Swimming Performance of Rainbow Trout and Westslope Cutthroat Trout in an Open-Channel Flume

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Abstract

We used an open-channel flume to characterize the swimming performance of Rainbow Trout *Oncorhynchus mykiss* and Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* ranging nominally in fork length from 15 to 30 cm. With an open-channel flume, we observed volitional swim performance of wild-caught Rainbow Trout and Westslope Cutthroat Trout; the fish were not coerced, prodded, or spooked into action. We also observed the maximum short-duration swim speed of the fish, providing important effective leap or velocity challenge information for the design of intentional barriers. We conducted the experiment with a consistently low water velocity challenge and characterized swim speeds by using weighted least-squares regression, revealing no evidence of a difference in swim speeds between the two species. We estimated the overall average swim speed for Rainbow Trout to be 0.84 m/s (SE = 0.02), with a 95% confidence interval of 0.79–0.89 m/s, and that for Westslope Cutthroat Trout to be 0.84 m/s (SE = 0.03), with a 95% confidence interval of 0.78–0.90 m/s. The maximum swim speeds observed were 2.72 m/s for Rainbow Trout and 3.55 m/s for Westslope Cutthroat Trout. The project results provide new information on the swimming ability of wild Rainbow Trout and Westslope Cutthroat Trout that can be used to improve fish passage or barrier design.

Keywords: Rainbow Trout; Westslope Cutthroat Trout; swimming; speed

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Introduction

The Western United States is renowned for pristine cold-water fisheries that support many species of Trout, a resource that drives tourism, real estate values, and other economic engines. Mobility and connectivity in aquatic systems are important to all life stages and species of Trout (Rieman and McIntyre 1995; Kahler and Quinn 1998). One management strategy for mitigating the potential impact of climate change and enhancing the long-term viability of aquatic species is to ensure that aquatic systems are connected (Hulme 2005). Culverts, for example, are potential physical barriers to upstream fish passage due to insufficient water depth, large outlet drop height, and excessive water velocity (Baker and Votapka 1990; Votapka 1991; Fitch 1995; Burford et al. 2009). There are other barriers to fish mobility, but mainstream incorporation of environmental concerns into culvert design and analyses has provided a clear view that a sound knowledge of fish swimming capabilities is a necessity. Intentional barriers installed to isolate native fish in certain stream reaches often rely on excessive leap or velocity challenges (Powers and Orsborn 1985). Again, these examples are but a few of the many situations where the need for knowledge of fish swimming performance is a fundamental component of sound design and assessment.

Understanding the swimming performance of fish and how swimming ability applies to the design and analysis of passage structures increases the ability to protect and enhance native fish populations (Katopodis 2005). In our project, two Trout species were examined: Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* and Rainbow Trout *Oncorhynchus mykiss*. Westslope Cutthroat Trout historically inhabited waters west of the Continental Divide, as well as the upper Missouri River drainage, including portions of several states and Canada (Behnke 1992). The preservation of Westslope Cutthroat Trout is often the impetus for connectivity concerns and restoration activities, and although in peril in some portions of its historic range, Westslope Cutthroat Trout remains widespread throughout the Pacific Basin of the United States, the Great Basin, and the Rocky Mountains. Rainbow Trout is an important game fish, and nonnative, hatchery-reared Rainbow Trout have been widely stocked throughout North America. Rainbow Trout are also commonly used as a surrogate species for salmonid fish passage assessment studies and models. In addition, fisheries professionals involved with native species conservation commonly deal with projects that must consider the interactions between Rainbow Trout and Westslope Cutthroat Trout.

A review of previous swimming performance studies for Rainbow Trout and Cutthroat Trout provides an interesting context regarding the purpose or intent of the studies, the variety of experimental techniques used, and the range of swimming information derived from them. As of this writing, there are no published reports that we are aware of concerning the swimming capabilities of Westslope Cutthroat Trout where the experiment was designed specifically to address that issue. There have been a few published studies that developed anecdotal information, for example, observations of fish overcoming a certain velocity challenge in a culvert (Belford and Gould 1989; Burford et al. 2009; Peterson et al. 2013), which establishes an at-least swim speed threshold.

