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Critical Swimming Speeds of Wild Bull Trout

Abstract

We estimated the critical swimming speeds (U_{crit}) of wild bull trout at 6°, 11°, and 15°C in laboratory experiments. At 11°C, 5 fish ranging from 11 to 19 cm in length had a mean U_{crit} of 48.24 cm/s or 3.22 body lengths per second (BL/s). Also at 11°C, 6 fish from 32 to 42 cm had a mean U_{crit} of 73.99 cm/s or 2.05 BL/s. At 15°C, 5 fish from 14 to 23 cm had a mean U_{crit} of 54.66 cm/s or 2.88 BL/s. No fish successfully swam at 6°C. Swim speed was significantly influenced by fish length. Many bull trout performed poorly in our enclosed respirometers: of 71 U_{crit} tests we attempted, only the 16 described above were successful. Bull trout that refused to swim held station within tunnels by using their pectoral fins as depressors, or they rested and later became impinged against a downstream screen. Several common techniques did not stimulate consistent swimming activity in these fish. Our estimates of U_{crit} for bull trout provide an understanding of their performance capacity and will be useful in modeling efforts aimed at improving fish passage structures. We recommend that fishway or culvert designers concerned with bull trout passage maintain velocities within their structures at or below our estimates of U_{crit}, thus taking a conservative approach to ensuring that these fish can ascend migratory obstacles safely.

Introduction

The ability of bull trout (*Salvelinus confluentus*) to successfully pass dams, culverts, and other diversion structures is a concern for fishery managers. Concern is warranted because little information exists on the performance of bull trout that may provide insight into their ability to pass through culverts or fishways. Specifically, no information is available on the swimming performance or exercise physiology of bull trout, which is prerequisite to addressing questions concerning their passage at various structures. In addition, bull trout prefer low water temperatures, complex forms of cover, and low velocity areas (Fraley and Shepard 1989, Rieman and McIntyre 1993, Goetz 1997, Dambacher and Jones 1997, Earle and McKenzie 2001). The combination of these preferences and the presence of resident and fluvial life history types may influence their performance at fish passage structures, but this notion has not been studied.

The U.S. Forest Service (USFS) is currently developing national protocols for adequate passage of aquatic organisms through culverts. As part of this effort, the USFS has developed an analytical model that evaluates different culvert designs for fish passage. Based on swimming ability of various North American fish species (determined previously in laboratory and field studies), their potential performance in different culvert types can be estimated using the model. For species for which there are no swimming performance data (such as bull trout), this model cannot be applied or must be applied using data from a similar species. However, because of species and life stage-specific differences that determine the swimming performance of fish, using data from one species to predict the capabilities of another is ill advised (Berry and Pimentel 1985, Mesa and Olson 1993). For this reason, the USFS is compiling data on the swimming performance of various species of fishes, particularly those listed as imperiled, threatened, or endangered. Bull trout in the western United States are currently listed as threatened under the Endangered Species Act.

For this study, we addressed the objective of determining the critical swimming speed (U_{crit}) of juvenile and adult bull trout at three temperatures. The critical swimming speed of fish is an important measure of their biological and physiological performance because U_{crit} is thought to be a close measure of the maximum aerobic capacity of fish (Hammer 1995). Thus, at speeds near and above U_{crit}, swimming involves increased

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recruitment of white muscle fibers and energetically costly anaerobic pathways for metabolism (Burgetz et al. 1998). A knowledge of U_{crit} indicates water velocities where fish may have difficulty swimming for long periods of time. This information would be useful for designing new, or modifying existing, fish passage structures that minimize impacts to bull trout.

