, often in groups of 3 to 5 fish, amongst boulders and similar cover which completely concealed them. Collected fish were transported to the Conte in an insulated and aerated 2 m^3 container filled with approximately 750 liters of water from the sampling site (Portz et al. 2006). At Conte fish were held outdoors in 1.8m diameter round tanks fed flow-through Connecticut River water.

PIT Tagging—Fish were allowed to acclimate for 24-hours to holding conditions at Conte before being surgically implanted with Passive Integrated Transponder (PIT) tags. Each fish was anesthetized, weighed, and their total length measured before a uniquely encoded PIT tag was implanted in the body cavity. The surgeries were performed by a well-practiced surgeon (Cooke et al. 2003) and the incisions were closed with surgical grade super glue . The fish quickly recovered from the anesthesia, and a single mortality occurred immediately after the surgical implantation. Passive integrated transponder tags properly implanted have limited to no effect on swimming ability (Knaepkens et al. 2007B; Newby et al. 2007; Makiguchi and Ueda 2009). Tagged fish were randomly divided into two study groups and given 24-hours for post surgery re-acclimation before the start of experimental trials (Mulcahy 2003).

Experimental flume trials—An extant open-channel experimental flume at Conte was modified for the volitional ascent trials. The experimental flume measured 1 m wide x 1 m deep x approx 24 m long, with a zero slope. The flume was constructed of wood, steel, and 2.5-cm-thick acrylic panels on one vertical side. The floor and other wall were constructed of plywood and coated with retroreflective material which was smoothed to prevent the formation of organized eddies (Haro et al. 2004). A manually operated headwater gate issued Connecticut River water from an adjacent hydroelectric power canal upstream of the power facility. The flume's downstream end was amended with a large wooden staging area that provided slowed water velocities from which fish could ascend the flume volitionally (Castro-Santos 2005). The open-channel flume was located outside and subject to the ambient photoperiod. The water used in each trial was drawn from the Connecticut River and subject to natural temperature fluctuations. Ten PIT antenna cables were looped twice around the outermost structure of the flume, each 2 m apart from the previous and the next in the series. Each antenna was connected to a PIT reader, and the readers to a laptop computer which logged all PIT tag readings (Castro-Santos et al. 1996). Pit tags were charged by the electrical field of the antennas and sent back fish-specific identification codes to the readers at a rate of 14Hz. The computer logged these codes with a time stamp to the nearest 0.01 s. To gain a perspective on fish ascent techniques an infrared camera and illumination source were placed between antennas two and three after the first trial, the camera was connected directly to a video cassette recorder (Beach 1978; Castro-Santos et al. 1996).

Each of the two experimental groups were introduced to two of the four water velocities tested to identify the velocities that challenged burbot (listed in trial sequence): $1.05 ms^{-1}$, $0.75 ms^{-1}$, $0.90 ms^{-1}$, and $1.25 ms^{-1}$. The velocity of each trial was achieved by adjusting the depth of the head water and the depth of water in the flume by adding or removing tail water weirs located in the staging area. Throughout the trials, the experimental velocity was monitored indirectly by monitoring the depth of water in the flume channel (Castro-Santos 2005). The trials were conducted overnight because burbot are more active at night. Fish were exchanged between the holding tanks and the flume staging area in the late morning. At the end of each trial the water velocity was measured midway up the flume in a 5 cm x 5 cm bisecting planar grid with a propeller Ott meter.

Model nature-like fishway — In the scale model nature-like fishway at Conte fish were introduced to a staging area and allowed to stage volitional ascent attempts up the length of the scale model fishway. The fishway model incorporates numerous slopes, depths, and arrangements of artificial stones to approximate a natural stream channel. Swimming activity is monitored by a series of PIT antennas along the length of the scale model fishway (Castro-Santos et al. 1996). Before burbot were introduced to the fishway it was amended with one inch plastic mesh at both the upstream and downstream of the apparatus to prevent burbot from escaping the laboratory. Nothing was done to exclude fish from narrow cracks between the plywood boards that held the artificial stones andmade up the base sections of the fishway. At the conclusion of the four open channel experimental flume velocity trials all the burbot were introduced to the scale model nature-like fishway.

Data handling— The thousands of raw readings collected from the antenna readers were amassed in a Microsoft Access database. Using selection queries, each observation pertaining to an individual fish across trials was then isolated and input to a Microsoft Excel workbook where the readings were interpreted as follows:

Groups of raw readings (comprised of a reader number and time stamp) were assigned to validated presences within the flume occurring within a minimum observation period. A presence was established when subsequent readings of a fish occurred within 0.25 sec of each subsequent reading.

Each established presence was then associated with a specific antenna based on the reader number associated with the constituent raw readings. The reader numbers associated with the raw readings comprising a given presence were averaged. Outlying antenna reading errors were eliminated by using the integer value of the averaged reader numbers.

Groups of presences were identified as attempts to ascend the flume. An attempt was defined as starting when a new presence occurred at the first antenna in the series a minimum of 60 sec after the previous presence. Once all the raw readings were classified and organized they were returned to a Microsoft Access database.

Each ascent attempt was characterized by the maximum distance of ascent and fatigue time. The maximum distance of ascent was defined as the distance of the furthest PIT antenna that recorded a presence during an attempt. Fatigue time was defined as the time that elapsed from the start of the trial, when the fish entered the flume, and the furthest PIT antenna reading during an attempt. Any fish that reached the end of the flume, i.e. failed to fatigue, was identified as a fish needing to be right-censored in subsequent analysis (Haro et al. 2004).