Nearly all experiments designed specifically to elucidate the swim capabilities of Rainbow Trout have been performed using respirometers (Bainbridge 1960, 1962; Jones 1971; Jones et al. 1974; Schneider and Connors 1982; Peake et al. 1997; Burgetz et al. 1998; Jain and Farrell 2003; Claireaux et al. 2005; Farrell 2008). The common term most often used in respirometer studies is the critical swim speed (i.e., U_{crit}), a measure of the maximum water velocity for which the fish could hold its position for some specified time duration that varied between studies. There are variations of the device itself and of the protocol for using the devices that are documented in each study; for example, some studies used electric shocking to motivate fish, whereas others used gentle nudging. There are also variations in the motivation for the studies: the effect of temperature, fish length, and experimental approach on swim performance (Webb et al. 1984; Keen and Farrel 1994; Jain et al. 1997; MacNutt et al. 2004), the effect of contaminants on swim performance (Jones and Moffit 2004), or the physiological response to environmental or biological conditions (Milligan and Wood 1986; Schulte et al. 1992). Under the common name Rainbow Trout (reported in different studies as *Oncorhynchus mykiss* or *Salmo gairdneri* or *Salmo irideus*), the fish in any one study may have been anadromous steelhead that can grow to 100 cm in length, or resident fish caught from streams where the adults measure one-tenth that size. Some studies used hatchery fish, experiments were performed worldwide, and in some studies the life history of the test fish was not well described. Some studies evaluated the potential effects of hybridization between Trout species (Hawkins and Quinn 1996; Seiler and Keeley 2007). The number of fish (n) in each of these published studies was also highly variable, from small studies ($n = 2$) to larger trials ($n > 100$). Hunter and Mayor (1986) summarized swimming information for Rainbow Trout and other species, generally using information from published studies that are referenced herein.

Although swim capabilities observed in respirometer studies are important and meaningful, the transferability of the results back to the natural stream or impediments therein are challenging. Researchers report that characterizing swimming performance using open-channel flumes may provide a more realistic measure of swimming performance than swim chamber studies (Peake 2004; Castro-Santos 2005; Peake and Farrel 2006). Field studies in Montana investigated the passage of Yellowstone Cutthroat Trout *Oncorhynchus clarkia bouvieri*, Rainbow Trout, and their hybrids through culverts and characterized the flow, depth, and velocity conditions through which fish passed or failed to pass (Belford and Gould 1989; Solcz 2007; Blank 2008; Burford et al. 2009). Solcz (2007) used these data to develop a probabilistic model of culvert passage relative to average water velocity within the culvert.

In summary, there is little published swim performance information for Westslope Cutthroat Trout. There is substantial information concerning swim performance for Rainbow Trout, but it is almost exclusively from respirometer studies with dramatic diversity in fish, settings, protocols, and other factors. The primary objective of this project was to characterize the volitional swimming performance of Rainbow Trout and Westslope Cutthroat Trout in an open-channel flume setting. The experimental design also afforded the opportunity to