We used our estimates of U_{crit} to assess the potential of bull trout to pass through fishways, culverts, or other migratory obstacles in a manner similar to Jones et al. (1974) and Peake et al. (1996, 1997, 2000). Estimates of U_{crit} from these studies have been used to determine fishway or culvert velocities that would allow passage of different species of fish within a certain period of time. For example, Jones et al. (1974) estimated the U_{crit10} (derived from U_{crit} tests with 10-min time intervals) of several species of fish from the McKenzie River to describe speeds that these fish could maintain for 10 min. Thus, assuming a 10 min transit time through a culvert with velocities similar to the U_{crit10}, one could calculate the maximum length of culvert that fish could realistically pass. Peake et al. (1997) took this analysis to a more refined level by deriving models from U_{crit2}, U_{crit5}, and U_{crit10} tests for various species of Newfoundland salmonids, thus providing more flexibility in determining culvert lengths and velocities that allow adequate passage of fish. Our results provide not only some basic biological information on bull trout, but also preliminary performance metrics needed for modeling and establishing guidelines for their passage through culverts and other structures.

Methods

Test Fish

Juvenile bull trout were collected from a screw trap on the Metolius River, Oregon, from 28 March to 2 May 2002 by personnel from the USGS Western Fisheries Research Center and the Portland General Electric Company (PGE) during their ongoing fish trapping operations. In August 2002, PGE personnel collected adult bull trout by angling in the Metolius River arm of Lake Billy Chinook. This lake was formed by Pelton Dam, a project that impounds the Crooked, Deschutes, and Metolius rivers in central Oregon. Fish from the screw trap were held initially in floating cages within the river and transferred, once per week, to the PGE owned and operated Round Butte Hatchery at Pelton Dam. Fish captured by angling were transported every day to the hatchery. When sufficient numbers of bull trout had been captured, we transported them to the Columbia River Research Laboratory (CRRL) using a truck equipped with an insulated tank and aerated water. A fish protector (Pond Polyaqua) was added to the water (about 6 ppm) to minimize physiological stress and maintain skin condition during transport. Dissolved oxygen levels and temperature were checked routinely during the 4 hr trip.

Upon arrival, fish were separated into 5-cm size classes (all lengths reported herein are fork lengths, FL) and held indoors under a simulated ambient photoperiod in circular tanks (0.76 m in diameter, 0.76 m deep) receiving well water. Separating fish into size classes was necessary to minimize cannibalism, which occurred during some of our early holding. Larger, adult fish were held outside in 1.5-m-diameter tanks. Initially, water temperature in all tanks was the same as water during transport, about 9-11°C. Thereafter, water temperature was adjusted at a rate of 2°C/d to within ± 1°C of the selected experimental temperature. The water was heated using single-pass electric heaters, and packed columns dissipated excess dissolved gases generated by heating. All fish were acclimated for at least 2 wk to the experimental temperature prior to testing. Small fish (about 10 cm) were fed two earthworms or several salmon eggs (obtained from a local hatchery) two to three times each week. Larger fish were fed one to two live fish (sub-yearling hatchery salmonids) two to three times each week. Selected characteristics of our well water were measured hourly with an automated meter.

Critical Swimming Speed Tests

Critical swimming speed tests on bull trout were conducted from early May to late September 2002 at 6°, 11°, and 15°C. These temperatures represent a range of water temperatures naturally encountered by bull trout in the wild (Ratliff 1992, Buchanan and Gregory 1997). Swimming tests were conducted in 7, 55, or 84 L Blazka-type respirometers, depending on size of fish. Water velocities in the respirometers were created by a propeller driven by a variable-speed electric motor. We used linear regression to describe the relation between motor speed and water velocity (measured with a flow meter inside the tunnel).

The resulting regression equations were used to calculate the motor speed necessary for each respirometer to achieve a desired velocity. All relations between motor speed and water velocity had r^2 values > 0.95.

One or two days before a U_{crit} test, a fish was netted from a holding tank and transferred to an isolation container. Fish < 30 cm were placed in a 50.8-cm-long, 26.7-cm-wide, 31.7-cm-deep aquarium and larger fish were placed in a 0.76-m-diameter, 0.76-m-deep circular tank. Fish showing signs of disease, injury, or other abnormalities were not tested. Food was withheld from isolated fish to ensure a post-absorptive state (Beamish 1964, Bernatchez and Dodson 1985). On the morning of a test, a respirometer was filled with water of the appropriate temperature. A fish was netted from an isolation aquarium or tank, lightly anesthetized by placing it in a 19-L bucket containing 50 mg/L of buffered tricaine (MS-222), rapidly weighed and measured, and placed into the respirometer. The fish was allowed to adjust for 2 hr at a water velocity of about 1.0 body length/s (BL/s).