Regression analyses—Distance of maximum ascent, fatigue time, and swim speed expressed as body lengths per second (BLs^{-1}), of every attempt made during all trials, were input into the program Statistical Analysis Software (SAS). Right-censored survival regressions were conducted using PROC LIFEREG, where an appropriate model form was selected from among log and nonlog forms of logistic, gamma, weibull, normal and exponential distributions based upon Akaike's Information Criterion (AIC) scores (Castro-Santos 2004). For the swim speed and fatigue time data, a moving slope break-point model was ran, i.e. models were ran iteratively with 0.01 incremental changes in the break-point through the observed range of swim speeds observed in the trials. Again, AIC scores, corrected for small sample size, were used to identify the best fitting model. In this instance, that model identified the swimming speed (in BLs^{-1}) that represented the break-point at which regressions above and below the value fit the data best. This slope break-point has been interpreted as an idealized maximum prolonged swimming speed above which the sprint swimming mode was implemented (Castro-Santos 2004).

Results

Fish collection— Fourty-two burbot were collected with a mean length of 191 mm TL (range 142-363 mm) and a mean weight of 40.0 g. The length and weight of the collected burbot are listed along with trial participation in Appendix A.

Experimental flume trials—The 5 cm velocity measurement grids taken after each trial were interpreted to assign nominal velocities to each trial based on the velocity profiles attained; there is always variation in velocities, even in a smooth flume, so we selected a widespread velocity to represent each trial. Figure 1 depicts the velocity distributions present during each trial. The first trial conducted was at a nominal velocity of 1.05ms^{-1}. Within the staging area, current at the drain weirs resulted in the impingement of eight fish on steel exclusion screens. Before the start of the second trial the tail weirs were refitted with plastic exclusion screens that kept fish a greater distance from the weirs. After the modifications to the staging area were made no fish were lost to impingement in subsequent trials.

Burbot readily entered the flume, regularly making more than one ascent attempt during a trial; each individual fish's performance is summarized in Appendix B. Activity within the flume was almost entirely limited to the night hours between sunset and sunrise. Figure 2 illustrates the proportion of flume activity occurring across all trials at a given hour. At nominal velocities above 0.90ms^{-1} burbot were less successful ascending the length of the flume in comparison to the 0.75ms^{-1} trial, during which burbot often ascended the entire length of the flume (Figure 3). The range of nominal velocities effectively challenged burbot swimming, as evidenced by the decline in maximum ascent distance in Figure 3.

The survival distribution, in this case the percent passing a given distance (in the flume) at each nominal velocity, was given by the following equation:

$$\ln Dmax = 3.144 - 2.547 Vnom + 0.401\beta_{scale} + 2.493\beta_{shape}$$

where $\ln Dmax$ is the logged maximum recorded distance of ascent during a single attempt, $Vnom$ is the nominal velocity in the flume, and β_{scale} and β_{shape} are terms produced when fitting the regression to the Weibull distribution. The slope, -2.547, had a 95% confidence interval bound by –2.902 and –2.192. The survival distributions are plotted in Figure 4.

When the infrared footage covering each trial was viewed, it revealed that burbot swam along the areas of the flume where the velocity was lowest. Burbot swam along the bottom and in the corners of the flume. It was also observed, that in apparent exhaustion upon completing an ascent attempt, burbot would turn their body perpendicular to the flow thus passively descend the flume in the current.