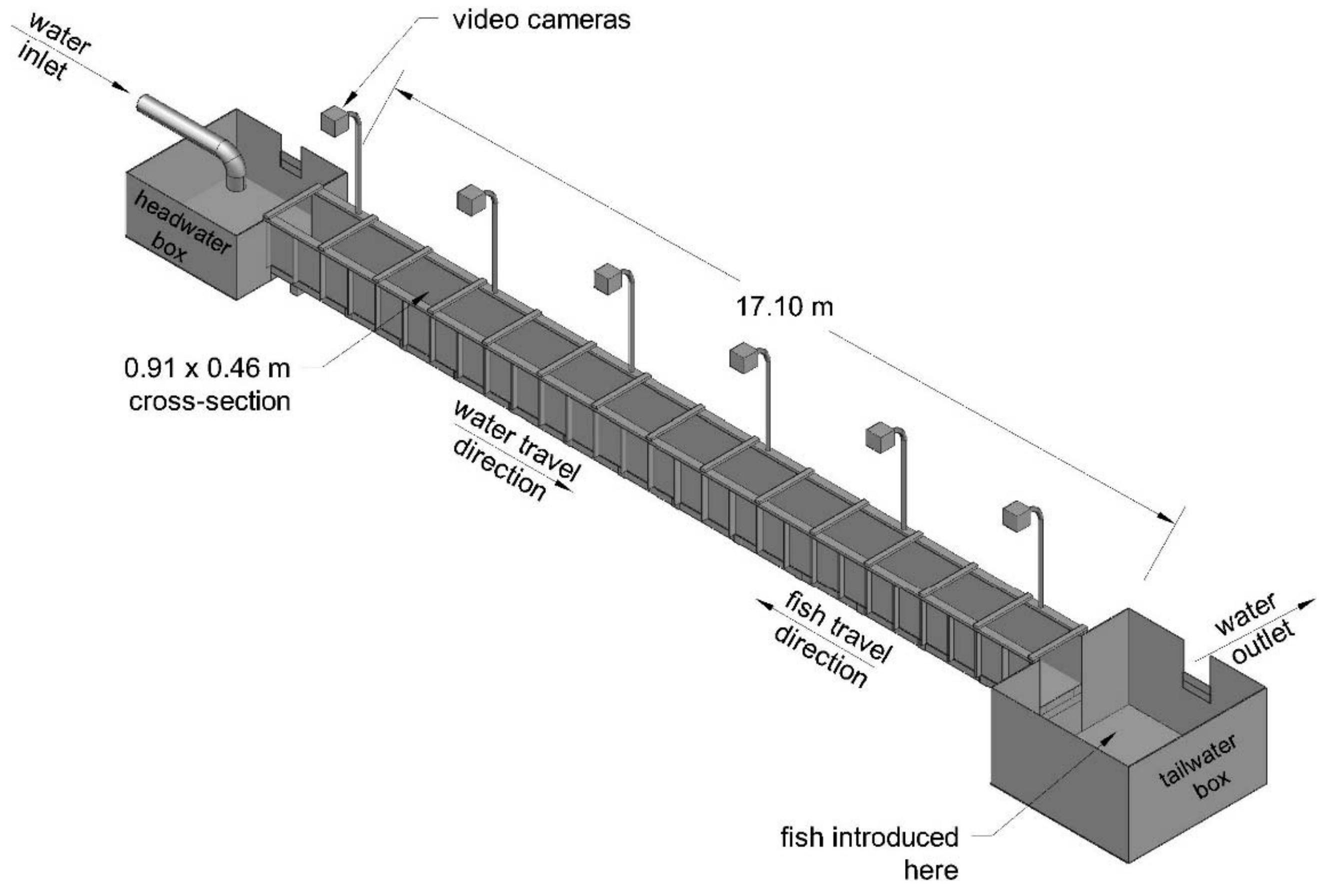

Figure 1. Schematic of the open-channel flume used in the experiment at the U.S. Fish and Wildlife Service Bozeman Fish Technology Center in Bozeman, Montana, in 2011. We introduced Rainbow Trout *Oncorhynchus mykiss* and Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* into the tailwater box. We also recorded fish travel on high-speed video cameras. We transformed travel time and distance to piece-wise fish velocities relative to the ground.

observe the maximum short-duration swim speed for both species.

