SWIMMING PERFORMANCE OF YELLOWSTONE CUTTHROAT TROUT

(*ONCORHYNCHUS VIRGINALIS BOUVIERI*)

by

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DEDICATION

This thesis is dedicated to my loving family (Karen, Curtis, and Charlie), my loving girlfriend (Emily), and all my friends for their incredible amounts of support and encouragement throughout my master's program. Thank you for teaching me that success comes from hard work, dedication, and passion in all aspects of life. And for instilling the idea that you can't have sunny days without rainy days. None of this would have been possible without your support.

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ABSTRACT

Yellowstone Cutthroat Trout (*Oncorhynchus virginalis bouvieri*) inhabit the upper portions of the Yellowstone and Snake River basins of Montana, Wyoming, and Idaho. Although individual populations remain intact in headwater streams, anthropogenic activities have resulted in substantial declines in their historic range and core population abundance, and the classification as a species of concern in Montana. To aid in Yellowstone Cutthroat Trout restoration and conservation, we conducted two studies to characterize their swimming performance. In the first study, we used an open-channel flume to observe the volitional swimming performance of 168 hatchery-raised Yellowstone Cutthroat Trout, ranging in total length from 292 to 450 mm. Fish were tested against a range of water velocities (0.61, 0.94, 1.75, and 2.00 $m \cdot s^{-1}$) and temperatures (8.0 and 12.0°C). We observed that passage success decreased with increasing water velocities, ranging from 98% at 0.61 $m \cdot s^{-1}$ to 19% at 2.00 $m \cdot s^{-1}$, and that water temperature did not affect the maximum distance of ascent within each hydraulic challenge (X^2 ranged from 0.0 to 1.0, p-value $\geq$ 0.3, df = 1). The overall maximum sprinting velocity was 4.59 $m \cdot s^{-1}$, mean maximum swimming velocity was 2.15 $m \cdot s^{-1}$, and average water velocity at gait transitions was 0.61 $m \cdot s^{-1}$ from sustained to prolonged, 0.94 $m \cdot s^{-1}$ from prolonged to unsteady burst glide, and <1.73 $m \cdot s^{-1}$ from unsteady burst glide to steady burst. In the second study, we quantified the U_{sprint} swimming mode of Yellowstone Cutthroat Trout using a swim chamber. Sixty fish were individually tested, which resulted in a mean U_{sprint} velocity of 3.91 body lengths$\cdot s^{-1}$ (SD = 0.56), equivalent to 1.48 $m \cdot s^{-1}$ (SD = 0.18). U_{sprint} values ranged from 0.86 to 1.85 $m \cdot s^{-1}$ for Yellowstone Cutthroat Trout with total lengths of 314 mm to 456 mm. Gait transitions were observed from sustained-prolonged to burst-glide swim mode at a mean water velocity of 0.88 $m \cdot s^{-1}$ (SD = 0.15) and from burst-glide to strictly burst at 1.13 $m \cdot s^{-1}$ (SD = 0.18). These findings provide valuable information for assessing passage success probability and guiding the design of fish passage structures, which are essential for the restoration and conservation of native Yellowstone Cutthroat Trout populations.

CHAPTER ONE

LITERATURE REVIEW

Background

Construction of dams in river systems has resulted in habitat fragmentation for freshwater ecosystems around the world. When fish movement is limited, issues regarding migration for spawning, searching for food, and avoiding suboptimal temperatures at high and low flows arise. To restore the longitudinal connectivity of rivers and access to critical life cycle habitat, researchers, biologists, and engineers have implemented fish passage structures. When fishways were first constructed limited information was available regarding fish swimming abilities or fishway design criteria, and therefore many fishways were relatively unsuccessful (Katopodis & Williams, 2012). Research has focused on optimizing passage efficiencies through passage studies, as well as quantifying the swimming performances of individual fish species. Historically fishway design and research focused on salmonid species due to their cultural, commercial, and recreational value. This research led to improvements in salmonid passage, but other species remained isolated above and below barriers. Several impacted species native to Montana have minimal research quantifying their swimming abilities, such as Yellowstone Cutthroat Trout (*Oncorhynchus virginalis* bouvieri; YCT), which is currently a species of concern (MNHP & MFWP, n.d.).

Theoretical quantification of different species swimming abilities is critical for engineers and biologists designing fish passage structure and barriers. Historically sustained, prolonged, and burst swim modes have been determined to relate energy exertion to swimming velocities

(Blake, 2004). Sustained swimming is quantified as long periods (>200 minutes) without muscle fatigue. Sustained swimming is rarely tested in ecohydraulic studies since it is not a meaningful metric in the context of fishway designs. Prolonged swimming can be maintained for 20 seconds to 200 minutes and ends in muscle fatigue. Burst swimming can be maintained for <20 seconds and ends in muscle fatigue (Beamish, 1978). Typically, respirometers or swim chambers are used to test sustained, prolonged, and burst swim mode metrics given their ability to precisely increase water velocity at specific time intervals (Blake, 2004). Additionally, burst swimming can be measured with a stimulated predator attack or a spook test, which attempt to induce the maximum physiological swimming velocity (Aedo et al., 2009). Sustained, prolonged, and burst swimming modes have also been tested in open-channel volitional studies, but video cameras or constant visual monitoring of tail beat frequencies are required to assign observed velocity to the swim mode used. Open-channel studies are preferred when testing passage success compared to different velocity barriers (Haro et al., 2004). The swimming velocities produced in open-channel studies are referred to as maximum swimming velocities.

Other swimming metrics that are frequently reported in ecohydraulic literature are critical swimming velocity (U_{crit}) and the approximate maximum sprinting swimming velocity (U_{sprint}) (Dockery et al., 2017a; L. A. Hunter & Mayor, 1986). These swimming metrics were developed to test the maximum aerobic and anaerobic capabilities of fish and have explicit procedures to ensure the standardization of these metrics. The U_{crit} metric is defined as the highest velocity that can be sustained for a 5 to 10-minute interval and is generally considered the velocity that fish switch from aerobic to anaerobic respiration (Aedo, 2008; Brett, 1964; Underwood et al., 2014). U_{sprint} is defined as the maximum velocity a fish could swim for 15 seconds, which is the approximate maximum duration that sprint swimming can be sustained (Dockery et al., 2017). U_{crit} and U_{sprint} metrics are tested in respirometers. These five swimming metrics can be compiled to generate a theoretical swim curve that can be used when designing fishway structures. For fish passage structures, oncoming water velocities should not exceed the capabilities of all species that inhabit the ecosystem. For fish barriers, oncoming water velocities should exceed the capabilities of species that should be excluded from passing upstream.

This literature review provides an overview of general swimming studies, as well as the swimming performance data and life history of YCT. Additionally, it will examine rock-ramp design standards, rock-ramp open-channel passage studies, and the application of computational fluid dynamic (CFD) modeling to rock-ramps.

General Swimming Studies

The methods and procedures used to quantify fish swimming abilities have been modified over the years to provide more accurate characterization of swimming performance. The goal of evaluating swimming performance of all fish species is to quantify the duration that they can maintain a specific swimming velocity before they reach fatigue. These metrics can then be applied to fishway designs. Two main types of fish passage studies currently exist: attraction-entrance-passage (AEP) studies and swimming performance studies.

AEP studies evaluate the percentage of fish that are attracted to the fishway, the number that enter the fishway, and the number that can successfully pass through the specific type of fishway. This type of study can be conducted either in a laboratory or at an existing fishway field site. Different types of technical fishways include Denil, pool and weir, pool and slot, lock and lift, and nature-like fishways (Noonan et al., 2012). The main objective of these studies is to determine passage success rates for different species at varying hydraulic conditions within the fishways. Blank et al. (2005) studied the passage success rates of several species of trout, sculpin, and sticklebacks through 46 different culverts in the Clearwater River drainage in Montana (Blank et al., 2005). A similar study on the Big Hole River basin in Montana examined the AEP of Arctic Grayling *(Thymallus arcticus)*, trout, and suckers through Denil-type fishways (Triano et al., 2022). Peake (2008a) conducted an AEP study using an experimental raceway to evaluate how Northern Pike *(Esox lucius)*, Walleye *(Sander vitreus)*, and White Suckers *(Catostomus commersonii)* entrance and passage success differed at varying velocity challenges. Unlike other AEP studies, Peake (2008a) did not test a specific type of fishway, but rather assessed swimming performance without calculating swimming velocities. Although AEP studies can provide information regarding the passage success of specific fishway design, they do not typically produce fish swimming metrics needed for designing new and more efficient fishways.

Swimming performance studies are designed to measure specific metrics associated with how fast and far fish can swim before exhaustion. When fish encounter areas of high velocity, they must switch from a slow, energy-efficient mode (sustained swimming) to a more energy-expensive swimming mode such as prolonged or burst swimming (Castro-Santos, 2005). Velocities of each swim mode differ among fish species therefore must be quantified separately (Castro-Santos, 2005). Understanding the swimming abilities of all fish in an ecosystem of interest is critical when designing a structure meant to improve longitudinal connectivity or prevent migration of unwanted fish such as invasive species. Without fish swimming metrics assessment of fishways would be limited to AEP studies.

First attempts to quantify fish's swimming abilities were performed in swim chambers. Swim chambers are circular networks in which water velocities can be regulated. In these studies, fish were placed into a chamber and coerced to swim, either by tapping on the chamber walls or flashing lights (Aedo, 2008; Bainbridge, 1958). Although swim chamber studies allow researchers to examine specific swimming metrics, they do not simulate the conditions present when navigating a velocity barrier. Physical and behavioral factors that influence successful passage include motivation, hydraulic conditions, turbulence, fishway geometry and location, number of attempts, and rate of fatigue. Therefore, laboratory swimming performance studies have shifted to open-channel flumes that better imitate conditions that fish would encounter in a natural stream, river, or fishway.

Some of the first volitional open-channel swimming studies were conducted by Dow (1962) and Weaver (1963, 1965). A flume with adjustable bed slope and inlet water depths was constructed at an existing dam to allow migrating fish to volitionally attempt to ascend the flume (Weaver, 1963, 1965). Rather than calculating swimming velocities, Weaver (1963, 1965) measured the distance of ascent in relation to downstream water velocity and bed slope of the flume. Dow (1962) calculated the swim speeds of Atlantic Herring *(Clupea harengus)* in an open-channel flume and observed velocities significantly higher than those reported by Bainbridge (1960) in an enclosed swim chamber. The idea that fish perform significantly better in volitional open-channel studies is now widely accepted in the field of ecohydraulics.