Scale model nature-like fishway — At

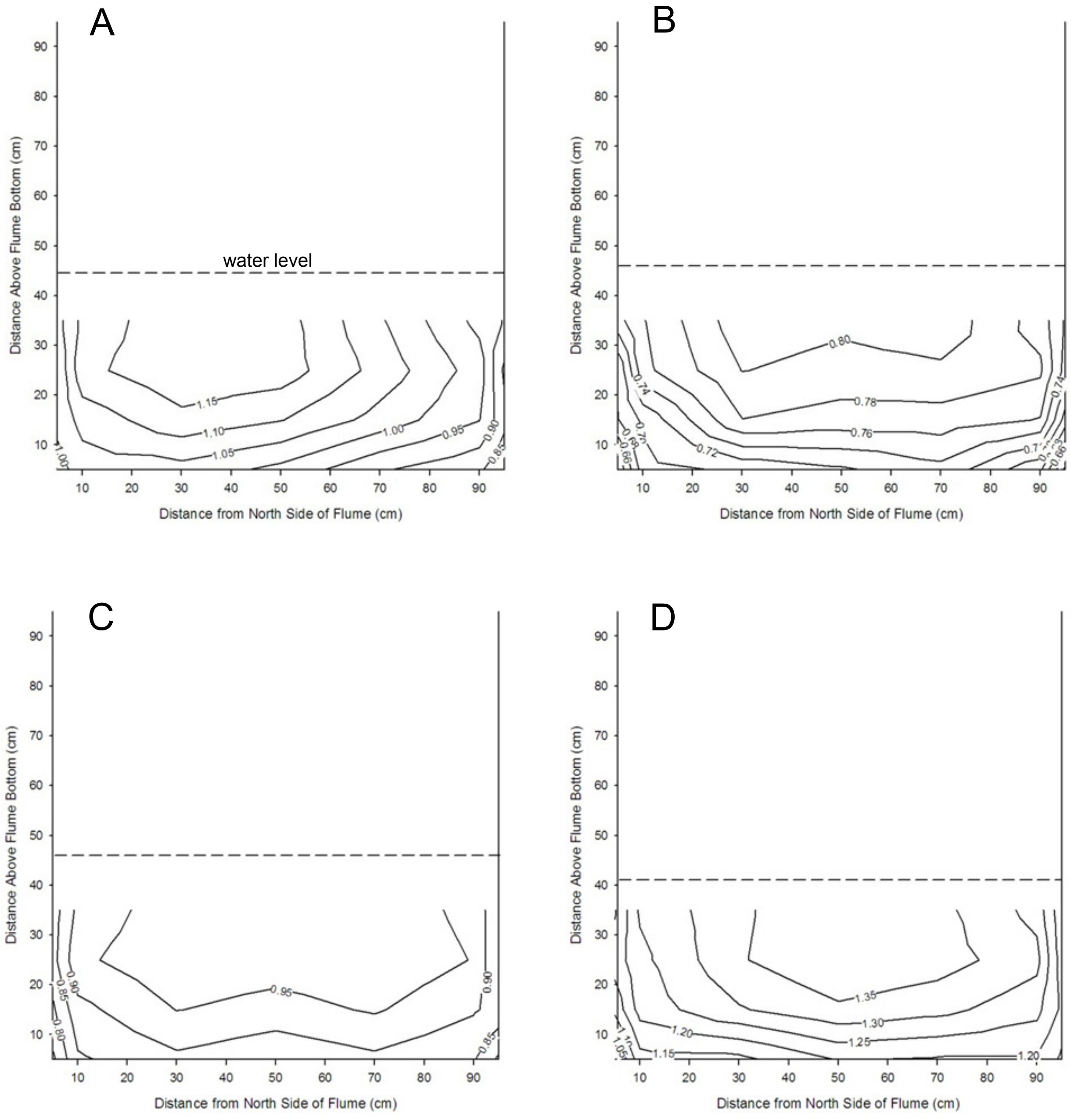

Figure 1.—Velocity profile series presented in trial sequence, nominal velocities: A) 1.05ms^{-1} B) 0.75ms^{-1} C) 0.90ms^{-1} D) 1.25ms^{-1}. Note the slower velocities in the areas of highest friction along the bottom and sides of the flume.

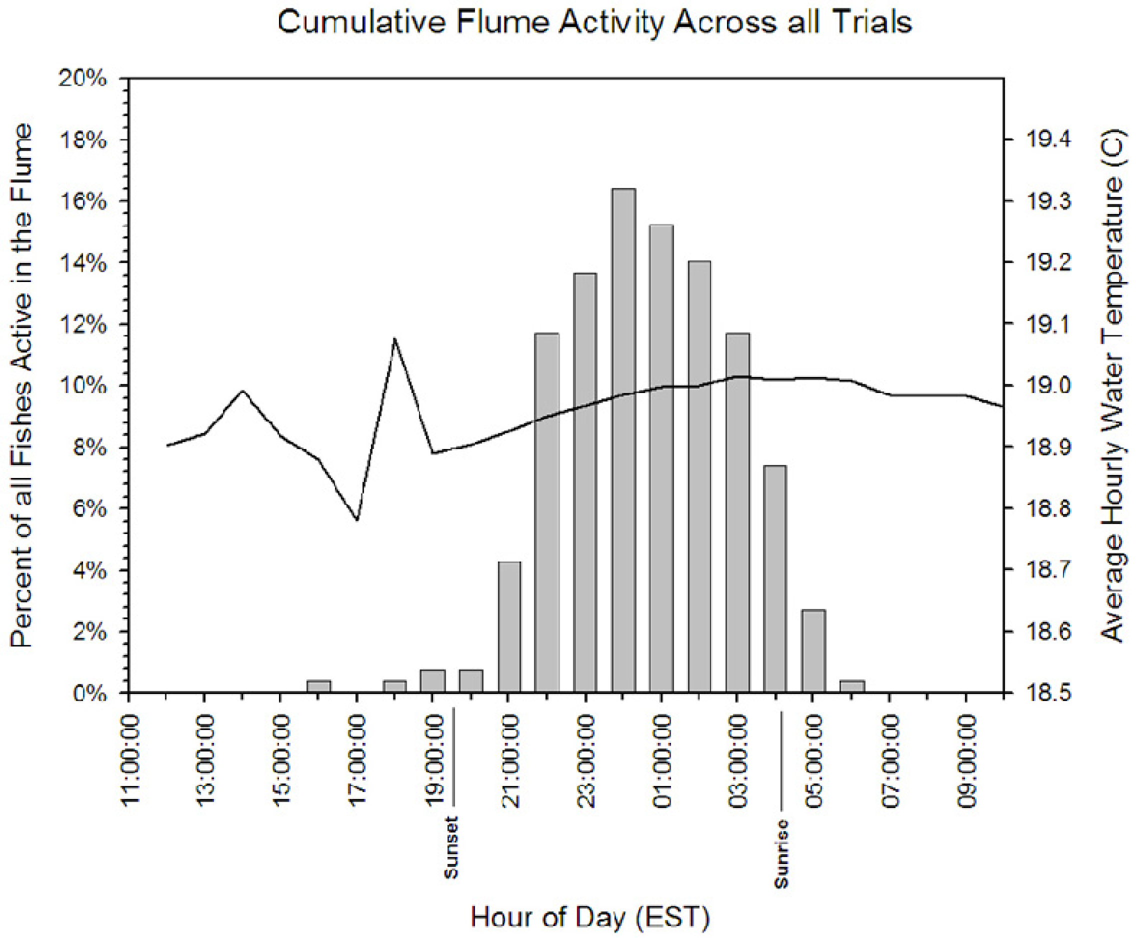

Figure 2.—Representation of flume activity across all trials proportionally over one hour increments (bars) plotted with the average hourly water temperatures (line) during all trials. Note the peak in nocturnal activity between the hours of midnight and 1am.

the conclusion of the open channel experimental flume trials, 33 burbot were introduced to the staging area of the scale-model nature-like fishway. The first night the burbot were in the model nature-like fishway the recording computers malfunctioned and recorded nothing. The fish were allowed to remain in the flume for a second night, but no activity was observed. When the water was removed from the flume at the end of the second trial, most of the burbot were located wedged under the artificial stones and between the plywood that made up the bottom support of the fishway. Because burbot were able to infiltrate the substructure of the model, the trial did not provide any useful data for analyses.