Following adjustment at 1.0 BL/s, we subjected fish to a brief practice swim test. Based on preliminary work, we noted that fish performed somewhat better in the swim tunnels if they had prior experience with U_{crit} procedures. For this practice swim, water velocity was increased by 10 cm/s and the fish was required to swim for a maximum of 2 min (normally 30 min in our standard U_{crit} protocol). The water velocity was then increased by 10 cm/s every 2 min until the fish stopped swimming. The velocity was returned to 1.0 BL/s and the fish was allowed to recover for 3 hr, after which we started the actual U_{crit} test. For our tests, we modified the ramped U_{crit} protocol described by Jain et al. (1997). Water velocity was increased to 20 cm/s above the velocity at 1 BL/s and the fish was required to swim for 30 min. Thereafter, the velocity was increased by 10 cm/s every 30 min until the fish fatigued. Fatigue was confirmed when a fish stopped swimming and fell back on a downstream screen within the tunnel three times. Rapid changes in water velocity (i.e., quickly turning the motor off and on) were used to encourage fish to leave the downstream screen. Following a test, fish were removed, lightly anesthetized with buffered MS-222, tagged with a small passive integrated transponder (PIT) tag to facilitate individual identification, and placed in a holding tank for future testing.

Critical swimming speed was calculated in BL/s and absolute speed (cm/s) using the formula described by Beamish (1978). None of our fish had a girth that exceeded 10% of the cross sectional area of a swim tunnel, thus we did not correct swim speed estimates for solid blocking. To assess the influence of fish length on swim performance, we plotted U_{crit} against fish length at each water temperature. Within each temperature, we calculated mean values for U_{crit} using pooled data from similar sized individuals.

Collection and Holding

In total, 160 bull trout were collected from the Metolius River and Lake Billy Chinook (Table 1). All bull trout survived the stress associated with capture, handling, and transportation and arrived in good condition at our laboratory. Within a couple days, bull trout were feeding aggressively. Our feeding regime was successful in producing growth in many fish. We measured 29 PIT-tagged individuals from mid-May to early August and again in early November. On average, fish gained 69 g in weight (range 0-246 g) and 4 cm in length (range 0.2-7.3 cm).

Little is known about the long-term maintenance of wild bull trout in laboratory facilities

TABLE 1. Bull trout collection dates, sites, methods, sizes, and total number of fish collected during 2002.

Date	Site	Method	Size (cm)		Total collected
			< 20	>20	
5 Apr	Metolius River	Screw trap	45	0	45
19 Apr	Metolius River	Screw trap	55	0	55
3 May	Metolius River	Screw trap	27	0	27
5 Jun	Lake Billy Chinook	Angling	0	1	1
31 Jul	Metolius River	Fyke net	0	1	1
16 Aug	Lake Billy Chinook	Angling	0	31	31

and we encountered two general problems. First, early in the study we observed cannibalism and agonistic behavior that was stressful to subordinate fish and led to a few mortalities. To minimize the effects of these behaviors, we separated fish into 5-cm size intervals, held similar sized fish together, and placed several 15 to 30-cm-long pieces of PVC pipe (5, 7.5, and 10-cm-diameter) in each tank to provide cover. Second, several fish showed signs of disease or injury during the study (e.g., overtly lethargic behavior, unusually dark coloration, damaged snouts, frayed fins, cloudy eyes, external pustules or sores, or bleeding). These fish were euthanized and given a complete bacterial, viral, and parasitic screening by personnel from the USFWS Lower Columbia River Fish Health Center.