Haro et al. (2004) and Castro-Santos (2004) expanded on the Dow (1962) and Weaver (1963, 1965) studies by conducting swimming studies in open-channel flumes that evaluated swimming capabilities and predicted passage success through velocity barriers (Castro-Santos, 2004; Haro et al., 2004). Haro et al. (2004) performed a fish swimming study in a 24-m long, flat, smooth open-channel flume with six migratory fish species. He observed volitional fish passage through a high-velocity flow profile to relate anaerobic swim modes to the maximum distance ascended (Haro et al., 2004). Haro aimed to quantify behavioral metrics rather than physiological fatigue. Passive Integrated Transponders (PIT) tag antennas were placed along the length of the flume to record the distance ascended and to determine the swimming velocities of the fish between each consecutive antenna (Haro et al., 2004). Haro observed that fish swam at a higher maximum velocity and increased distance of ascent than in earlier non-volitional studies (Beamish, 1978; Videler, 1993). The main takeaway is that fish do not voluntarily swim to fatigue and that passage performance is largely dependent on testing fish in an apparatus that mimics a more natural setting compared to a swim chamber (Haro et al., 2004).

Castro-Santos (2004) used a 23-m open-channel flume to compare the rate and number of passage attempts to the maximum distance ascended by White Suckers and Walleyes. PIT tags were used to record the number of attempts and the distance ascended at water velocities of 1.5 $\mathrm{m \cdot s^{-1}}$, 2.5 $\mathrm{m \cdot s^{-1}}$, 3.5 $\mathrm{m \cdot s^{-1}}$, and 4.5 $\mathrm{m \cdot s^{-1}}$ (Castro-Santos, 2004). White Suckers had increased rates of attempts when flow velocities were 3.5 $\mathrm{m \cdot s^{-1}}$ to 4.5 $\mathrm{m \cdot s^{-1}}$, which indicated an increased attraction to the fishway when higher flow rates were present (Castro-Santos, 2004). This study updates Haro et al. (2004) by presenting two new concepts relevant to our current study for analyzing fish swimming performance studies: 1) swimming performance is quantified based on distance ascended over successive attempts, and 2) passage success is a continuous, time-dependent process (Castro-Santos, 2004). Open-channel volitional studies should be conducted over several hours to allow fish multiple attempts to pass the flume.

Peake & Farrell (2004) were among the first to show that a strong relationship exists between exercise physiology and different swimming strategies when faced with various velocity barriers. Smallmouth Bass *(Micropterus dolomieu)* with fork lengths of 24 to 38 cm were volitionally tested in a 25-m long flume against water velocities ranging from 40 to 120 $cm \cdot s^{-1}$. Maximum steady gait, an equivalent of prolonged swimming, ranged from 53.6 to 97.3 $cm \cdot s^{-1}$ and minimum unsteady gait velocities, an equivalent of burst mode, ranged from 81.4 to 122.9 $cm \cdot s^{-1}$. Smallmouth Bass maintained a ground speed of roughly 20 $cm \cdot s^{-1}$ when using a steady gait and about 40 $cm \cdot s^{-1}$ with unsteady gait regardless of the oncoming water velocity (Peake & Farrell, 2004). As the water velocities increased, swim speeds increased until a more energetic mode was required to maintain a constant ground speed, which suggests that an optimal ground speed for each swimming mode exists.

Castro-Santos (2005) further explored the ideal of optimal ground speed using a 23-m open-channel flume with six East Coast fish species. He evaluated if fish in high-velocity flows will switch from a prolonged swim mode to a burst swim mode after water velocities exceed the U_{crit} value of each species (Castro-Santos, 2005). Castro-Santos (2005) stated that "optimum groundspeed exists for each mode and failure to swim at the correct speed can result in reduced distances of ascent" yet in his study fish rarely used the predicted U_{crit} value or the optimum ground speed when switching modes or in passage attempts (Castro-Santos, 2005). He did note that White Suckers were the only species that used the low-velocity zone within the flume to improve the maximum distance ascended (Castro-Santos, 2005).

Castro-Santos et al. (2013) performed another open-channel swim study using the same 23-m long smooth flume with the same methods for data collection as the 2004 and 2005 studies.

They volitionally swam Brook Trout *(Salvelinus fontinalis)* and Brown Trout *(Salmo trutta)* at flow velocities of 1.6 $m \cdot s^{-1}$ and 2.5 $m \cdot s^{-1}$ to quantify their burst swim speeds (Castro-Santos et al., 2013). Both species of trout did not swim at their distance-maximizing speed, the optimal ground speed associated with the speed of the oncoming water, yet the absolute swimming speed and endurance time were significantly higher than any previous swim chamber studies reported (Castro-Santos et al., 2013). Castro-Santos et al. (2013) emphasized "that physiological limits alone are poor predictors of swimming performance." To develop metrics that accurately express the swimming ability of a fish, both the physiological limits and behavioral influences must be compared to hydraulic conditions such as flow rates, depths, temperatures, and seasonal timing.

Researchers at the Bozeman Fish Technology Center have examined the volitional swimming performance of fish in a straight smooth flume (Blank et al., 2020; Dockery et al., 2017a, 2019). These three studies used a 17.1 m long flume to determine swimming velocities and distances ascended. A straight, smooth flume creates steady flow conditions, close to uniform flow, which eliminate areas of reduced water velocity that fish could potentially use when swimming upstream. Video cameras placed along the length of the flume were used to determine swimming velocities. Dockery et al. (2017) reported that the burst velocity of Longnose Dace *(Rhinichthys cataractae)* was 1.75 $m \cdot s^{-1}$, which was 0.50 $m \cdot s^{-1}$ faster than previously observed (Aedo et al., 2009; Dockery et al., 2017a). Blank et al. (2020) reported the prolonged swim speed of Westslope Cutthroat Trout *(Oncorhynchus clarkii lewisi)* and Rainbow Trout *(Oncorhynchus mykiss)* was 0.84 $m \cdot s^{-1}$ and burst swim speeds were 3.55 $m \cdot s^{-1}$ and 2.73 $m \cdot s^{-1}$ respectively. These metrics were within the range reported for other open-channel studies. Dockery et al. (2020) evaluated the swimming performance of age 1+ Arctic Grayling in a shortened, 12.25 m, section of the flume. This study coupled maximum swimming velocities to the duration a fish could sustain said speed (Dockery et al., 2019). Overall, these open-channel swim studies have provided improved fish swimming metrics by testing fish in an apparatus that mimics a more natural setting compared to a swim chamber.

YCT Swim Performance and Life History

The design of fish passage structures must be improved to increase passage success for all fish to restore longitudinal connectivity to freshwater ecosystems. Life cycle information and swimming performance metrics can help practitioners evaluate if fish species are motivated and theoretically capable of ascending a structure. I will discuss the life history, natural habitat, and swimming performance of native YCT in the following section. Although extensive information on their life cycles exists in the literature, to date limited published research regarding swimming performance metrics is available.

Yellowstone Cutthroat Trout

The two native subspecies of Cutthroat Trout in Montana are YCT and Westslope Cutthroat Trout (MNHP & MFWP, n.d.). YCT can be distinguished from other trout species by the reddish-orange slashes that extend from their lower jaw to the bottom of the gills, and by medium-large round black spots that are concentrated on their back and sides (Holton & Johnson, 2003). Fish range in size based on the environment where they spawn and mature into adults (Brown, 1971). Populations of YCT that mature in high elevation headwater streams are typically less than 25.4 cm, whereas fish that develop in larger rivers and lakes can reach lengths of 45.7 cm (Brown, 1971; MNHP & MFWP, n.d.). Yellowstone Cutthroat Trout prefer to live in clear, cold lakes and streams where temperatures range from 4°C to 15°C (MNHP & MFWP, n.d.). Mature fish, 3 to 4 years old, typically spawn on gravel beds from April to July on the descending limb of the annual hydrograph (Gresswell, 2011; MNHP & MFWP, n.d.). Thurow and King (1994) conducted an observational YCT reproduction study on Pine Creek, Idaho. They suggested that physical cues control when YCT initiate redd construction and spawning. Optimal physical cues include temperature (4 to 20°C), depth (10 to 30 cm), velocity (25 to 60 $\mathrm{cm{\cdot}s^{-1}}$), and substrate particle size (0.063 mm to 100 mm) (Thurow & King, 1994). Fish will typically spawn earlier in the spring at lower elevations compared to fish that spawn at higher elevations later in the spring (Gresswell, 1995). Gresswell (1995) also reported that males generally migrate to spawning locations earlier than females, and that older and larger YCT will migrate farther upstream to spawn compared to younger smaller fish. Repeat spawning in consecutive or alternating years is common for YCT, and all fish will exhibit one of three spawning patterns: resident, fluvial, or adfluvial. Resident fish remain in the same stream reach for their entire life. Fluvial fish migrate upstream from main-stem rivers into tributaries to spawn. Adfluvial fish migrate from lakes into tributaries to spawn (Gresswell, 1995). In addition to reproductive migration, YCT also migrate to find food and to seek thermal refuge (Gresswell, 2011).

Yellowstone Cutthroat Trout are currently listed as a “species of concern” in Montana (MNHP & MFWP, n.d.). Gresswell (2011) reported that over the past century, anthropogenic activities have reduced YCT to 42% of their historic range and 28% of their core population. YCT inhabit both sides of the continental divide (Thurow & King, 1994). The current range of YCT includes the Yellowstone River, the Clarks Fork of the Yellowstone, the Bighorn River, the

Tongue River, and upper portions of the Snake River (MNHP & MFWP, n.d.; Thurow & King, 1994). Habitat degradation associated with reduced water quality and barriers to longitudinal connectivity has negatively affected the YCT population (Gresswell, 2011), but the introduction of non-native fish is considered the largest threat (MNHP & MFWP, n.d.). When non-native Rainbow Trout and YCT interbreed they produce fertile hybrids (Kovach et al., 2011; Rosenthal et al., 2022; Seiler & Keeley, 2007). The morphology of these hybrids is dominated by Rainbow Trout characteristics, including a deeper body and larger fins, which result in better swimming stamina for the hybrids, one of the factors allowing hybrids to outcompete YCT (Seiler & Keeley, 2007). Rosenthal et al. (2022) reported that YCT are capable of outperforming Rainbow Trout in terms of reproductive success. Furthermore, they suggested that the exclusion of Rainbow Trout from the spawning locations of YCT would promote the recovery of genetically pure YCT (Rosenthal et al., 2022). Additionally, the introduction of non-native Lake Trout *(Salvelinus namaycush)* into Yellowstone Lake, Wyoming, in 1994 caused the largest population of inland nonhybridized YCT to decline (Glassic et al., 2024). Additionally, outbreaks of whirling disease and drought induced by climate change have negatively impacted YCT throughout North America (Glassic et al., 2024).