Methods

Flume and water source

We conducted this study in a flume that was located at the U.S. Fish and Wildlife Service Bozeman Fish Technology Center (BFTC) in summer 2011. Similar fish swim studies have been conducted at the facility since then, for example, a study of Arctic Grayling *Thymallus arcticus* by Dockery et al. (2019), with refinements to the facility and methods based on lessons learned in previous studies. The flume (Figure 1) was 0.91 m in height, 0.46 m in width, and 17.10 m in length. We marked a discernable grid on the opaque floor before the experiment, with 0.15-m increments across the width of the flume and 0.60-m increments in the direction of flow. We blended inflow water from groundwater wells by using pumps to control temperature and flow rate. Water entered a headwater box, flowed through the flume, and exited into a tailwater box. We used a nominal flow rate of 0.05 m^3/s for all trials, with minimal variation in rate (Table 1). Six high-definition digital video cameras (Handicam HDR-XR-150; Sony) aimed vertically downward in an array above the flume recorded fish movement.

Fish collection and handling

We collected Rainbow Trout that ranged in fork-length (FL) size from 15.0 to 30.5 cm from Hyalite Creek near Bozeman, Montana, in May 2011 by electrofishing. We placed captured Rainbow Trout in a bucket containing creek-water; we then transferred them to live-wells and trucked them to the BFTC. We collected Westslope Cutthroat Trout that ranged in size from 15.0 to 29.0 cm FL by using the same methods as for Rainbow Trout from streams near Kalispell, Montana, in October 2010. We held the Westslope Cutthroat Trout at the Sekokini Springs Hatchery in Glacier County, Montana, over the winter, and we transported them to the BFTC in April 2011. We regulated the live-well temperature during transport to within 2°C of that of the source river or hatchery and held the oxygen concentration in the live-well at a constant value of 8 mg/L. At the BFTC, we held Rainbow Trout and Westslope Cutthroat Trout in separate tanks near the flume. We implanted all fish with a passive integrated transponder tag. Because of

Table 1. We placed Rainbow Trout *Oncorhynchus mykiss* or Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* in the outlet pool of an open-channel flume in Bozeman, Montana, USA, in 2011 and allowed fish to enter and traverse the flume volitionally. We used video cameras to track fish trajectory against an observed combination of water flow depth and velocity. In each trial, we introduced fish of one species and within a size class to the flume in a batch. The conditions and participants in each experimental trial are summarized. The abbreviation std dev is the standard deviation of the mean water velocity.

Trial no.	Water flow rate (m^3/s)	Mean water velocity (std dev) (m/s)	Mean water depth (m)	Nominal fork length (cm)	Water temp (°C)	No. of fish in trial
Rainbow Trout						
1	0.043	0.44 (0.03)	0.21	16.5	9.6	14
2	0.055	0.51 (0.02)	0.24	19.1	9.8	21
3	0.051	0.46 (0.04)	0.24	21.6	9.5	9
4	0.044	0.49 (0.03)	0.20	24.1	9.5	15
Westslope Cutthroat Trout						
5	0.055	0.46 (0.04)	0.26	16.5	11.0	9
6	0.049	0.43 (0.03)	0.25	19.1	11.5	13
7	0.049	0.49 (0.03)	0.22	21.6	11.5	8

interference from the flume structure, however, we did not use passive integrated transponder technology during the swim trials. We inserted the 12-mm tags into the abdomen through a small incision on the ventral surface anterior to the pelvic girdle, as described by Forty et al. (2016). Insertion wounds were small and did not require sutures; previous studies indicated that sutures are not necessary for such small incisions and that the effects of tags do not significantly affect swimming performance (Bolland et al. 2009; Larsen et al. 2013). We gave fish adequate time (weeks) to completely heal before testing began. We weighed and measured fish, but we did not determine sex, before the swimming trials. The water temperature in the holding tanks was consistently within 1.0°C of that in the flume, with the flume water temperature ranging from 9.5 to 12.0°C (Table 1). We fed the fish daily with commercial Trout feed, but food was withheld for 24 h in advance of a swim trial.