Results

We attempted to swim 5 fish at 6°C, 46 fish at 11°C, and 20 fish at 15°C. Of these 71 fish, 16 of them successfully completed a U_{crit} test; no tests were successful at 6°C. Swim speed was significantly influenced by fish length and, because there were no significant differences in slopes or elevations between lines fit for each temperature, the data were described by single regression lines (Figure 1). Estimates of U_{crit} in BL/s for large fish were lower than those of smaller fish, but when expressed in absolute speeds, swimming speed was positively related to fish size (Figure 1). Water temperature had a minor, but significant, influence on mean swim speed as evidenced by fish 11-19 cm at 11°C having a lower U_{crit} than those swum at 15°C (Table 2; $P < 0.05$)

The behavior of bull trout in the enclosed swim tunnels was problematic: only 22.5% of our fish completed the U_{crit} test. We defined a test as successful if the fish showed steady swimming with minimal erratic behavior and provided the data needed to calculate a valid estimate of U_{crit}. Specifically, fish had to swim for 30 min for two velocity steps above the initial adjustment velocity (i.e., 1 BL/s). All 16 of the successful fish did this, and some also swam during a third or fourth velocity increment. The behavior of bull trout resulting in a failed U_{crit} test typically consisted of fish flaring out their pectoral fins and maintaining position on the bottom of the tunnel or resting against the downstream screen instead of swimming. As velocity was increased, fish showing this type of behavior would usually maintain position on the bottom of the tunnel until the velocity was too high, at which point they began to behave erratically and soon became impinged on the back screen.

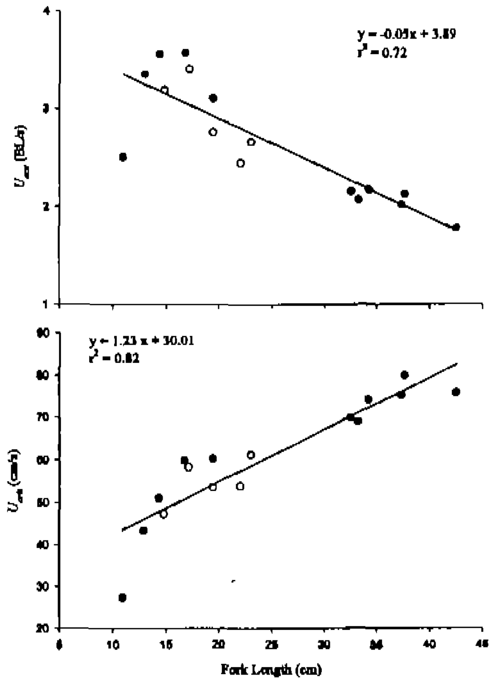

Figure 1. Linear regressions of U_{crit} (top panel = BL/s; bottom panel = cm/s) as a function of length for eleven fish swam at 11°C (black circles) and five fish at 15°C (open circles).

TABLE 2. Mean (SE) fork length and estimates of U_{crit} for three groups of bull trout at two temperatures.

Size range (cm)	Temperature (°C)	Sample size	Mean length (cm)	U_{crit} (cm/s)	U_{crit} (BL/s)
11-19	11	5	14.8 (1.5)	48.24 (6.10)	3.22 (0.20)
32-42	11	6	36.2 (1.5)	73.99 (1.67)	2.05 (0.06)
14-23	15	5	19.3 (1.5)	54.66 (2.35)	2.89 (0.17)

Discussion

Our estimates of U_{crit} for wild bull trout represent the first laboratory-based swimming performance metrics for these fish and a good first step toward understanding their capacity for exercise and ability to negotiate fish passage structures. The critical swimming speeds of wild bull trout compare favorably with those from rainbow trout (*Oncorhynchus mykiss)*, but only for fish of about 30 cm or greater (Webb 1971, Pearson and Stevens 1991, Jain et al. 1997, Burgetz et al. 1998). Because of the different protocols used to estimate U_{crit} and the numerous factors that can influence the swimming performance of fishes, it is difficult to compare estimates of U_{crit} between or within species. Indeed, we were unable to find many results from other studies on salmonids that we could validly compare to the swimming performance of our 12-20 cm fish. Brook trout (*S. fontinalis)* of about 11-12 cm had U_{crit} estimates from 4.63 to 4.86 BL/s at 15°C (Petersen 1974), which is much higher than our estimates for smaller bull trout. Also, the U_{crit} of sockeye salmon (*O. nerka)* 9-16 cm in length was 3.3-4.4 BL/s at 10-15°C (Brett and Glass 1973), which is also higher than our estimates for smaller bull trout. Critical swimming speed is influenced by the velocity increments and the time between increments used in a study (see Hammer 1995 for a review). Further, the swimming performance of fish depends on numerous other factors, including species, life history type, temperature, body size, fish training, and metabolic condition. For example, differences in stamina between coho salmon (*O. kisutch)* from different streams had a genetic basis (Taylor and McPhail 1985). Also, anadromous sockeye salmon had a greater mean U_{crit} than non-anadromous forms raised under identical conditions (Taylor and Foote 1991). As alluded to by Hammer (1995), a standardization of protocols for critical swimming speed tests, and more understanding of the factors that influence these tests, would facilitate comparisons between species and help make U_{crit} a more complete measure of fish performance.