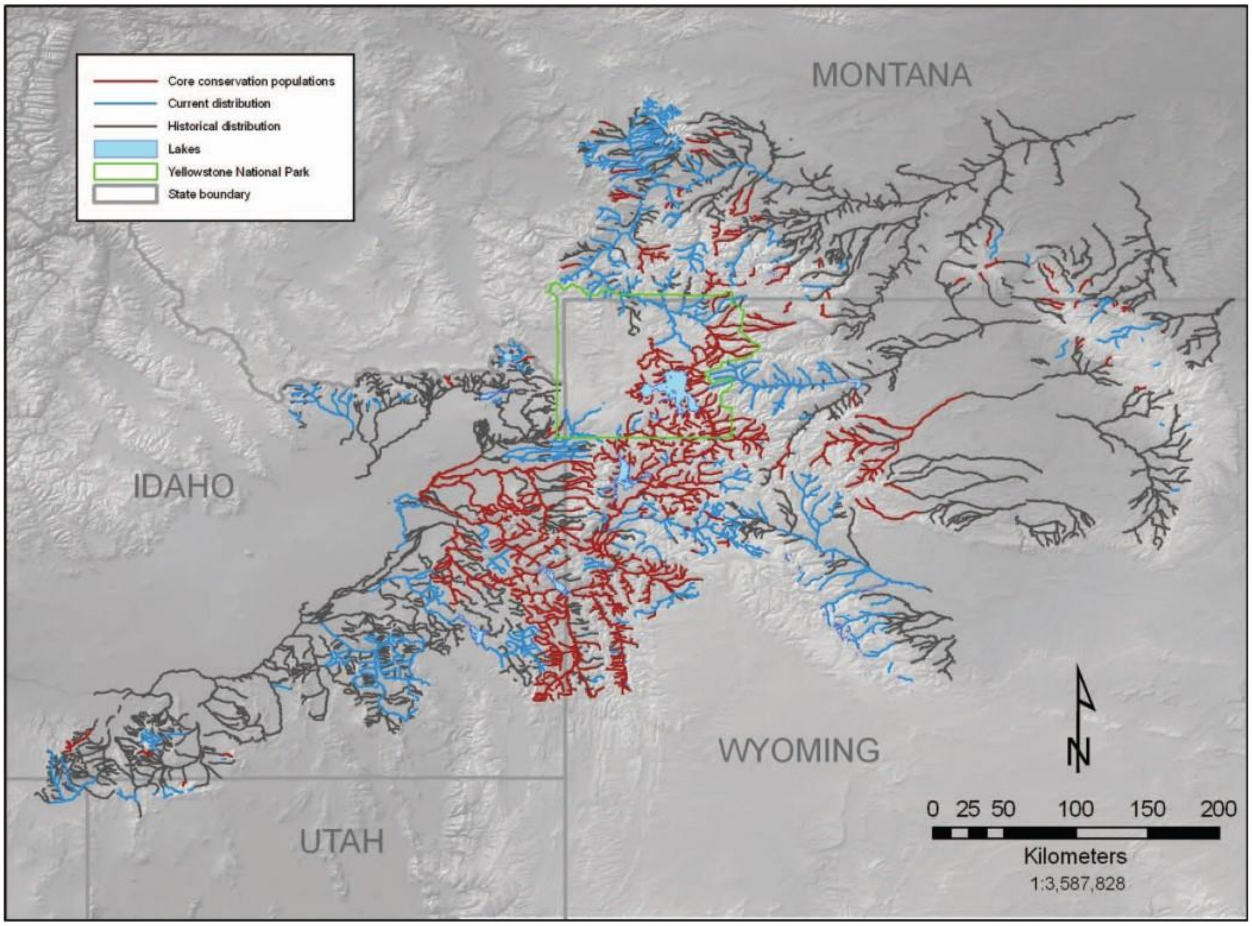

Figure 1.1: The core (red), current (blue), and historical (gray) population distribution of YCT in Montana, Idaho, and Wyoming (Gresswell, 2011).

The swimming ability of YCT is relatively undefined by the current literature. Seiler and Keeley (2007) compared body morphology to the swimming ability of YCT, Rainbow Trout, and their hybrid offspring. The critical swimming methodology (U_{crit}) was used to evaluate the maximum aerobic velocity a fish can maintain for a fixed amount of time in a swim chamber (Underwood et al., 2014). This approach can provide useful results to compare swimming abilities between species but does not provide data that can be directly applied to fish passage design (Underwood et al., 2014). Seiler and Keeley (2007) reported that YCT, with fork lengths

(FL) ranging from 78 to 98 mm, had an estimated U_{crit} of 7.7 body-lengths per second ($BL \cdot s^{-1}$), which was the lowest U_{crit} of all the species studied.

Although minimal swim performance data is available for YCT, studies have evaluated the swimming velocities of other subspecies of Cutthroat Trout. Blank et al. (2020) performed an open-channel flume study to characterize the swimming abilities of Rainbow Trout and Westslope Cutthroat Trout. Westslope Cutthroat Trout (FL: 15 to 29 cm) were reported to have an average swimming speed of 0.84 $m \cdot s^{-1}$ with a 95% confidence interval of 0.79 to 0.89 $m \cdot s^{-1}$, and a maximum swimming velocity of 3.55 $m \cdot s^{-1}$ (Blank et al., 2020). Hawkins and Quinn (1996) used a Blazka-type swim chamber to quantify the difference in mean U_{crit} between steelhead *(Oncorhynchus mykiss)*, Coastal Cutthroat Trout *(Oncorhynchus clarkii clarkii)* raised at the Shelton hatchery, and Coastal Cutthroat Trout raised at the Aberdeen hatchery. Steelhead (FL ± standard deviation: 100.1 ± 9.9 mm) had the highest U_{crit} of 7.69 ± 0.17 $BL \cdot s^{-1}$, followed by Aberdeen Cutthroat Trout (FL: 88.6 ± 7.7 mm) with a U_{crit} of 6.69 ± 0.23 $BL \cdot s^{-1}$, and then Shelton Cutthroat Trout (FL: 89.6 ± 12.0 mm) with a U_{crit} of 5.58 ± 0.15 $BL \cdot s^{-1}$ (Hawkins & Quinn, 1996). The swimming metrics reported for Westslope Cutthroat and Coastal Cutthroat Trout may be comparable to that of YCT, but differences in body morphology justify the need for further research.

Rock-Ramp Design

Throughout history, humans have built dams on rivers for flood control, irrigation, and energy production. These dams have, in turn, disrupted natural fish migration. To address this issue, fish passage structures have been developed and have seen significant technological advancements in recent decades. In the 1970s, researchers introduced "nature-like fishways" as a solution (Katopodis & Williams, 2012). These fishways aim to mimic the natural conditions of rivers, thus providing fish passage. They create bypass channels that replicate the river's original course and encompass diverse hydraulic conditions found in natural river systems. Nature-like fishways cater to the passage and habitat needs of various species in the ecosystem (Katopodis & Williams, 2012). One specific type of nature-like fishway is the "rock-ramp" structure. Rock-ramp fishways consist of gently sloping channels with large rocks that create low-velocity areas for fish to rest (Katopodis & Williams, 2012). These structures usually have slopes of less than 5% and are constructed using locally available materials such as large boulders, sand, gravel, and soil (Katopodis & Williams, 2012). The success of rock-ramp fishways in facilitating fish passage depends on their ability to replicate the natural hydraulic conditions of the river (Katopodis & Williams, 2012). Nature-like fishways, including rock ramps, have emerged as effective solutions for providing safe passage and habitat for fish while closely imitating natural river conditions (Katopodis & Williams, 2012).

Fish in rivers and streams regularly encounter turbulent water conditions. Liao et al. (2003) and Liao (2007), stated that fish can either be repelled or attracted to turbulent flows based on their ability to maintain stability while swimming. Chaotic flow profiles characterized by wide fluctuations in velocity tend to repel fish, whereas flows that have regions of predictable turbulence, such as vortices, attract fish. Turbulent regions can reduce the energy required to hold position when foraging for drifting aquatic invertebrates (Seiler & Keeley, 2007). Turbulence in rivers often results from water interactions with stationary objects, like rocks and logs, creating irregular and chaotic flow patterns. During migration and foraging, fish have developed strategies to navigate these conditions, such as using bow wakes in front of obstructions, exploiting suction regions behind obstacles where water flows upstream, and harnessing vortex streets or Kármán gait to minimize locomotion energy expenditure (J. Liao et al., 2003; J. C. Liao, 2007). Vortex streets, occurring when opposing water velocity vectors collide, create alternating vortices that fish can use to move upstream with minimal energy consumption (J. C. Liao, 2007). Vortex streets are located downstream and on either side of an obstacle in a river or stream (e.g. an eddyline). All salmonids are grouped into the sub-carangiform locomotion mode, which is defined as the rear half of the body displacing laterally when creating thrust and is characterized by fish with a fusiform body shape and a deep caudal peduncle. Fish that utilize a sub-carangiform form can leverage the vortices generated by the vortex street by positioning their tails at an angle to the incoming water of less than 90 degrees from the head, resulting in an extremely energy-efficient propulsion method that allows for rest while moving upstream or staying stationary (J. Liao et al., 2003; J. C. Liao, 2007; Webb, 1975). In the context of fish passage, incorporating features like rocks, which induces predictable vortices within unsteady flows that migrating fish can use to their advantage, into fishway designs can enhance their success.

Rock-ramp designs can be broadly categorized into those incorporating rock sills and notches, which function as weirs, and those employing dispersed boulders as roughness elements (D’Enno et al., 2002). Rock-ramp configurations are associated with three distinct flow regimes: plunging (or weir) flow, transitional flow, and streaming flow (Baki et al., 2020). Plunging flow is characterized by brief, high-velocity phases when water flows over rock sills and around boulders. These high-velocity zones must be relatively short to allow fish to navigate using a burst swim mode. Directly downstream of these high-velocity areas, transitional flow conditions prevail, marked by reduced flow velocities and increased water depths. Eddies are often observed behind roughness elements within the transitional flow regime, providing fish with resting spots before they employ their burst swim mode to navigate the high-velocity weir flow. Finally, streaming flows are found directly upstream of a weir, where eddies caused by roughness elements have dissipated, resulting in a more uniform flow profile (Baki et al., 2020). The presence of streaming flows is crucial in a rock-ramp design, as their absence can be attributed to rock weirs being placed too close together, potentially inducing excess turbulence within the fishway (Baki et al., 2020; D'Enno et al., 2002).

When designing a rock-ramp fishway, it is essential to adhere to the criteria outlined in the literature to create a successful fishway. D'Enno et al. (2002) outlined key requirements for rock-ramp designs, which include a mean water depth ranging from 30 to 40 cm, critical depth > 20 cm, a longitudinal slope of 1:20 to 1:30 (equivalent to 3% to 5% gradient), a maximum flow velocity between 1.6 $m \cdot s^{-1}$ and 2.0 $m \cdot s^{-1}$, a maximum length of 30 m unless design modifications are considered, and a minimum channel width of 2 m, with potential adjustments based on discharge. Additionally, hydraulic models and calculations must ensure that the critical water depth and maximum water velocities are sufficient for the target fish species and do not exceed their swimming abilities (D'Enno et al., 2002). In a study conducted by Dumitran & Vuţă (2017), various physical aspects of rock-ramp designs were assessed to determine an optimal configuration. This study employed the previously mentioned design criteria and concluded that a trapezoidal channel with 1:2 slide slopes (horizontal : vertical) is ideal for maintaining velocities below 2 $m \cdot s^{-1}$ (Dumitran & Vuţă, 2017).