Swim mode shift— The moving-point survival regression analysis of the relation between swim speed and fatigue time was best modeled with natural-logged fatigue times and a generalized Gamma distribution. The incremental fitting of the range of swim speeds identified 4.72 as the break-point in the cresenct-shaped data cloud above and below which the data could be better fit-

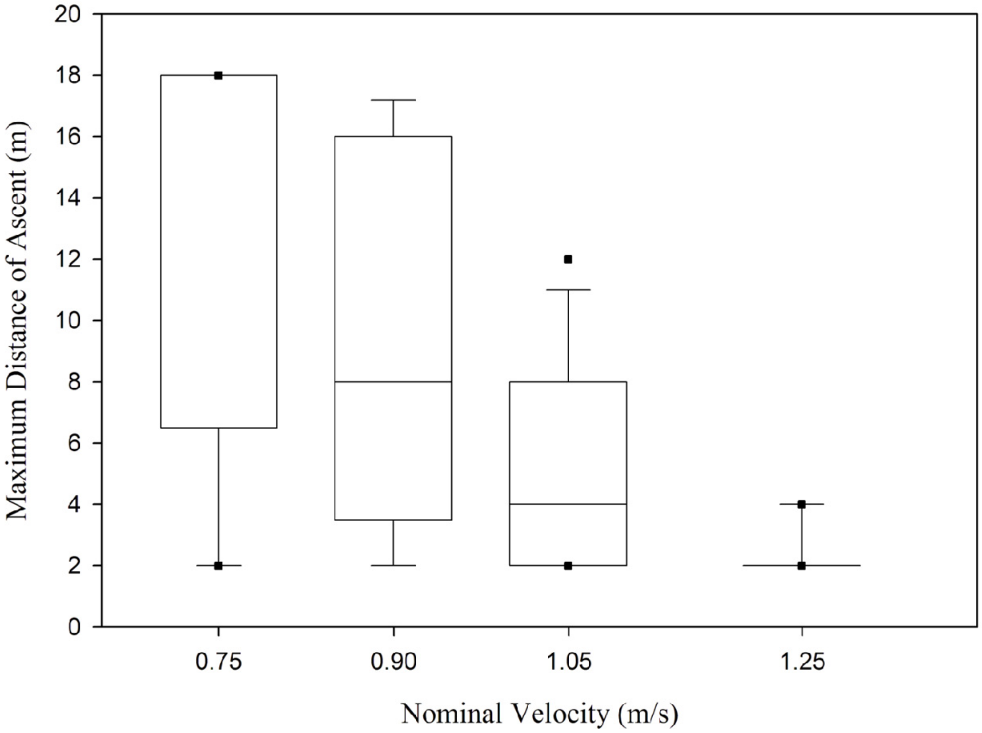

Figure 3.—Maximum distance of ascent by nominal water velocity present in the flume; upper and lower bounds of the boxes represent the 75th and 25th percentiles respectively, whiskers represent the 90th and 10th percentiles, solid black squares represent the 95th and 5th percentiles, and the lines within each box are the median.

ted by separate slopes. This represented an idealized swim speed at which a swimming mode shift between prolonged swimming and sprint swimming occurred (Figure 5). As such, the maximum predicted prolonged swimming speed of burbot is 4.72 BLs^{-1}.

Below 4.72 BLs^{-1}, the burbot swim speed to fatigue time relationship fit the following equation:

$$\ln T = 1.875 + 0.040BLs^{-1} + 0.167\beta_{scale} + 1.259\beta_{shape}$$

where $\ln T$ is the logged fatigue time, BLs^{-1} is the swim speed, and β_{scale} and β_{shape} are terms produced when fitting the regression to the generalized gamma distribution. The slope, 0.040, had a 95% confidence interval bound by –0.176 and 0.256.

Above 4.72 BLs^{-1} , the burbot swim speed to fatigue time relationship fit the following equation:

$$\ln T = 3.0778 - 0.268BLs^{-1} + 0.274\beta_{scale} + 0.675\beta_{shape}$$

The slope, -0.268, had a 95% confidence interval bound by –0.290 and –0.247.

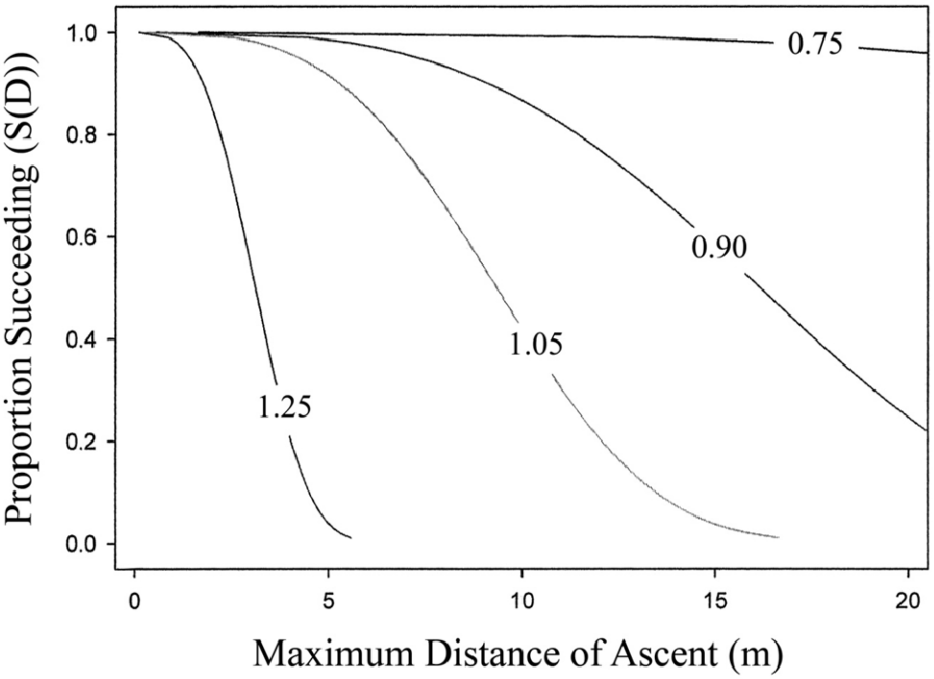

Figure 4.—Proportion succeeding at distance for each nominal velocity (curves labeled in m/s) trialed in the smooth flume.