Hydraulics

To initiate a trial, water was introduced to the flume and allowed to reach steady conditions (45–60 min). On-site hydraulic measurements, corroborated with a gradually varied flow hydraulic model, characterized the flow environment in the flume for each trial. We used a graduated rod to measure the water depth at each grid interval over the length of the flume and continuously logged flow depth in the headwater and tailwater tanks with TruTrack WT-HR data loggers (TruTrack Ltd., Christchurch, New Zealand). A Flexus F601 flow recorder (Flexim Aericas Corp., Edgewood, NY) was installed in the supply pipe to measure inflow rate. We corroborated inflow rate values with a U.S. Geological Service method in the flume itself (Rantz et al. 1982), where we measured in-flume water velocities with a Marsh McBirney Flo-Mate velocimeter (Hach Corp., Loveland, CO) approximately 7.3 m upstream from the tailwater tank. Together, these observations resulted in estimates of the flow depth and bulk water velocity at each 0.6-m grid interval along the length of the flume.

Swim performance experiments

For each trial indicated in Table 1, we placed the subset in the tailwater pool at the downstream end of the flume. We did not coerce fish to enter the flume, nor did we coerce or intentionally spook them during any part of the swim trial. Each trial lasted 4 h, a duration based on pilot studies that showed this was sufficient time for fish to make multiple attempts, explore, and often ascend the length of the flume. We recorded continuous video footage from all cameras over the duration of each trial as fish moved throughout the flume. We distilled the movement of individual fish (position in the flume versus time) from the camera array video footage from the video footage (the distilled data are in the Data S1, *Supplemental Material*). The cameras recorded still images at 30 frames/s. We processed the video streams by examining these still images and noting the spatial position of each fish in successive time-stamped images.

Data analysis

The fish exhibited multiple behaviors during the experiment. We observed fish to swim with their body facing in either the upstream or downstream direction; when facing upstream, fish could advance upstream, hold their position, or swim against the flow but move in the downstream direction. We only included observations of fish that entered the flume by more than 1.2 m and progressed in the upstream direction in the analysis, in an attempt to characterize swim speeds of forward-swimming fish. We made the 1.2-m cutoff criterion based on observations from a pilot study, where fish frequently entered the flume but then quickly turned and exited on their own volition before proceeding more than 1.2 m into the flume; we characterized this type of behavior as an exploratory entry. We determined the speed at which a fish swam through each flume grid interval ($v_{g,ij}$, the groundspeed, or fish velocity relative to the ground, positive in the upstream direction for the *i*th swim event in the *j*th flume segment) as the grid spacing (0.6 m) divided by the time over which fish traveled that distance. The fish swim speed ($v_{f,ij}$, the speed of the fish

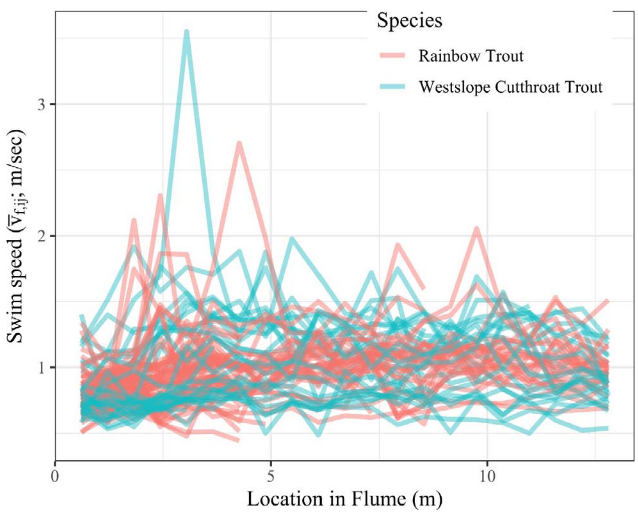

Figure 2. We placed Rainbow Trout *Oncorhynchus mykiss* or Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* in the outlet pool of an open-channel flume in Bozeman, Montana, in 2011 and allowed fish to enter and traverse the flume volitionally. The graph shows individual observations of fish swim velocities relative to the water, $v_{f_{ij}}$, for each swim event for Rainbow Trout (salmon-colored lines) and Westslope Cutthroat Trout (blue lines). Although observations are point-wise, the connecting lines show the dependence within a swim event (i.e., for a fish exhibiting constant forward motion in the flume).