Effective fishway design also necessitates careful consideration of the downstream entrance location to facilitate fish migration. Dumitran and Vuţă (2017) emphasized the importance of this aspect. Fish behavior plays a significant role in their ability to locate a fishway entrance. For instance, salmonid species are drawn to high-turbulence zones, which serve as a guide for their upstream passage (Baki et al., 2020). Conversely, species with weaker swimming capabilities tend to avoid highly turbulent areas due to their inability to navigate effectively in irregular flow regimes (Baki et al., 2020). Furthermore, the hydraulics below a dam can vary seasonally and with varying flow rates through spillways, adding complexity to the design challenge (Baki et al., 2020).

The key factor ensuring successful fish passage in rock-ramp design lies in the placement of rock weirs and dispersed boulders. Literature reports highlight the significance of numerical investigation and hydraulic analysis in determining the optimal spacing and size of boulders on the ramp. Baki et al. (2016) utilized ANSYS-CFX, a numerical computational fluid dynamics (CFD) model, to assess boulder spacing in both longitudinal and transverse directions for staggered and clustered patterns. Their findings recommend staggered boulders to be spaced 2.0-3.8 times and 2.7-3.5 times the boulder's diameter in the longitudinal and transverse directions, respectively. For clustered boulder patterns, each cluster should be 3.0-4.5 times the boulder's diameter in the longitudinal direction (Baki et al., 2016). Additionally, Baki et al. (2020) conducted a study on the hydraulic effects of different sizes and locations of notches in a "V"-shaped rock weir. They evaluated passage probability by comparing burst swim speed to the maximum velocity, U_{max}, in the fishway. The study reported that as the notch width increased from 0.08B to 0.38B, where B represents the ramp width, the recirculation zone in the pool expanded. This enlarged recirculation zone offered sufficient resting areas for configurations with one notch on either the same or alternating sides of the weir. In this context, sufficient resting area was defined as 40% of the pool area having velocities less than $0.4U_{max}$ (Baki et al., 2020). While it is important to note that each rock-ramp design is unique due to varying flows and spatial constraints, the metrics provided above offer a valuable starting point for hydraulic design considerations. Nevertheless, further research is warranted to explore the impact of turbulence on passage success and how different rock placements and natural weir geometries impact hydraulic conditions.

Rock-Ramp Passage Studies

Rock-ramps serve the purpose of facilitating fish passage around barriers, but to assess and enhance their effectiveness, passage studies are required. In a study conducted by Swarr (2018) at Colorado State University Foothills Fisheries Laboratory, a passage experiment was performed involving three small-bodied Great Plains fish species: Flathead Chubs *(Platygobio gracilis)*, Stonecats *(Noturus flavus)*, and Arkansas Darters *(Etheostoma cragini)*. The study used a trapezoidal rock-ramp measuring 6.1 m in length and 1.2 m in width. This ramp featured evenly distributed large roughness elements attached to a smooth PVC surface (Swarr, 2018). Passage success percentages were determined, using a PIT tag telemetry system, for five hydraulic challenges with varying slopes, ranging from 2% to 10%, at a constant flow rate of $0.082\ m^3 \cdot s^{-1}$ (Swarr, 2018). Although the maximum water velocities within the flume did not exceed $2\ m \cdot s^{-1}$, it's worth noting that water depths fell below the recommended range of 30 cm to 40 cm (D’Enno et al., 2002; Swarr, 2018). The study's overall findings indicate that fish passage decreases as the slope of the ramp increases. Additionally, it emphasizes the importance of designing fish passage structures with consideration for the weakest swimming species.

Richer et al. (2020) conducted a swim study on an existing rock-ramp fishway in Colorado. This study was situated on the Cache la Poudre River, a tributary to the South Platte River, which represents a transition zone from a steep, cold, and clear mountainous river to a flat, warm, and turbid plains river. The study's significance lies in its evaluation of passage success for both warm and cold-water species through a rock-ramp (Richer et al., 2020). To conduct the study, wild fish were collected, PIT-tagged, and placed at the base of the rock-ramp. The fishway was temporarily enclosed with screens for 46 hours to prevent fish from escaping up or downstream (Richer et al., 2020). Remarkably, the enclosed study reported that all nine fish species had individuals capable of ascending the 5% sloped rock-ramp. Notably, Longnose Suckers and White Suckers exhibited passage success rates of 71% and 100%, respectively (Richer et al., 2020). An additional 3-month extended study was carried out, involving the release of PIT-tagged fish below the fishway, allowing them to volitionally attempt navigating the rock-ramp. PIT-tag antennas recorded their passage attempts through the rock-ramp. Richer et al. (2020) reported that passage success significantly decreased for all species during this extended study. Longnose Suckers and White Suckers passage success rates of 12% and 25%, respectively (Richer et al., 2020). The study proposed that attraction and entrance conditions played a pivotal role in this reduced fish passage. Lastly, a hydraulic analysis was conducted, revealing that the roughness elements were effective in creating benthic zones of low velocity, even when surface and depth-averaged velocities exceeded fish swimming design criteria (Richer et al., 2020).

Masumoto et al. (2022) conducted a comprehensive study at the Miyanaka Intake Dam on the Shinano River in Japan, where three different fishways are located. Fish traps were strategically placed in all three fishways to capture fish utilizing each structure. The findings revealed that approximately 83.0% of bottom-dwelling fish preferred the rock-ramp. In contrast, the ice-harbor fishway and stair-type fishway attracted 22.3% and 78.1% of bottom-dwelling fish, respectively. Interestingly, the study highlighted that smaller fish, characterized by limited swimming abilities, exhibited a preference for the rock-ramp for their migration needs, while bottom-dwelling fish favored the rock-ramp as a stable habitat (Masumoto et al., 2022). The results also reported that fish catches increased upstream following the construction of the new rock-ramp (Masumoto et al., 2022).

Numerous rock-ramp passage studies have been conducted, and these investigations have been synthesized into meta-analyses aiming to provide insights into overall fishway passage success (Bunt et al., 2012; Hershey, 2021; Noonan et al., 2012). In a study by Bunt et al. (2012), which compared 19 monitoring studies, it was reported that nature-like fishways, specifically rock-ramps, exhibited the lowest attraction percentages among five fishway types, with a mean of 48% and a median of 50%. However, these nature-like fishways demonstrated the highest passage percentages, with a mean of 70% and a median of 86% (Bunt et al., 2012). Noonan et al. (2012) extracted data from 65 passage study papers and observed that salmonids achieved higher passage success rates for nature-like fishways, with 61.7% upstream and 39.6% downstream, compared to non-salmonids, which achieved 21.1% upstream and 39.6% downstream passage. The study also noted that nature-like fishways displayed some of the highest passage efficiencies compared to other fishway types. The mean upstream passage efficiencies (± 1 standard error) for salmonids using the five fishway types were: pool & weir passed 72% ± 21%, pool & slot passed 54% ± 3%, natural-like passed 62% ± 6%, Denil passed 21% ± 3%, and fish lock/elevator passed 35% ± 5% (Noonan et al., 2012). Hershey (2021) conducted another meta-analysis, using 60 peer-reviewed papers to synthesize attraction and passage efficiencies which updated the findings of the previous Bunt et al. (2012) study. In this report, nature-like fishways experienced lower attraction and passage efficiencies, 35% and 57%, respectively. This finding contradicted the previous results reported by Bunt et al. (2012) and Noonan et al. (2012) (Hershey, 2021). In summary, despite these comprehensive meta-analyses, more research is needed to accurately quantify attraction and passage efficiencies for rock-ramps and other fishway structures, particularly due to varying results across studies (Bunt et al., 2012; Hershey, 2021; Noonan et al., 2012).

Hydraulic CFD Rock-Ramp Modeling

Numerical and physical models serve as valuable tools for evaluating hydraulic conditions in fishway structures and natural open channels, such as rivers. The success of fish passage is directly related to the hydraulic conditions within these structures. Numerical and physical models are combined to validate the results generated by computational fluid dynamics (CFD) models. Numerical models come in varying levels of complexity and computational cost, generally categorized into three types: one-dimensional, two-dimensional, and three-dimensional models. Three-dimensional models are relatively rare in ecohydraulic studies, because of high computational costs as well as ecological and geomorphic processes on an ecological scale do not require the robustness of three-dimensional model results (Tonina & Jorde, 2013). As new methods for interpreting three-dimensional model results emerge, such as weighted usable volume, information on spatial flow properties is significant when examining how fluids interact with small particles and vegetation. Currently two-dimensional models are the preferred modelling method for ecohydraulic studies due to reduced computational run times compared to three-dimensional models (Tonina & Jorde, 2013). One-dimensional models provide cross-sectional averaged velocities and water surface elevations for longitudinal locations within a river or stream. Metrics produced by one-dimensional models provide flow information for aquatic habitat models such as the Physical Habitat Simulation Model (PHABSIM) (Tonina & Jorde, 2013).

In the context of fish passage studies, CFD models, primarily associated with two-dimensional and three-dimensional models, employ numerical methods to solve the Navier-Stokes equations and turbulence models (K. E. Plymesser, 2014). Researchers conducting hydraulic analyses have several CFD modeling programs at their disposal, all of which apply the same governing equations. Examples include OpenFOAM, ANSYS CFX, Star CCM+, and Flow-3D. The Navier-Stokes equations encompass the continuity, momentum, and energy equations. Although numerical CFD models are prevalent in the field of eco-hydraulics, it's worth noting that there is a relative scarcity of CFD studies specifically focusing on rock-ramp structures in the existing literature.

Two previous CFD models of rock ramp fishways were created by Baki et al. in 2016 and 2020. In both experiments, the researchers utilized ANSYS CFX software to solve the three-dimensional Reynolds-averaged Navier-Stokes equations. In the 2016 study, Baki et al. employed CFD models to investigate hydraulic conditions while varying discharge, channel slope, boulder size, spacing, and pattern. This comprehensive analysis evaluated each rock-ramp trial based on key factors such as water depth, maximum velocity, minimum velocity, and flow resistance within the structure. The validity of the CFD model was confirmed by comparing it to observations and measurements from a physical rock-ramp. Once a strong agreement was established between the numerical CFD model and the physical model, the study derived relationships relating water depth and velocity to discharge. These relationships provide valuable guidance for the design of future rock-ramp structures (Baki et al., 2016).

Another CFD modeling study performed by Baki et al. (2020) focused on assessing the hydraulic characteristics of rock-weir fishways featuring notch openings. The study considered various configurations of "V"-shaped rock weirs, including single notches on alternating sides of the "V," single notches on the same side of the "V," and double notches on both sides of the "V" (Baki et al., 2020). For this analysis, numerical CFD models were employed to evaluate water surface profiles, flow patterns, velocity fields, and depth-discharge relationships. By conducting a three-dimensional flow analysis, Baki et al. (2020) were able to identify areas of low velocity where fish could rest, as well as regions where fish would need to use a burst mode to pass upstream. These CFD models offer valuable hydraulic insights that can aid researchers and designers in assessing whether a fish can theoretically ascend a structure before its construction.

However, it's important to note that while CFD models provide valuable hydraulic information, they cannot replace the need for physical swimming studies to assess passage success (Baki et al., 2020).