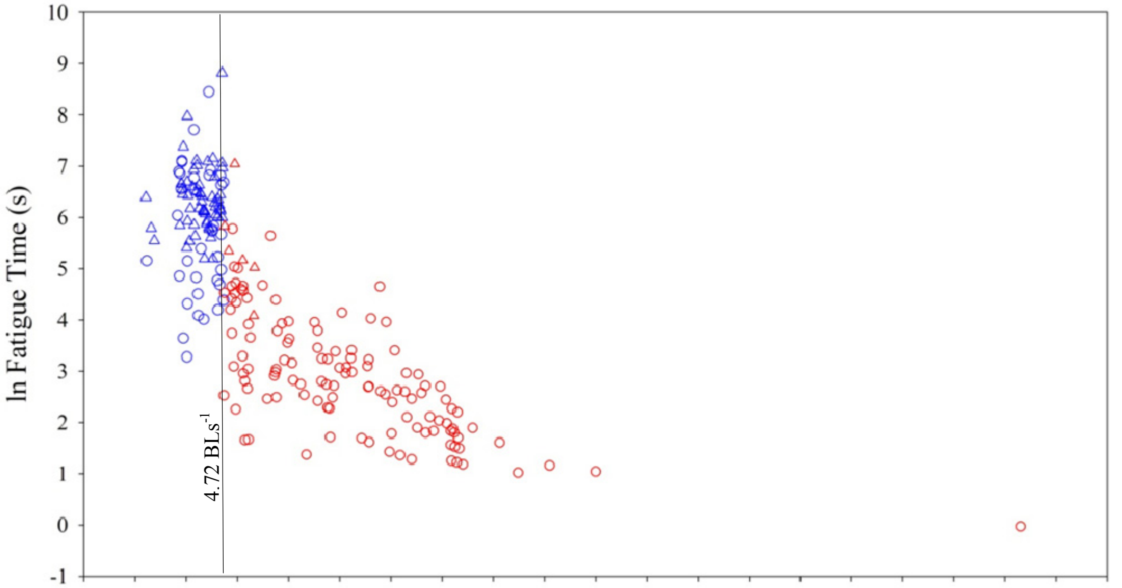

Figure 5.—Relationship of fatigue time to swim speed. Note fatigue times are logged and swim speed is expressed in body lengths per second. Data represents all attempts across all trials (i.e., individual fish are represented by more than one data point.) Prolonged swimming mode (blue) and sprint swimming mode (red) non-censored data indicated with circles; censored observations indicated by triangles.

Discussion

Burbot staged multiple attempts up the smooth flume at all trial velocities. This suggests that behaviorally, burbot may readily use technical fish passage solutions to pass barriers. The failure of the nature-like trials unfortunately leaves no room for interpretation. However, burbot have been sampled within nature-like fishways (Calles and Greenberg 2007). In Sweden, burbot passed nature-like fishway bypass channels with a 60% efficiency, although the authors report that burbot were spending extended periods in the fishways, and probably could have passed with high efficiency if so motivated (Calles and Greenberg 2007).

The burbot included in this study were small compared to ‘typical’ populations, but closely matched the size distribution of the state-endangered Connecticut populations, which are considered truncated (Vokoun and Dixon 2007). It is possible that many of the fish collected in Vermont may have been juveniles due to their small size. Adult burbot may have different swimming abilities. Burbot populations studied in Washington represented a more typical range in length, with adults ranging from 430 to 640 mm (Bonar et al. 2000), compared to the 142 to 363 mm range of the subject burbot. The limited size range of the individuals studied limits the application of these results to similarly sized fish (Ojanguren and Braña 2003).

The infrared video captured burbot characteristically utilizing low velocity areas within the flume at the bottom corners. Cardinal shiners (*Luxilus cardinalis*) and longear sunfish (*Lepomis megalotis*) both were documented to seek low velocity zones within the experimental structure in similar swimming performance studies in smooth flumes (Scott and Magoulick 2008). In contrast Castro-Santos (2005) reported walleye (*Sander vitreus*), striped bass (*Morone saxatilis*), American shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) avoided the walls of the flume and were generally within 200mm of the bottom, but typically not at the bottom. White sucker (*Catostomus commersonii*), however, like the burbot, used the corners, although at higher velocities the suckers swam more centrally in the flume (Castro-Santos 2005).

The trial velocities selected were successful in challenging burbot as evidenced by the marked decrease in maximum distance of ascent as trial velocities climbed from 0.90 ms^{-1} to 1.05 ms^{-1} and the near complete failure to ascend even to the second antenna (4 m) when challenged by a water velocity of 1.25ms^{-1}. In general these velocities are considered at the low end of those commonly found in many technical fish passage solutions such as steep-pass and vertical slot fishways. Successful technical fishway designs for burbot will need to carefully consider maximum velocities as distance of ascent decreased quickly with moderate increases in velocity. Common focal species for fish passage such as American shad, blueback herring, and striped bass all had high proportions of the population reach the top of a 20m flume at 1.5 ms^{-1} (Haro et al. 2004), a velocity beyond the range of testing performed here and probably beyond the range of volitional swimming for burbot.

Burbot were found to be among the species that switch from prolonged to sprint swimming modes when challenged by increased velocities. Not all species make such a switch, alewife for example only displayed sprint swimming in similar trials (Castro-Santos 2005); alewife, of course, do not always swim in sprint mode, but appear to do so when attempting to pass a velocity barrier. However, burbot exhibited a much narrower range of prolonged swim speeds than other fish studied, i.e. they switched to sprint swimming mode at relatively lower velocities. Walleye, striped bass, and white sucker all displayed larger ranges of prolonged swimming than burbot, extending from about 5 BLs^{-1} to 10 BLs^{-1} (Castro-Santos 2005). Burbot performed most similarly to American shad which also exhibited a relatively narrow range of prolonged swim speeds, from 0 BLs^{-1} to 5 BLs^{-1}. Sprint swimming performance was more comparable with other species tested, but in general was associated with faster fatigue times. The slope of the sprint swimming speed to fatigue time relationship was steeper than that of walleye (-0.13), striped bass (-0.19), white sucker (-0.15), and both blueback herring (-0.20) and alewife (-0.20). Again burbot were most similar to American shad which had a slope of –0.33. Overall, however, burbot sprint swimming was slower, with few fish exceeding 10 BLs^{-1}. White sucker, sympatric with burbot in Connecticut, did not switch to sprint swimming until around 10 BLs^{-1} (Castro-Santos 2005).