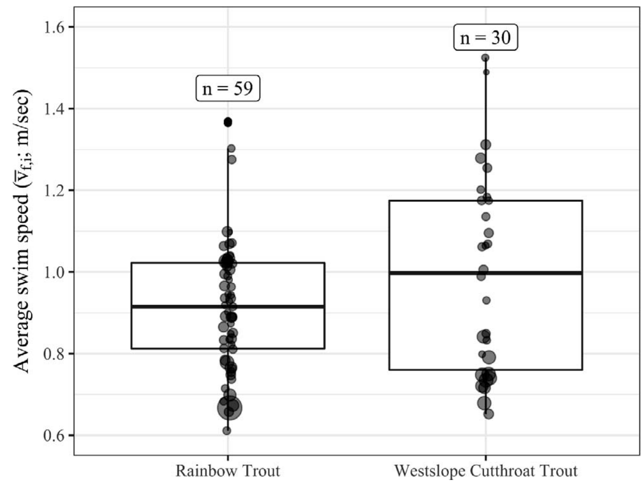

Figure 3. We placed Rainbow Trout *Oncorhynchus mykiss* or Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* in the outlet pool of an open-channel flume in Bozeman, Montana, in 2011 and allowed fish to enter and traverse the flume volitionally. The graph shows the average swim speed, $\bar{v}_{f_i}$, where each symbol corresponds to the mean swim speed for an individual fish. The box plots show the median, the first quantile, the third quantile, and fences for the unweighted observations. The symbol size for each fish corresponds to the weights used in the regression analysis to estimate the (weighted) overall average swim speeds for each species. We calculated the weights as the total number of observations divided by the variance in observations (sample variance) from an individual swim event.

relative to the water for the *i*th swim event in the *j*th flume segment) was calculated for each fish in each flume grid increment by adding the local water velocity ($v_{a,ij}$, a positive number for water flowing in the downstream direction corresponding to the *i*th swim event in the *j*th flume segment) to the fish ground speed:

$$v_{f,ij} = v_{g,ij} + v_{a,ij} \quad (1)$$

Overall, there were 89 observations (unique combinations of entries in the columns labeled fish and event in Data S1) of fish exhibiting forward facing direction and forward travel (both species combined), as shown in Figure 2. Missing data are the result of camera malfunctions or multiple fish crossing paths through the frame, making it impossible to uniquely identify fish in subsequent frames. For swim events with missing observations, it is assumed that the fish would have continued along a path similar to the path they were on while available for observation. Because of the relatively constant nature of the swim events exhibited in these data, this assumption is reasonable (Figure 2). To account for dependencies within multiple observations during the same swim event, which varied between 4 and 21 observations, we calculated the average swim velocity for each swim event (Figure 3).

Fish of the same species and size class were run in the same swim trial on the same day. Although it is expected that variation due to size class and water temperature (constant for each trial) is relatively low, we estimated the overall average of the average individual fish swim speeds for each species, with variation due to these factors being absorbed into the residuals, denoted $\in_i$. That is, the quantity of interest was the overall average of average swim speeds for the two species. Although it is clear from Figure 2 that there is no evidence of a difference between the overall average swim speeds of the two species, weighted least-squares regression was used to model overall average swim speeds for the two species to obtain ranges of plausible swim speed values for each species. The regression model used was as follows:

$$\bar{v}_{f_i} = \beta_0 + \beta_1 \mathrm{WCT}_i + \in_i \quad (2)$$

where $\in_i \sim N(0, n_i/\sigma_i^2)$, $i = 1,2,\ldots,89$. In this linear model, $\bar{v}_{f_i}$ is the average swim speed (m/s) for the *i*th swim event, WCT_i is a species indicator variable taking on the value 1 if the *i*th swim event was made by a Westslope Cutthroat Trout and the value 0 if by a Rainbow Trout. The parameters β_0 and β_1 represent the true overall mean swim speed for the Rainbow Trout and the additive adjustment to the true overall mean swim speed when moving from a Rainbow Trout to a Westslope Cutthroat Trout, respectively (i.e., $\beta_0 + \beta_1$ represents the true overall mean swim speed for Westslope Cutthroat Trout). The errors, $\in_i$, are assumed to be independent, but not identically distributed (i.e., they are assumed to be normal, but do not have the same variance). Specifically, weights for each observed average were computed as n_i/s_i^2, where n_i is the number of observed velocities used to calculate the average swim speed for the ith swim event, and s_i^2 is the sample variance of the velocities for the ith swim event $i = 1,2,\ldots,89$. We also identified the maximum value of $v_{f,ij}$ exhibited by any fish of each species. These values can be seen in Figure 2 as the peak value for each species. The R code used in the analysis is provided in an annotated text file in the supplemental materials (Data S2, *Supplemental Material*).

Results

The boxplots of Figure 3 display the average swim speed observed for each fish $\bar{v}_{f_i}$. There was no evidence of a difference between the overall average swim speeds of Rainbow Trout ($n = 59$) and Westslope Cutthroat Trout ($n = 30$) in volitional, open-flume swim trials ($t_{87} = 0.09$, $P = 0.93$). For Rainbow Trout, we estimated the overall average swim speed to be 0.84 m/s (SE = 0.02), with a 95% confidence interval of 0.79–0.89 m/s, and that for the Westslope Cutthroat Trout to be 0.84 m/s (SE = 0.03), with a 95% confidence interval of 0.78–0.90 m/s. These intervals provide a range of plausible swim speeds for the fish in this study. The maximum observed swim speed within an 0.6-m flume segment, $v_{f,ij}$, was 2.73 m/s for Rainbow Trout and 3.55 m/s for Westslope Cutthroat Trout.

Discussion

Fish swim studies have inherent limitations. This study represents the first that we are aware of in which swim trials were volitional in an open flume for two species of Trout. We took the fish used in the study from two specific streams in Montana, and any inference beyond the Trout used in this study should be approached with caution. We only performed the volitional trials under one hydraulic challenge. The range of size (length) of the fish tested was relatively narrow because we captured the fish in the wild for the study, enough so that no attempt to characterize swim speed by fish length was made. Lastly, we implanted the fish with passive integrated transponder tags before the experiment.

The maximum swim speed observed in this study for Westslope Cutthroat Trout (3.55 m/s) is similar to the average water velocity that Coastal Cutthroat Trout *Oncorhynchus clarkii clarkia* were able to overcome in the culvert test bed flume study by Peterson et al. (2013). However, it is less than the upper limit of the burst swim range ($\sim$4.12 m/s) for Cutthroat Trout reported by Bell (1991). For Rainbow Trout, the maximum observed swim speed in this study (2.73 m/s) is toward the upper end of values reported in other studies. The maximum Rainbow Trout velocity in all studies reviewed in the preparation of this report was 8.17 m/s for a fish of length 81.0 cm. For a comparison to other Trout species, Mesa et al. (2008) evaluated sprint swimming performance of wild Bull Trout *Salvelinus confluentus* by using a similar method to the experiment described herein (but coerced instead of volitional) and found their maximum swim velocity ranged between 1.3 and 2.3 m/s.