Conclusion

This literature review investigated the swimming abilities, life history, and range of Yellowstone Cutthroat Trout as well as general and rock-ramp open channel swimming studies, rock-ramp design standards and numerical computational fluid dynamic modeling of rock-ramps. The main conclusions are:

- The swimming ability of YCT is relatively unknown. There is only one study that has provided a U_{crit} value of ~7.7 $BL \cdot s^{-1}$ (Seiler & Keeley, 2007), as of September 22, 2022.
- Open-channel swimming studies that allow fish to swim volitionally with adequate time to attempt multiple passages produced the most accurate results.
- Rock-ramp fishways have exhibited a range of passage success and therefore need to be studied further. Overall rock-ramps have great potential to provide passage and habitat for a variety of species of fish.
- There have been very few three-dimensional CFD models on nature-like or rock-ramp fishways.

Overall, fish passage success can be improved by quantifying the swimming abilities of all fish that are present in a river reach. Further research for different geometries of rock-ramps could produce higher passage success rates and emulate more natural river conditions in the fishway. Finally, CFD models can be used to relate hydraulic conditions to fish swimming behaviors and therefore can be used to predict fish passage success before physical trials are conducted.

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CHAPTER TWO

USPRINT ABILITIES OF YELLOWSTONE CUTTHROAT TROUT (*ONCORHYNCHUS VIRGINALIS BOUVIERI*) IN A SWIM CHAMBER

Contribution of Authors and Co-Authors

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Manuscript Information

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Abstract

Yellowstone Cutthroat Trout (*Oncorhynchus virginalis bouvieri*; YCT) inhabit the upper portions of the Yellowstone and Snake River basins of Montana, Wyoming, and Idaho. Although individual populations of YCT remain intact in headwater streams, anthropogenic activities have resulted in substantial declines in their historic range and core population abundance. We quantified the U_{sprint} swimming mode of YCT to aid in passage assessment, design, and other projects involving YCT restoration and conservation. Sixty hatchery raised YCT were swum individually in a swim chamber. We used a Loligo 185L swim chamber and standardized U_{sprint} methods to quantify the maximum anaerobic swimming velocity that YCT can sustain for 15 seconds, defined as maximum anaerobic sprinting velocity (U_{sprint}). Overall, the mean U_{sprint} velocity observed was 3.91 body lengths$\cdot s^{-1}$ (standard deviation (SD) = 0.56 body length$\cdot s^{-1}$), which was equivalent to an absolute velocity of 1.48 $m\cdot s^{-1}$ (SD = 0.18 $m\cdot s^{-1}$). U_{sprint} values ranged from 0.86 $m\cdot s^{-1}$ to 1.85 $m\cdot s^{-1}$ for YCT with total lengths of 314 mm to 456 mm. YCT preformed gait transitions from sustained-prolonged to burst-glide swim mode at a mean water velocity of 0.88 $m\cdot s^{-1}$ (SD = 0.15 $m\cdot s^{-1}$) and from burst-glide to strictly burst at 1.13 $m\cdot s^{-1}$ (SD = 0.18 $m\cdot s^{-1}$). Results suggest passage structures with water velocities less than 0.88 $m\cdot s^{-1}$ should provide high probability of successful passage of YCT, whereas structures with water velocities exceeding 1.85 $m\cdot s^{-1}$ may be impassable. When applying U_{sprint} metrics to fishway designs, engineers and biologists should ensure fishway velocities do not exceed U_{sprint} values for YCT. Overall, these metrics are valuable for assessing existing passage success probability and guiding the design of future fishway projects, which is essential for the restoration and conservation of YCT populations.

Introduction

Yellowstone Cutthroat Trout (*Oncorhynchus virginalis bouvieri*; YCT) are a subspecies of cutthroat found in Montana. Native populations of YCT exists in Pacific and Atlantic drainages, but are limited to rivers, lakes, and streams of Montana, Idaho, and Wyoming (MNHP & MFWP, n.d.). Non-native populations are present in western Montana because of fish stocking in several watersheds (Gresswell, 1995; MNHP & MFWP, n.d.). Native populations of YCT in Montana are currently listed as a "species of concern" because of declining population numbers and reductions in range and habitat (MNHP & MFWP, n.d.). Gresswell (2011) reported that over the past century, anthropogenic activities have caused the historic range and core (genetically unaltered) population of YCT to be reduced to 42% and 28% respectively.

When longitudinal connectivity is fragmented, fish passage structures (e.g., ladders, rock-ramps, or culverts) are often constructed to reestablish the fish's ability to migrate. The ability of fish to move upstream, specifically to ascend a fishway or structure, is dependent on their swimming abilities. Fish swimming abilities are categorized into three modes; sustained, prolonged, and burst (Beamish, 1978; Brett, 1964). Each subsequent swim mode has higher mean maximum velocity, but the duration that the velocity can be maintained will decrease (Underwood et al., 2014). Quantifying the swimming ability of fish, using controlled experiments where fish are subjected to a varying range of velocities, can aid in fishway design. Swimming abilities can be measured in open-channel flumes and swim chambers to develop fish passage criteria (Cahoon et al., 2018). Open-channel swimming studies which allow fish to swim volitionally in a realistic setting are believed to produce better predictions of swimming abilities (Cahoon et al., 2018; Castro-Santos, 2004; Haro et al., 2004). Swim chamber studies are advantageous because numerous trials can be conducted in a relatively short time frame. Further, swim chambers are designed to precisely control experimental conditions and subject test fish to replicated treatments (Cahoon et al., 2018; Dockery et al., 2017b). In swim chamber studies a time-to-fatigue relationship can be determined at a fixed velocity and used to estimate traversable distance. Water velocities can also be incrementally increased at specifics time intervals to determine a maximum aerobic (U_{crit}) or anaerobic capacity (U_{sprint}). Although swim chambers usually underestimate swimming metrics, they have been proven to provide useful metrics for sprinting endurance abilities as well as general estimates of swim speeds at gait transitions (Dockery et al., 2017b). In engineering applications, aerobic and anaerobic swimming metrics can be used to design fishway hydraulics to either allow fish to migrate upstream or create velocity barriers to isolate different fish populations.

Swimming performance metrics for YCT are relatively undefined in the current literature. A study that examined the U_{crit} swimming metrics for YCT was performed by Seiler and Keeley (2007). This study swam 7-month-old YCT in a swim chamber. U_{crit} is defined as the maximum aerobic velocity a fish can maintain for a fixed amount of time (Beamish, 1978; Blake, 2004; Brett, 1964). The YCT eggs and sperm were collected from Henry's Lake near Island Park Idaho on April 23rd, 2004. The juvenile fish were then used in sustained swimming velocity trials from November 24th, 2004, to December 23rd, 2004. Seiler and Keeley (2007) reported that fish fork lengths (FL) ranged from 78 mm to 98 mm. To encourage fish to swim mild electrical stimulus (1 volt, $^1/_2$ amp) was applied to the downstream screen when fish started to rest or impinge on the screen. A mean U_{crit} value of 7.7 $BL \cdot s^{-1}$ (body lengths per second) was reported for YCT (Seiler & Keeley, 2007). Although there are almost no swim performance metrics reported for YCT, there have been other swim studies that report metrics for different subspecies of Cutthroat Trout (*O. clarkii*).

Another study was conducted with mature adfluvial Cutthroat Trout in Yellowstone Lake, Yellowstone National Park, Wyoming. Fish were collected from tributaries of Yellowstone Lake, these fish were then displaced from their spawning tributaries and released into the open waters of Yellowstone Lake. The mean total length was 359 mm with fish ranging from 310 mm to 400 mm. Ultrasonic tracking of fish reported swim speeds of 0.29 $m{\cdot}s^{-1}$ through open-water and 0.37 $m{\cdot}s^{-1}$ along-shore. Swimming velocities were averaged over 5 hours 54 minutes for fish swim paths through open-water and 2 hours 38 minutes along-shore (McCleave & LaBar, 1972). The reported swim metrics represent sustained or prolonged swim modes for YCT.

Other subspecies of Cutthroat Trout have been studied, and their reported metrics can provide baseline metrics for YCT examined in this study. Blank et al. (2020) performed an open-channel flume study to characterize the swimming abilities of Westslope Cutthroat Trout *(O. clarkii lewisi)*. Westslope Cutthroat Trout, with FL ranging from 150 mm to 290 mm, were reported to have an average swimming speed of 0.84 $m{\cdot}s^{-1}$ with a 95% confidence interval of 0.79 to 0.89 $m{\cdot}s^{-1}$, and a maximum swimming velocity of 3.55 $m{\cdot}s^{-1}$ (Blank et al., 2020). Hawkins and Quinn (1996) used a Blazka-type swim chamber to quantify the mean critical swim velocity (U_{crit}) of Coastal Cutthroat Trout *(O. clarkii clarkii)* for two hatchery stocks. They reported U_{crit} values of 5.58 ± 0.15 $BL{\cdot}s^{-1}$ (mean FL ± standard deviation (SD): 89.6 ± 12.0 mm) for Shelton Cutthroat Trout and 6.69 ± 0.23 $BL{\cdot}s^{-1}$ (mean FL: 88.6 ± 7.7 mm) for Aberdeen Cutthroat Trout. The swimming metrics reported for Westslope Cutthroat and Coastal Cutthroat

Trout may be comparable to that of YCT, but differences in body morphology justify the need for further research.

The primary goal of this study was to characterize the swimming abilities of YCT which can be used to improve fishway designs and restore longitudinal connectivity. This study used a swim chamber to quantify the maximum anaerobic swimming velocity that YCT can sustain for 15 seconds, defined as U_{sprint} (Beamish, 1978; Cahoon et al., 2018; Dockery et al., 2017b). All U_{sprint} trials were tested at 12°C. This temperature was selected because YCT commonly occupy habitats with water temperatures ranging from 4.5°C to 15.5°C (Gresswell, 1995, 2011), and YCT (age 1+) maximum scope for activity occurs at 15°C (Dwyer & Kramer, 1975). Additionally, the open-channel volitional study that was conducted in parallel with this U_{sprint} study used a temperature treatment of 12°C. Therefore 12°C was selected so future researchers can compare metrics produced in a swim chamber versus an open-channel flume. When applying U_{sprint} metrics to fishway designs, engineers and biologists should ensure fishway velocities do not exceed U_{sprint} values for YCT. Additionally, if a rock-ramp or pool and weir type fishway have high velocity regions comparable to reported U_{sprint} values then these regions should be short enough, in length, for YCT to pass utilizing a burst swimming mode and bracketed with velocity refuges. The application of U_{sprint} metrics is critical for successful fishway designs.

Methods and Materials

Test Fish

We swam 60 healthy hatchery raised YCT between July 25th and August 9th, 2023. The YCT used in this study originated from brood stock at the Yellowstone Cutthroat Trout Hatchery in Big Timber, Montana. The embryos were sourced from the hatchery's spawning operations and then moved to the Bozeman Fish Technology Center (BFTC) where they were incubated at 12°C. Test fish were progressively moved to larger tanks to maintain a density below 0.023 kg/L and reared according to standard techniques and parameters described for trout culture by Piper et al. (1982). At the time of this study the fish were age 4 and ranged in total length from 314 mm to 456 mm and ranged in weight from 315 g to 1083 g total weight. All fish that swam in this study were determined to be in good condition through a visual inspection, and therefore represented healthy fish assumed to be capable of demonstrating the swimming ability of their wild counterpart. Fish that appeared injured in any way were not used.