We must note some caveats to the data as presented here. First, we analyzed data including multiple ascent attempts from the same individuals, which constitutes psuedoreplication as defined by Hurlbert (1984). It is possible the multiple attempts from the same individual are not truly independent. Further, we did not attempt to account for any effect of previous attempts on subsequent attempts. It is possible the previous attempts may both increase or decrease subsequent performance (Castro-Santos 2004; 2005). However, we can say that burbot showed no obvious signs of fatigue at the end of trials and no significant mortality occurred within 24 h after each trial. Given the number of attempts burbot made during trials, it appears that the fish did not swim to physiological exhaustion when attempting to ascend the flume. This is consistent with other observations for a wide range of species in volitional flume studies (Haro et al. 2004; Peake 2008).

In conclusion burbot had decreased absolute distances of ascent at relatively low velocities and a limited prolonged swim speed range. Burbot displayed markedly slower swim speeds than other species tested. Low gradient pool and weir fishways have proven suitable for passing benthic species, including burbot, in the United Kingdom (Knapekens et al. 2007a) and the Czech Republic (Slavik and Bartos 2002) and may prove a suitable option in Connecticut. (along with the mentioned nature-like fishways), especially given the small discharges available in the two occupied watersheds. Also, the switch to sprint swimming may allow some flexibility in design strategies, so long as distances are within physical capabilities and characteristic swimming behavior.

References

Angermeier, P. L. 1995. Ecological attributes of extinction-probe species: Loss of freshwater fishes of Virginia. Conservation Biology 9(1):143-158.

Beach, M. H. 1978. The use of infra-red light and closed circuit TV to validate records from automatic fish counters. Journal of Fish Biology 13:639-644.

Bonar, S. A., L. G. Brown, P. E. Mongillo, and K. Williams. 2000. Biology, distribution and management of burbot (*Lota lota*) in Washington state. Northwest Science 74(2):87-96.

Calles, E. O., and L. A. Greenberg. 2007. The use of two nature-like fishways by some fish species in the Swedish river Emån. Ecology of Freshwater Fish 16(2):183-190.

Castro-Santos, T. 2004. quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences 61: 1602-1615.

Castro-Santos, T. 2005. Optimal swim speeds for traversing velocity barriers: An analysis of volitional high-speed swimming behavior of migratory fishes. Journal of Experimental Biology 208(3):421-432.

Castro-Santos, T. 2006. Modeling the effect of varying swim speeds on fish passage through velocity barriers. Transactions of the American Fisheries Society 135 (5):1230-1237.

Castro-Santos, T., and A. Haro. 2003. Quantifying migratory delay: A new application of survival analysis methods. Canadian Journal of Fisheries and Aquatic Sciences 60(8):986-996.

Castro-Santos, T., A. Haro, and S. Walk. 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. Fisheries Research 28(3):253-261.

Catalano, M. J., M. A. Bozek, and T. D. Pellett. 2007. Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. North American Journal of Fisheries Management 27(2):519-530.

Cheong, T. S., M. L. Kavvas, and E. K. Anderson. 2006. Evaluation of adult white sturgeon swimming capabilities and applications to fishway design. Environmental Biology of Fishes 77(2):197-208.

Cooke, S. J., B. D. S. Graeb, C. D. Suski, and K. G. Ostrand. 2003. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: Case study of a novice and experienced fish surgeon. Journal of Fish Biology 62(6):1366-1380.

Dauble, D. D., R. A. Moursund, and M. D. Bleich. 2006. Swimming behavior of juvenile pacific lamprey, *Lampetra tridentata*. Environmental Biology of Fishes 75(2):167-171.

Gherardi, F., S. Bertolino, M. Bodon, S. Casellato, S. Cianfanelli, M. Ferraguti, E. Lori, G. Mura, A. Nocita, N. Riccardi, G. Rossetti, E. Rota, R. Scalera, S. Zerunian, and E. Tricarico. 2008. Animal xenodiversity in Italian inland waters: Distribution, modes of arrival, and pathways. Biological Invasions 10(4):435-454.

Haro, A., T. Castro-Santos, J. Noreika, and M. Odeh. 2004. Swimming performance of upstream migrant fishes in open-channel flow: A new approach to predicting passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences 61(9):1590-1601.

Holthe, E., E. Lund, B. Finstad, E. B. Thorstad, and R. S. McKinley. 2009. Swimming performance of the European minnow. Boreal Environment Research 14(2):272-278.

Knaepkens, G., E. Maerten, and M. Eens. 2007a. Performance of a pool-and-weir fish pass for small bottom-dwelling freshwater fish species in a regulated lowland river. Animal Biology 57(4):423-432.

Knaepkens, G., E. Maerten, C. Tudorache, G. De Boeck, and M. Eens. 2007. Evaluation of passive integrated transponder tags for marking the bullhead (*Cottus gobio*), a small benthic freshwater fish: Effects on survival, growth and swimming capacity. Ecology of Freshwater Fish 16(3):404-409.

Lorang, M. S., and G. Aggett. 2005. Potential sedimentation impacts related to dam removal: Icicle creek, Washington, U.S.A. Geomorphology 71(1-2):182-201.

Makiguchi, Y., and H. Ueda. 2009. Effects of external and surgically implanted dummy radio transmitters on mortality, swimming performance and physiological status of juvenile masu salmon *Oncorhynchus masou*. Journal of Fish Biology 74 (1):304-311.

Mulcahy, D. M. 2003. Surgical implantation of transmitters into fish. ILAR Journal 44 (4):295-306.