For Rainbow Trout, the overall average swim speed observed in this study was estimated to be 0.84 m/s. The results of this study should not be compared directly with results of respirometers studies, but it is interesting to note results of the respirometer studies when the fish lengths and water temperatures of the tests were reasonably similar. Bainbridge (1960) reported a U_{crit} of 0.55 m/s (length = 18 cm, temperature not reported, $n = 4$), Bainbridge (1962) reported a U_{crit} of 0.58 m/s (length = 26 cm, temperature = 14°C, $n = 13$), Jones (1971) reported a U_{crit} of 0.66 m/s (length = 11 cm, temperature = 12°C, $n = 150$), and Schneider and Connors (1982) reported a U_{crit} of 0.90 m/s (length = 29 cm, temperature = 10°C, $n = 21$). The average Rainbow Trout swim speed observed in our volitional trials is within the range of U_{crit} values reported in previous respirometer studies that had comparable fish lengths and water temperatures.

One major design goal of fish passage structures is to ensure that Trout and other fish species are able to easily pass upstream without exhaustion. The Washington Department of Fish and Wildlife (Barnard et al. 2013) recommends maintaining culvert water velocities that decrease as the culvert length increases, ranging from 1.2 m/s in short culverts (3–30 m long) to 0.6 m/s in long culverts (length >60 m). These guidelines are recommended for culvert installations using a hydraulic design approach, which creates specific water depths and velocities for a range of fish passage flows in culverts. The results of our volitional trials fall within these values for conservative passage design: Rainbow Trout ascended the test flume at overall average swim velocities in a plausible range from 0.79 to 0.89 m/s, and Westslope Cutthroat Trout ascended at overall average swim velocities in a plausible range from 0.78 to 0.90 m/s.

Practitioners using swimming abilities to infer passage probability, whether assessing structures (such as culverts), identifying barriers, or purposefully creating barriers are advised to synthesize the relevant data specific to their application and apply conservative values to ensure the success of specific goals. The results from this study provide information to a growing body of Trout swimming ability literature; we characterized the swimming performance of similar-sized individuals of two Trout species, Rainbow Trout and Westslope Cutthroat Trout, under specific laboratory test conditions. The results might be useful for evaluating velocity or leap (a velocity-based calculation) barriers to Rainbow Trout or Westslope Cutthroat Trout and suggest that velocities <3.55 m/s for Westslope Cutthroat Trout and <2.73 m/s for Rainbow Trout may not be barriers to passage for the fish investigated herein. Passage probability models are only as good as the representative swimming data for the specific physiological aspects of a species and environmental conditions surrounding the observation. Although our study was limited in scope and more studies investigating the leap and velocity metrics associated with identifying barriers for Trout species would be valuable, our results provide new information on the swimming ability of wild Trout that can be used to refine passage models.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Supplemental file that archives the experimental observations of Rainbow Trout *Oncorhynchus mykiss* or Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* that we placed in the outlet pool of an open-channel flume in Bozeman, Montana, USA, in 2011 and that we allowed to enter and traverse the flume volitionally. Each observation of a fish traversing a 0.6-m-long segment of the flume length is represented by a row in the file. The file is in Excel format, there are 3,430 rows by 18 columns in the data set, and the file is annotated to fully describe the contents of each column. Each row in the file includes fish identifiers, fish length, water velocity, fish ground speed, fish speed relative to the water, water temperature, and categorical variables that aid in automating the analyses.

Found at DOI: https://doi.org/10.3996/052019-JFWM-040.S1 (345 KB XLSX).

Data S2. An annotated text file containing the R code used in the swim speed analysis of Rainbow Trout *Oncorhynchus mykiss* or Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* that we placed in the outlet pool of an open-channel flume in Bozeman, Montana, USA, in 2011 and that we allowed to enter and traverse the flume volitionally. The R code performs statistical analyses and prepares the graphs that summarize the analysis.

Found at DOI: https://doi.org/10.3996/052019-JFWM-040.S2 (8 KB R).

Reference S1. Baker CO, Votapka FE. 1990. Fish passage through culverts. FHWA-FL-09-006. U.S. Department of Agriculture Forest Service–Technology and Development Center, San Dimas, California.

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