The poor performance we observed in many of our bull trout may be in part due to constraints of the swim tunnels and certain aspects of their life history. The wild bull trout we used in our study may have found the tunnels too confining, perhaps eliciting a behavioral stress reaction leading to poor performance. Juvenile bull trout are closely associated with stream substrates and extensive in-stream cover, and prefer low velocity areas (Fraley and Shepard 1989, Goetz 1997, Dambacher and Jones 1997, Earle and McKenzie 2001). This cryptic, relatively inactive, life style of bull trout may make them less inclined to perform adequately in confined tunnels under a forced swimming regime, at least relative to other salmonids. On the other hand, bull trout migrate long distances for spawning and rearing (Fraley and Shepard 1989, Swanberg 1997, Burrows et al. 2001), indicating that their capacity for swimming can be substantial. Further research will be necessary to elucidate the factors that may influence the performance of bull trout in laboratory experiments and provide a more complete understanding of bull trout swimming performance.

Fish managers and engineers can use our data for modeling and establishing guidelines for the passage of bull trout through culverts and other structures. Using our U_{crit30} model (Figure 1) would yield conservative estimates of water velocities in culverts of different lengths that bull trout could pass. Such an analysis, based on that of Peake et al. (2000), is shown in Figure 2. For example, at 11-15°C, a 25 cm bull trout could pass a 60 m

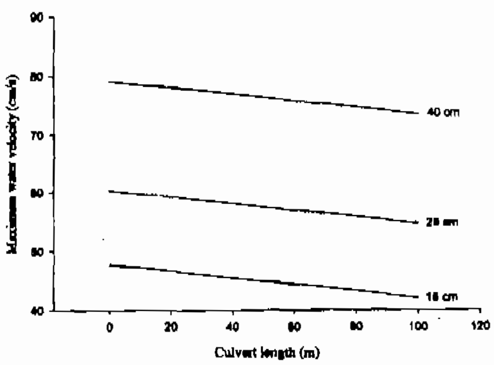

Figure 2. Maximum water velocities that will allow bull trout of three sizes to pass culverts of various lengths in 11° to 15°C water. The lines were determined as follows: maximum water velocity within a culvert equals the highest speed a fish can maintain for 30 min (U_{crit30}) minus the minimum ground speed required to pass the culvert in 30 min (culvert length/1,800 s). The U_{crit30} values were calculated by substituting length values into the appropriate equation from Figure 1.

culvert if water velocities were kept below 57 cm/s. Taking the most conservative approach, the models in Figure 2 would predict that bull trout from 15 to 40 cm FL could pass culverts up to 100 m in length provided water velocities were below 42 cm/s at 11-15°C. Further research would be needed to include the influence of different water temperatures, fish sizes, and swim speeds on our models of bull trout passage through culverts.

We believe our estimates of U_{crit} for bull trout represent an important benchmark towards understanding their capacity for exercise. As such, these estimates should serve as a good starting point for efforts aimed at designing or improving passage structures for bull trout. Until more information becomes available, we recommend that fishway or culvert designers concerned with bull trout passage work to maintain velocities within their structures at or below our estimates of U_{crit}, thus taking a conservative approach to ensuring that these fish can ascend migratory obstacles safely.

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