Newby, N. C., T. R. Binder, and E. Don Stevens. 2007. Passive integrated transponder (PIT) tagging did not negatively affect the short-term feeding behavior or swimming performance of juvenile rainbow trout. Transactions of the American Fisheries Society 136(2):341-345.

Ojanguren, A. F., F. Braña. 2003. Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish 12: 241-246.

Paragamian, V. L., R. Hardy, and B. Gunderman. 2005. Effects of regulated discharge on burbot migration. Journal of Fish Biology 66(5):1199-1213.

Peake, S. 2004. An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. Transactions of the American Fisheries Society 133(6):1472-1479.

Peake, S. J. 2008. Behavior and passage performance of northern pike, walleyes, and white suckers in an experimental raceway. North American Journal of Fisheries Management 28(1):321-327.

Peake, S. J., and A. P. Farrell. 2006. Fatigue is a behavioral response in respirometer-confined smallmouth bass. Journal of Fish Biology 68(6):1742-1755.

Pon, L. B., S. G. Hinch, S. J. Cooke, D. A. Patterson, and A. P. Farrell. 2009. Physiological, energetic and behavioral correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia. Journal of Fish Biology 74(6):1323-1336.

Portz, D. E., C. M. Woodley, and J. J. Cech Jr. 2006. Stress-associated impacts of short-term holding on fishes. Reviews in Fish Biology and Fisheries 16(2):125-

170.

Scott, M. K., and D. D. Magoulick. 2008. Swimming performance of five warmwater stream fish species. Transactions of the American Fisheries Society 137(1):209-215.

Slavík, O., and L. Bartoš. 2002. Factors affecting migrations of burbot. Journal of Fish Biology 60(4):989-998.

Thomson, J. R., D. D. Hart, D. F. Charles, T. L. Nightengale, and D. M. Winter. 2005. Effects of removal of a small dam on downstream macroinvertebrate and algal assemblages in a Pennsylvania stream. Journal of the North American Benthological Society 24(1):192-207.

Vokoun, J. and C. Dixon. 2007. Habitat Use and Population Demographics of State-endangered Burbot Lota lota in Northwestern Connecticut. State Wildlife Grant and Income Tax Check-Off Fund-Endangered Species Program Final Report to Connecticut Department of Environmental Protection. Department of Natural Resources Management and Engineering, University of Connecticut, Storrs. 102pp.

Appendices

Appendix Table 1. PIT tag IDs of individual burbot, associated experimental groups, length (mm), weight (g), and trial assignments.

Pit tag ID	Group	Length (mm)	Weight (g)	Trial 1	Trial 2	Trial 3	Trial 4	Nature-like
2000	6FTE	164	23.2	•				
2001	6FTE	154	18.4	•				
2002	6FTE	245	78.1	•		•		•
2003	6FTE	183	32.2	•		•		•
2004	6FTE	185	34.5	•		•		•
2005	6FTE	199	39.1	•		•		•
2006	6FTE	193	33.3	•		•		•
2007	6FTE	185	34.3	•				
2008	6FTE	192	38.2	•				
2009	6FTE	192	36.3	•		•		•
2010	6FTE	182	32.7	•		•		•
2011	6FTE	191	39.8	•		•		•
2012	6FTE	160	22.5	•				
2013	6FTE	249	76.5	•		•		•
2014	6FTE	201	43.5	•		•		•
2015	6FTE	163	23.5	•				
2016	6FTE	180	33.6	•				
2017	6FTE	191	35.3	•		•		•
2018	6FTE	199	40.5	•		•		•
2019	6FTE	363	234.7	•				
2020	6FTW	142	14.8					
2021	6FTW	202	45.2		•		•	•
2022	6FTW	193	38.2		•		•	•
2023	6FTW	188	35.3		•		•	•
2024	6FTW	185	28.2		•		•	•
2025	6FTW	198	35.4		•		•	•
2026	6FTW	171	28.3		•		•	•
2027	6FTW	173	29		•		•	•
2028	6FTW	195	43.2		•		•	•
2029	6FTW	172	24.3		•		•	•
2030	6FTW	163	21.3		•		•	•
2031	6FTW	182	34.3		•		•	•
2032	6FTW	182	33.7		•		•	•
2033	6FTW	207	51		•		•	•
2034	6FTW	192	41		•		•	•
2035	6FTW	243	39.3		•		•	•
2036	6FTW	215	47.5		•		•	•
2037	6FTW	169	26.9		•		•	•
2038	6FTW	169	24.7		•		•	•
2039	6FTW	167	25.6		•		•	•
2040	6FTW	182	33.9		•		•	•
2041	6FTW	181	29.7		•		•	•

Appendix Table 2. Individual attempts within each trial summarized by average distance of maximum ascent, average duration of attempt, average time between attempts, the start of the first and end of the last attempts made during a trial and total amount of time spent in the flume during a trial.

ID	Trial	Vnom	# of Attempts	Mean Dmax (Body Lengths)	Mean Attempt Duration (s)	Mean Time Between Attempts (s)
2002	1	1.05	7	8.2	3.4	1750.5
	3	0.90	27	9.1	22.4	806.4
2004	1	1.05	2	37.8	13.5	1245.2
	3	0.90	4	40.5	297.2	1590.4
2005	1	1.05	2	30.2	30.9	763.9
2009	1	1.05	5	27.1	9.1	2397.9
	3	0.90	3	41.7	2524.7	3571.8
2010	1	1.05	1	44.0	15.1	0.0
	3	0.90	3	51.3	21.6	11044.5
2011	1	1.05	19	12.7	21.4	972.7
	3	0.90	15	25.1	34.1	1007.5
2013	1	1.05	7	12.6	7.0	1244.5
	3	0.90	3	2.7	1.7	4680.4
2014	1	1.05	17	8.8	7.4	829.4
	3	0.90	24	11.2	55.2	731.3
2015	1	1.05	1	0.0	0.0	0.0
2017	1	1.05	4	2.6	1.3	1547.3
	3	0.90	22	7.6	5.0	695.3
2018	1	1.05	5	20.1	9.6	1916.1
	3	0.90	3	16.8	6.5	4846.2
2021	2	0.75	9	17.6	47.2	1588.0
	4	1.25	5	0.0	0.0	967.7
2022	2	0.75	20	25.4	165.2	1223.4
	4	1.25	2	10.4	3.3	3389.5
2023	2	0.75	6	47.9	635.4	1461.8
	4	1.25	15	0.7	0.2	1196.0
2024	2	0.75	11	48.2	351.9	2448.0
2025	2	0.75	15	43.1	269.7	1395.4
	4	1.25	15	8.8	7.4	1684.5
2026	2	0.75	3	31.2	339.8	4061.5
	4	1.25	3	7.8	4.1	3770.8

Appendix Table 2 expanded.