An unmarked but small subset of this group of fish were swum in 2021 as pilot study fish in determining passage through a scaled Denil fishway (Buller, 2023). All the fish used in the U_{sprint} study were swum in 2023 to quantify swimming performance in an open-channel flume as discussed in Chapter 3 of this manuscript. To ensure sufficient resting time between swimming in the open-channel flume trials and the U_{sprint} experiment, fish were given a minimum of 9 days rest between swimming trials.

Fish Handling

The group of 60 YCT were haphazardly divided into two 1.83-meter diameter circular flow-through tanks (29 fish and 31 fish) with the same circular velocity, water temperature, and feeding regiments. Each holding tank was outfitted with a water inflow pipe; the inflow pipe was directed toward the side of the tank and provided water velocities within the tank between 0.003 $m \cdot s^{-1}$ and 0.165 $cm \cdot s^{-1}$ to build fitness; exercised hatchery fish have been tested and demonstrated abilities similar to their wild counter parts (Cahoon et al., 2018; Dockery et al., 2019).

To ensure a post absorptive state during the swim trials, fish were moved from the holding tank and grouped into six smaller, 0.914 m diameter, staging tanks (five fish per tank) supplied with reuse water set to 12°C. Once in the staging tanks food could be removed from specific staging tanks 24 hours prior to a swimming trial, which ensured a post absorptive state, while the rest of the staging tanks continued to receive food. All fish spent from one to four days in the staging tanks. After a swimming trial was complete, the fish were returned to their original holding tank. During the swim trials all holding tanks and staging tanks were set to 12°C, with temperatures varying less than ± 0.2°C. Additionally, all the fish used in the U_{sprint} study were held at 12°C for a minimum of 15 days prior to the experiment.

Fish were fed 5.5 mm float feed (Classic Trout; Skretting, Tooele, UT) once daily using a timed belt feeder, with the food quantity adjusted based on the number of fish in each tank. Passive integrated transponders (PIT) tags were surgically implanted into all fish at least 34 days prior to the swim trials. Food was withheld from fish 24 hours before tagging; individual fish were lightly anesthetized using MS-222 (25 mg/L) and a 23 mm preloaded half duplex (HDX) PIT tag (OregonRFID, Portland, OR) was implanted in the peritoneal cavity through a small incision and no sutures needed (Gries & Letcher, 2002). All fish were weighed to the nearest 0.1 g and total length was measured to the nearest 1.0 mm, 5 days after all trials were completed.

U_{sprint} Test

The U_{sprint} test measures the maximum velocity a fish can swim for 15 seconds, which is related to the approximate maximum duration sprint swimming can be sustained (Dockery et al., 2017b). Tests were conducted in a swim chamber located at the U.S, Fish and Wildlife Service Bozeman Fish Technology Center (BFTC; Bozeman, Montana, USA). The swim chamber (185L;

Loligo System, Tjele, Denmark) was supplied with air-saturated flow through water from warm and cold artesian wells. The temperature in the swim chamber was controlled by adjusting the ratio of warm and cold water into the chamber (18.9-30.3 $L \cdot min^{-1}$ total flow). In this study, U_{sprint} swim metrics were evaluated at 12°C. The test section had a cross-section of 25 cm x 25 cm and a length of 87.5 cm. At the upstream end of the test section, flow straighteners provided rectilinear microturbulent flow and an approximately uniform velocity profile (Dockery et al., 2017b). A metal grate was placed at the downstream end to prevent fish from escaping as well as to indicate when a fish became impinged. A white tarp was hung around the swim chamber to prevent disturbances during the trials. A video camera (Handicam HDR-XR-150, Sony, Tokyo, Japan) was used to record the trials. The recorded video allowed for the total swim time and the water velocity associated with gait transitions to be determined.

A rating curve that related pump frequency output to water velocity in the test section was established using a Marsh McBirney Flo-Mate velocimeter (Hach Corp., Loveland, CO). The rating curve allowed the researcher to increase the water velocity quickly and accurately by setting the pump frequency on the control panel. Water temperatures in the swim chamber were taken before and after a trial with an Ertco-Eutechnics Model 4400 digital thermometer (Alpha Technics Oceanside, CA) to monitor temperatures within the swim chamber. Temperature did not change significantly over the duration of a trial, so the initial temperature was used in the data analysis.

Fish were netted from the staging tank and identified using a hand-held PIT tag reader (Model 601, Biomark, Boise, ID) before being placed into the swim chamber test section. The trial began with a 10-minute acclimation period at a water velocity of 45.7 $cm \cdot s^{-1}$, then the water velocity was increased (7.6 $cm \cdot s^{-1}$) every 15 second until the fish became impinged on the downstream screen (Brett, 1964; Dockery et al., 2017b; Starrs et al., 2011). If a fish remained impinged on the downstream grate for more than 3 seconds, the pump motor was rapidly turned off and then on to encourage the fish to continue swimming. This 3 second window provided time for the fish to attempt to free itself volitionally. If a fish remained impinged, the trial was ended, and the time and velocity of impingement was recorded. The recorded video was then used to correct the recorded time of impingement to the initial time of impingement (removing the 3 to 5 seconds when attempting to free the fish).

Data Analysis

The data analysis for the U_{sprint} study was conducted with program R Studio version 4.3.0 (R Core Team, 2023). Fish were selected to participate in the U_{sprint} study in a haphazard order. The Shapiro-Wilks test, at the 95% confidence level, was used to test normal distributions of all variables. Variables recorded in the U_{sprint} study included: total length, weight, initial temperature, U_{sprint} ($m \cdot s^{-1}$), and U_{sprint} ($BL \cdot s^{-1}$). Normal distributions were confirmed for total length (p-value = 0.9811) and weight (p-value = 0.4516), based on the Shapiro-Wilks normality test. All other variables were determined to not be normally distributed (p-value < 0.0001). Normal probabilities plots were also made for each variable and confirmed the results of the Wilks-Shapiro normality test.

Further investigation of the U_{sprint} ($m \cdot s^{-1}$) values from Holding Tank 1 and Holding Tank 2 were conducted with the Anderson-Darling and Cramer-von Mises normality test. The U_{sprint} values from Tank 2 were determined to be not normally distributed for the Anderson-Darling test (A = 1.6471, p-value = 0.0002) or for the Carmer-von Mises test (W = 0.2718, p-value = 0.0007).

The U_{sprint} values from Tank 1 were determined to be normally distributed for the Anderson-Darling test (A = 0.4883, p-value = 0.2054) and for the Carmer-von Mises test (W = 0.08984, p-value = 0.1474). The non-normal distribution for the U_{sprint} values for Tank 2 was due to three low U_{sprint} values that were determined to be outliers. When these outliers were removed from the dataset, the Anderson-Darling (A = 0.2739, p-value = 0.6370) and Cramer-von Mises (W = 0.0537, p-value = 0.4442) tests indicated the assumption of normality was adequately met for Tank 2 U_{sprint} values. A two-sample t-test with a two-sided alternative, the difference in the means equals zero, was also conducted to evaluate the U_{sprint} values from Tank 2 and Tank 1. This t-test resulted in very weak evidence to reject the null hypothesis (p-value = 0.103) that the means of Tank 2 and Tank 1 U_{sprint} values were equal. Levene's test was also conducted to test for equal variance between the U_{sprint} values from Tank 2 and Tank 1. The Levene's test resulted in a large p-value (p-value = 0.487) which indicated the assumption of homogeneity was adequately met. Therefore, for this data analysis all fish will be treated as a single sample.

Multiple linear regression was used to assess the relationship between total length, initial temperature, and U_{sprint} values (i.e., time to fatigue of sprint swimming). U_{sprint} values calculated with the formula provided in Equation 1 (Brett, 1964):

$$(1) \qquad U_{sprint} = U_i + [U(t_i \times t^{-1})]$$

where U_i is the penultimate velocity ($cm \cdot s^{-1}$), t_i is the amount of time (seconds) the fish swam in the final increment, t is the increment between velocity increases (15 seconds), and U is the water-velocity increment (7.6 $cm \cdot s^{-1}$). All U_{sprint} values have been converted to ($m \cdot s^{-1}$) for the following analysis. Water velocities in the swim chamber were not expected to be affected by the presence of fish, since test fish mean weight was less than the recommended range of 750 g to

5000 g for the 185L swim chamber (*Loligo Systems*, 2024), thus a velocity correction was not used (Webb, 1975).

The U_{sprint} data was used to predict the maximum distance that YCT could ascend upstream at high velocities using the Equation 2 (Peake et al., 1997). Equation 2 is as follows:

$$D = \left(U_{sprint} - V_f\right) \times 15\ s \qquad (2)$$

where D is the distance (m), U_{sprint} is the maximum swimming velocity sustainable for 15 seconds ($m \cdot s^{-1}$), and V_f is the water velocity ($m \cdot s^{-1}$).

Results

All YCT tested in U_{sprint} trials swam vigorously during the test, and there is clear evidence of fatigue shown by rapid tail beats and the inability to maintain positive rheotaxis as water velocity increased. Of the sixty fish that participated in the U_{sprint} study, two fish were excluded from the analysis; one was removed due to the camera stopping mid trial and the other was removed due to a data collection error during the swim trial. Generally, fish transitioned from a steady sustained/prolonged (SP) swim mode to unsteady burst/glide (BG) and finally to steady strictly burst (B) as water velocities increased. Based on video analysis, fish performed gait transitions from SP to BG at a mean time of 89 seconds (SD = 27 seconds) when water velocities reached 0.88 $m \cdot s^{-1}$ (SD = 0.15 $m \cdot s^{-1}$) and from BG to B at a mean time of 140 seconds (SD = 35 seconds) when water velocities reached 1.13 $m \cdot s^{-1}$ (SD = 0.18 $m \cdot s^{-1}$). After the final gait transition fish used a burst swim mode until they reached fatigue and became impinged on the downstream grate. The mean time YCT spent in burst mode was 78 seconds (SD = 38 seconds). Over the duration of a trial YCT spent an average of 42.4% of time in SP, 22.5% of time in BG, and 35.1% of time in strictly B.

Three fish did not follow the expected progression of swim modes, but only one of these fish produced a low U_{sprint} value which was highlighted as an outlier in the data. Two additional U_{sprint} values were highlighted as outliers, these fish exhibited low motivation levels which caused low U_{sprint} values. All outliers were kept in the data set and were used in the analysis since nothing justified their removal.