Start of First Attempt	End of Last Attempt	Sum of Attempt Durations (s)
6/4/08 23:04	6/5/08 2:29	23.6
6/6/08 21:51	6/7/08 4:04	604.4
6/5/08 2:08	6/5/08 2:50	27.1
6/7/08 1:36	6/7/08 3:41	1188.9
6/5/08 3:47	6/5/08 4:13	61.9
6/5/08 0:03	6/5/08 3:23	45.5
6/6/08 22:55	6/7/08 4:00	7574.0
6/5/08 1:26	6/5/08 1:26	15.1
6/6/08 16:11	6/7/08 1:24	64.8
6/4/08 23:02	6/5/08 4:17	406.9
6/6/08 21:58	6/7/08 2:19	511.0
6/5/08 0:50	6/5/08 3:16	49.2
6/6/08 22:32	6/7/08 2:26	5.2
6/5/08 1:12	6/5/08 5:09	125.7
6/6/08 21:32	6/7/08 2:46	1325.4
6/4/08 19:05	6/4/08 19:05	0.0
6/5/08 1:19	6/5/08 3:03	5.0
6/6/08 22:58	6/7/08 3:15	109.9
6/5/08 1:50	6/5/08 4:31	48.1
6/6/08 23:18	6/7/08 3:20	19.4
6/5/08 22:31	6/6/08 2:36	424.7
6/7/08 22:54	6/8/08 0:14	0.0
6/5/08 22:21	6/6/08 6:04	3304.5
6/7/08 21:41	6/7/08 23:34	6.6
6/6/08 0:47	6/6/08 4:17	3812.4
6/7/08 21:23	6/8/08 2:22	2.8
6/5/08 19:43	6/6/08 4:17	3871.2
6/5/08 22:13	6/6/08 5:10	4044.8
6/7/08 21:26	6/8/08 4:29	110.3
6/5/08 22:40	6/6/08 2:20	1019.3
6/7/08 21:50	6/8/08 0:58	12.4

Appendix Table 2. Continued.

ID	Trial	Vnom	# of Attempts	Mean Dmax (Body Lengths)	Mean Attempt Duration (s)	Mean Time Between Attempts (s)
2027	2	0.75	21	27.0	125.0	1632.9
2028	2	0.75	7	36.6	367.9	1615.7
	4	1.25	11	0.0	0.0	1347.9
2029	2	0.75	11	28.5	131.1	1646.5
	4	1.25	1	0.0	0.0	0.0
2030	2	0.75	28	19.7	157.4	755.3
	4	1.25	40	2.5	5.7	610.0
2031	2	0.75	26	17.8	138.2	801.9
	4	1.25	15	0.7	4.2	1380.8
2032	2	0.75	4	63.2	287.4	1659.0
2033	2	0.75	3	58.0	189.8	6371.8
2034	2	0.75	16	18.2	223.3	720.3
	4	1.25	24	0.4	0.9	637.2
2035	2	0.75	16	19.0	88.7	1318.1
2036	2	0.75	1	0.0	0.0	0.0
2037	2	0.75	13	42.8	530.5	1252.5
	4	1.25	3	0.0	0.0	2391.0
2038	2	0.75	22	33.9	212.4	797.7
	4	1.25	19	3.7	5.2	915.3
2039	2	0.75	13	19.3	70.3	1040.5
2040	2	0.75	10	52.7	412.6	1766.3
	4	1.25	6	12.8	5.9	1732.1
2041	2	0.75	11	63.3	252.0	1710.3
	4	1.25	1	22.1	9.7	0.0

Appendix Table 3 expanded.

Start of First Attempt	End of Last Attempt	Sum of Attempt Durations (s)
6/5/08 19:44	6/6/08 6:00	2626.0
6/6/08 2:59	6/6/08 6:50	2575.2
6/7/08 22:57	6/8/08 3:04	0.0
6/5/08 22:16	6/6/08 3:42	1442.5
6/7/08 22:16	6/7/08 22:16	0.0
6/5/08 22:51	6/6/08 5:57	4406.3
6/7/08 21:42	6/8/08 4:33	228.7
6/5/08 22:38	6/6/08 5:26	3592.6
6/7/08 21:35	6/8/08 3:21	62.9
6/5/08 22:20	6/6/08 0:30	1149.5
6/5/08 23:54	6/6/08 5:22	569.5
6/5/08 22:32	6/6/08 2:43	3572.3
6/7/08 22:31	6/8/08 2:46	21.5
6/5/08 22:23	6/6/08 4:38	1418.9
6/6/08 4:09	6/6/08 4:09	0.0
6/5/08 22:47	6/6/08 5:13	6896.1
6/7/08 22:27	6/8/08 0:26	0.0
6/5/08 22:27	6/6/08 4:38	4672.4
6/7/08 21:18	6/8/08 2:09	98.8
6/5/08 23:09	6/6/08 3:10	914.5
6/5/08 22:19	6/6/08 4:22	4126.4
6/7/08 21:33	6/8/08 0:27	35.6
6/5/08 22:52	6/6/08 4:52	2772.1
6/7/08 23:07	6/7/08 23:07	9.7