The mean maximum velocity sustainable for 15 seconds in the U_{sprint} test was 3.91 $BL{\cdot}s^{-1}$ (SD = 0.56 $BL{\cdot}s^{-1}$) with values ranging from 2.22 $BL{\cdot}s^{-1}$ to 4.84 $BL{\cdot}s^{-1}$ for all YCT tested in this study. In absolute terms, the mean U_{sprint} value was 1.48 $m{\cdot}s^{-1}$ (SD = 0.18 $m{\cdot}s^{-1}$) with values ranging from 0.86 $m{\cdot}s^{-1}$ to 1.85 $m{\cdot}s^{-1}$. Multiple linear regressions were conducted to evaluate trends between the continuous fish total length variable and the discrete initial temperature, at the start of the trial, variable compared to the continuous response variable absolute U_{sprint} ($m{\cdot}s^{-1}$). The regression did not indicate there was a relationship between absolute U_{sprint} ($m{\cdot}s^{-1}$) and initial temperature (p-value = 0.521) or a relationship absolute U_{sprint} ($m{\cdot}s^{-1}$) and fish total length (p-value = 0.766). Additional multiple linear regressions were conducted to evaluate trends between discrete variables; fish total length and the initial temperature compared to the continuous response variable U_{sprint} ($BL{\cdot}s^{-1}$). The regression did not indicate there was a relationship between U_{sprint} ($BL{\cdot}s^{-1}$) and initial temperature (p-value = 0.515). However, the linear regression analysis relating fish total length and U_{sprint} ($BL{\cdot}s^{-1}$) indicated that the slope (p-value < 0.001) was significantly different than zero. In this model the slope is negative which indicates that U_{sprint} ($BL{\cdot}s^{-1}$) decreased as total length increased. Table 2.1 displays the regression results produced by R Studio for U_{sprint} ($m{\cdot}s^{-1}$) and U_{sprint} ($BL{\cdot}s^{-1}$).

Table 2.1: Linear regression equation coefficients for the U_{sprint} ($m \cdot s^{-1}$) and the U_{sprint} ($BL \cdot s^{-1}$) models during the YCT swim chamber study.

Response Variable	Explanatory Variable	Coefficients	Standard Error	P-value	Lower 95%	Upper 95%	R^2
U_{sprint} ($m \cdot s^{-1}$)	Intercept	1.3821	0.3275	< 0.001	0.726	2.038	0.002
	TL (mm)	0.0003	0.0009	0.766	-0.001	0.002	
U_{sprint} ($m \cdot s^{-1}$)	Intercept	3.1725	2.6181	0.231	-2.072	8.417	0.007
	IT (°C)	-0.1402	0.2168	0.521	-0.574	0.294	
U_{sprint} ($BL \cdot s^{-1}$)	Intercept	7.4984	0.8701	< 0.001	5.755	9.241	0.234
	TL (mm)	-0.0094	0.0023	< 0.001	-0.014	-0.005	
U_{sprint} ($BL \cdot s^{-1}$)	Intercept	9.1102	7.9405	0.256	-6.797	25.017	0.008
	IT (°C)	-0.4307	0.6574	0.515	-1.748	0.886	

Note: Total length (TL), initial temperature (IT), and body lengths per second ($BL \cdot s^{-1}$)

The mean absolute U_{sprint} ($m \cdot s^{-1}$) value of 1.48 $m \cdot s^{-1}$ was used in Eq. 2 to predict maximum passable distance at high water velocities for YCT. The distance that YCT could ascend against a water velocity of 1.13 $m \cdot s^{-1}$ (the mean water velocity that induces a burst swim mode) was 5.25 m. When higher oncoming water velocities were entered into Eq. 2 the maximum distance of ascent rapidly decreased.

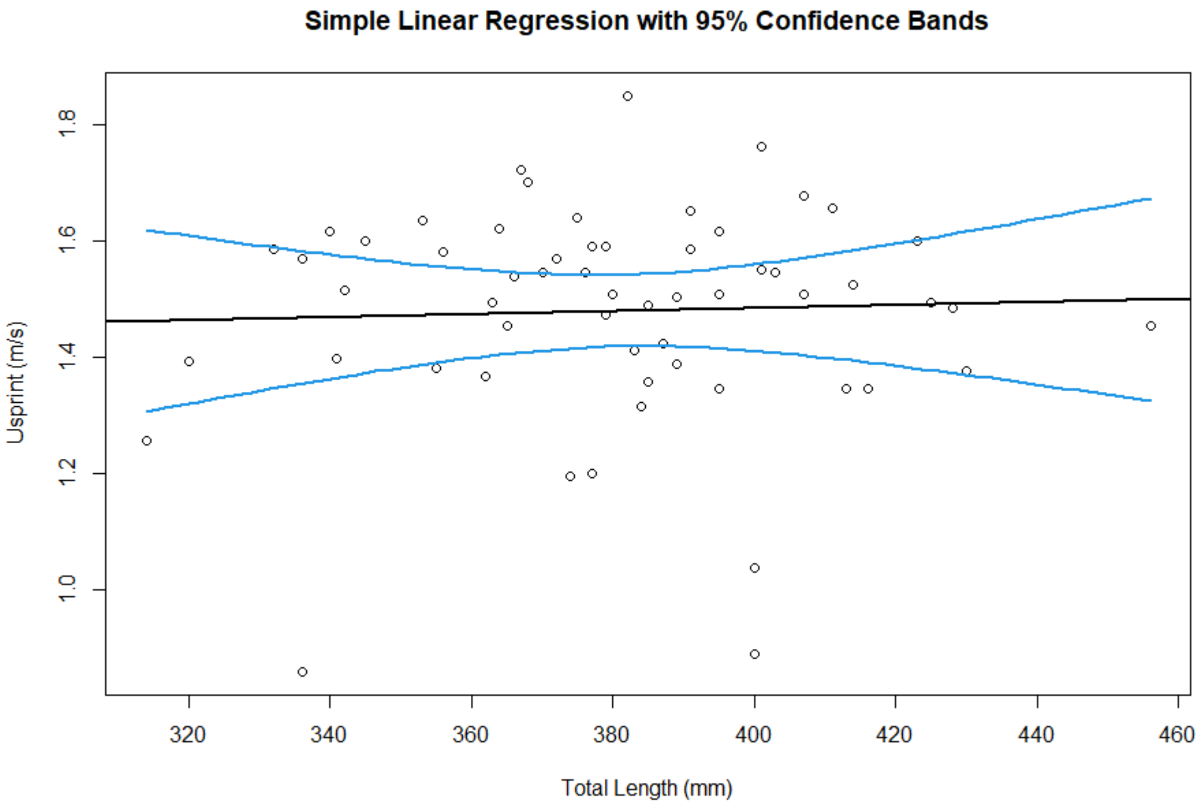

Figure 2.1: Simple linear regression for U_{sprint} ($m{\cdot}s^{-1}$) compared to fish total length (mm). A regression line has been fitted to the data to correlate U_{sprint} values to fish total lengths. Confidence interval bands, 95% confidence interval, have been calculated for the data set and are displayed in blue.

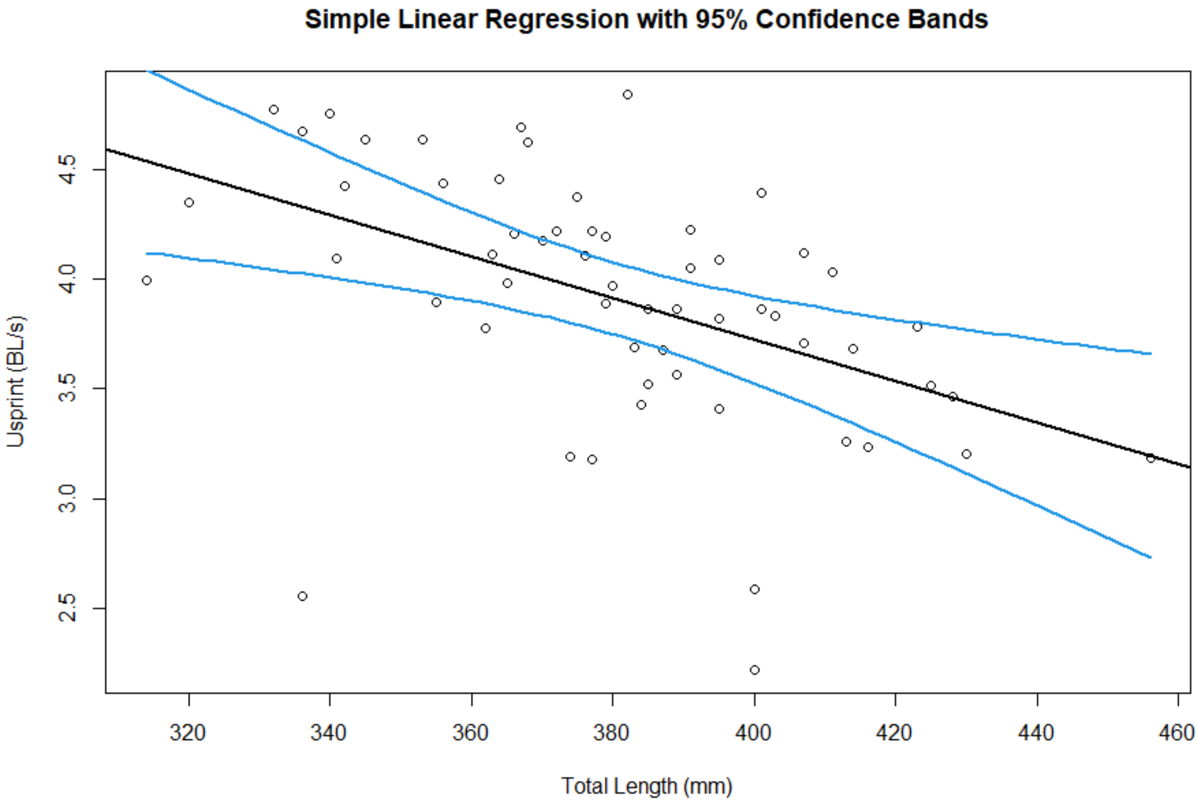

Figure 2.2: Simple linear regression for U_{sprint} (BL·s^{-1}) compared to fish total length (mm). A regression line has been fitted to the data to correlate U_{sprint} values to fish total lengths. Confidence interval bands, 95% confidence interval, have been calculated for the data set and are displayed in blue.

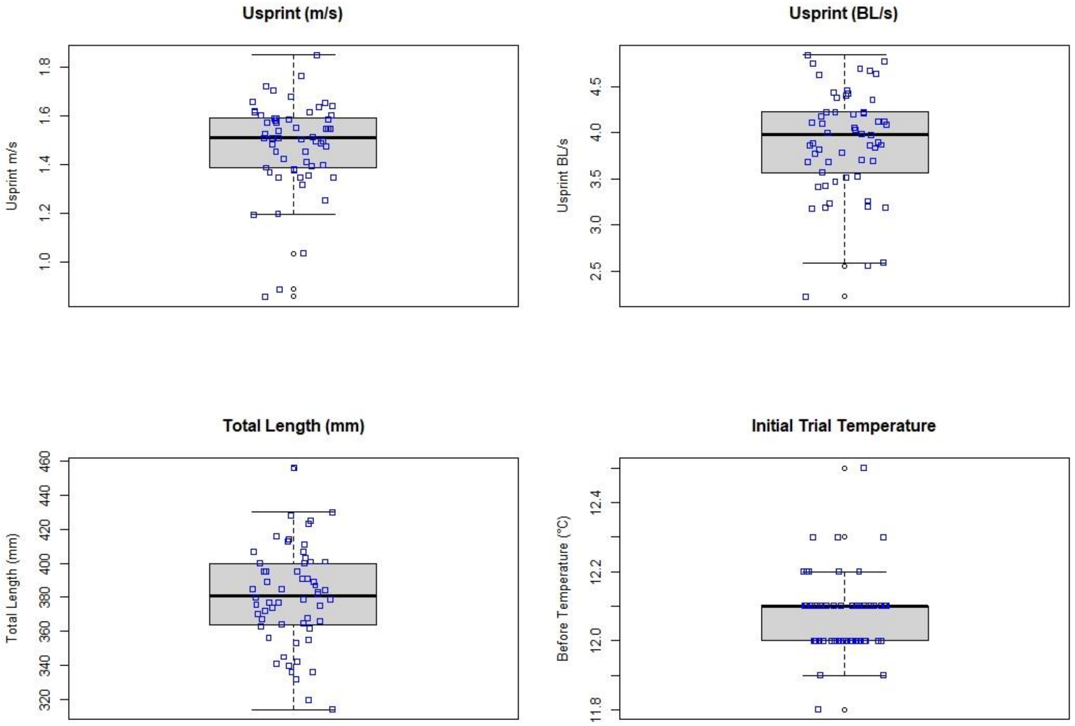

Figure 2.3: Boxplots for the U_{sprint} study variables with all fish participates data represented by blue squares. Variables include: U_{sprint} ($m{\cdot}s^{-1}$), U_{sprint} ($BL{\cdot}s^{-1}$), total length (mm), and before trial temperature (°C).

Figure 2.4: The swim chamber used to conduct the U_{sprint} experiment with a YCT in the test section.

Discussion

Fisheries professionals are faced with balancing human demand for surface water resources and maintaining healthy sustainable freshwater ecosystems. Many competing issues exist regarding how humans interact with fisheries such as land ownership, water rights, public safety, economic forces, energy production, agricultural use, and recreational demands (Cahoon et al., 2018). Projects with fisheries implications vary from large scale hydroelectric dams and transportation infrastructure to small scale irrigation diversions. These structures have the potential to cause habitat fragmentation by creating barriers (drops, velocity, depth, etc.) that fish are unable to navigate up or downstream. Regardless of scale, setting, or fish species, fishway structures are designed to facilitate successful migration. High quality swimming metrics for different species are crucial when designing fishways and assessing passage success probability. The primary goal of this study was to evaluate YCT's maximum anaerobic swim capabilities for a specific duration as well as to predict the water velocities that cause gait transitions. This U_{sprint} study will aid in determining the swimming capabilities as well as the limitations of YCT.

Although knowledge of the swimming capabilities of YCT is limited, several studies have examined the swimming metrics of YCT and other subspecies of Cutthroat Trout. Swim speeds previously reported for YCT include SP swim mode speeds of 0.81 to 1.03 $BL \cdot s^{-1}$ or in absolute terms 0.29 to 0.37 $m \cdot s^{-1}$ (mean FL: 359 mm) (McCleave & LaBar, 1972) and swim chamber U_{crit} values of 7.7 $BL \cdot s^{-1}$ or in absolute terms of 0.60 to 0.76 $m \cdot s^{-1}$ (FL: 78 mm to 98 mm) (Seiler & Keeley, 2007). The metrics reported by McCleave and LaBar (1972) cannot be directly compared to the results from this study as they were studying lower energetic swim modes. However, they do provide meaningful metrics for less energetic swim modes of YCT.

The U_{crit} value of 7.7 $BL \cdot s^{-1}$ observed by Seiler and Keeley (2007) was larger than our mean U_{sprint} value of 3.91 $BL \cdot s^{-1}$. Although these studies analyzed different swimming metrics, it is interesting that the maximum aerobic capabilities (U_{crit}) study reported higher swimming metrics than our maximum anaerobic capabilities (U_{sprint}) study. This discrepancy could be caused by the small fish size used in the Seiler and Keeley (2007) study, which confirms the generally observed idea that increased fish size will result in decreased swimming capabilities, when expressed in body lengths per second (Fry & Cox, 1970).

In our study, we observed gait transitions from a SP swim mode to an BG swim mode when mean water velocities exceeded 0.88 $m \cdot s^{-1}$, a threshold slightly higher than the U_{crit} metrics reported by Seiler and Keeley (2007). Both U_{crit} metrics and gait transitions from SP to BG swim mode serve as indicators of maximum aerobic swimming capabilities, allowing for meaningful comparisons between the Seiler and Keeley (2007) study and our findings. This comparison supports the quantification of YCTs maximum aerobic capabilities, estimated to range from 0.60 to 0.88 $m \cdot s^{-1}$.

YCT tested at the BFTC had a mean U_{sprint} of 3.91 $BL \cdot s^{-1}$ (SD = 0.56 $BL \cdot s^{-1}$) and in absolute terms of 1.48 $m \cdot s^{-1}$ (SD = 0.18 $m \cdot s^{-1}$) (total length: 314 mm to 456 mm). Additionally, gait transitions from SP to BG swim mode occurred at water velocities of 0.88 $m \cdot s^{-1}$ and from BG to B swim mode at 1.13 $m \cdot s^{-1}$. Combining the metrics produced in our study with the metrics reported by McCleave and LaBar (1972) and Seiler and Keeley (2007) a swimming performance curve can be created for YCT.

Developing a swimming performance curve for YCT based on various swimming metrics and methodologies is crucial for understanding their abilities in different hydraulic conditions.

For instance, if water velocities in a fishway exceed 1.13 $m \cdot s^{-1}$ (the velocity at which YCT gait transition from BG to B swim mode), designers should ensure that this velocity is sustained for less than 5.25 meters longitudinally. Exceeding this distance could lead to overexertion of YCT swimming endurance, hindering upstream migration. Developing such a curve is essential for informing the design of fishways to ensure they are suitable for YCT passage, contributing to the restoration of longitudinal connectivity and the protection of native fish populations. Additional swimming studies for YCT must be conducted to further develop a robust and comprehensive understanding of their swimming capabilities.

Limited studies have observed the swimming abilities of YCT, therefore comparisons to subspecies of Cutthroat Trout with similar physical and morphological characteristics can provide good proxies for developing applicable passage criteria. Blank et al. (2020) observed the swimming abilities of Westslope Cutthroat Trout (FL: 150 to 290 mm) in an open-channel flume and observed average swimming speeds of 0.79 $m \cdot s^{-1}$ to 0.89 $m \cdot s^{-1}$ and maximum swimming speeds of 3.55 $m \cdot s^{-1}$. In the current study, U_{sprint} for YCT was observed at an overall mean of 1.48 $m \cdot s^{-1}$ (SD = 0.18 $m \cdot s^{-1}$) which was significantly lower than the maximum swimming speeds reported by Blank et al. (2020) and provides evidence to support the idea that swim chambers underestimate swim speeds (Dockery et al., 2017b).

Hawkins and Quinn (1996) used a Blazka-type swim chamber to quantify the U_{crit} of Coastal Cutthroat Trout from two hatchery stocks. They reported U_{crit} values of 0.50 ± 0.002 $m \cdot s^{-1}$ (mean FL: 89.6 ± 12.0 mm) for Shelton Cutthroat Trout and 0.59 ± 0.002 $m \cdot s^{-1}$ (mean FL: 88.6 ± 7.7 mm) for Aberdeen Cutthroat Trout (Hawkins & Quinn, 1996). In the current study, mean U_{sprint} for YCT was observed at 1.48 $m \cdot s^{-1}$ (SD = 0.18 $m \cdot s^{-1}$) which was significantly higher than the U_{crit} values reported by Hawkins and Quinn (1996). U_{crit} metrics are measurements of aerobic swimming capacity whereas U_{sprint} metrics is a measure of anaerobic swimming capacities, therefore U_{sprint} metrics (in $m \cdot s^{-1}$) should result in higher values which is consistent with the comparison between Hawkins and Quinn (1996) and our results. In general, absolute swimming ability ($m \cdot s^{-1}$) increases with fish size while swimming abilities (in $BL \cdot s^{-1}$) decreases with fish size (Cahoon et al., 2018). This result was consistent with the U_{sprint} ($BL \cdot s^{-1}$) regression, see Figure 2.2. However, no significant relation between fish size and U_{sprint} ($m \cdot s^{-1}$) was observed in our study, see Figure 2.1, which was most likely due to the narrow range of fish lengths used in our study.

Comparisons between current and previous studies caution against interpreting performance metrics across different studies due to variations in swim trial procedures and the life history of the fish studied (Blank et al., 2020). Additionally, swim chamber results are difficult to compartmentalize into specific swim modes (sustained, prolonged, and burst) as swim chamber water velocities are continually increasing and are inevitably a very artificial environment (Cahoon et al., 2018). Overall, the mean U_{sprint} velocity observed was 1.48 $m \cdot s^{-1}$ (SD = 0.18 $m \cdot s^{-1}$) and ranged from 0.86 $m \cdot s^{-1}$ to 1.85 $m \cdot s^{-1}$ for YCT with total lengths of 314 mm to 456 mm. YCT preformed gait transitions from SP to BG swim mode at a mean water velocity of 0.88 $m \cdot s^{-1}$ (SD = 0.15 $m \cdot s^{-1}$) and from BG to B at 1.13 $m \cdot s^{-1}$ (SD = 0.18 $m \cdot s^{-1}$). Results suggest passage structures with water velocities less than 0.88 $m \cdot s^{-1}$ should provide high probability of successful passage of YCT for fish in this size range. However, structures with water velocities exceeding 1.85 $m \cdot s^{-1}$ may be impassable.

Of the sixty fish that participated in the U_{sprint} study, three did not follow the expected progression of swim modes. One of these fish produced a low U_{sprint} value, highlighted as a potential outlier in the data. Another fish that deviated from the normal swim mode progression produced the highest U_{sprint} value in this study. This fish initially skipped the BG mode and went from SP to steady B then back to BG and then to steady B again. These observed outliers provide evidence that fish swimming abilities are highly dependent on the motivation of an individual and are not strictly correlated to physical characteristics such as fish condition and length (Castro-Santos, 2005).

This study aims to expand on previous swim metrics studies to develop a comprehensive understanding of YCT swimming capabilities. To fully understand the swimming capabilities of YCT, large scale studies with a diverse range of fish ages, sizes, and life development are required. Unfortunately, this type of study is expensive and dependent on large scale infrastructure to product robust data. The authors of this project encourage the sharing of all information regarding the swimming capabilities of YCT in hopes that a meta-analysis can produce a comprehensive overview which can be used in successful fishway designs.

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CHAPTER THREE

SWIMMING PERFORMANCE OF YELLOWSTONE CUTTHROAT TROUT (*ONCORHYNCHUS VIRGINALIS BOUVIERI*) IN AN OPEN-CHANNEL FLUME

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Collected data, analyzed data, interpreted results, wrote manuscript.

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Contributions: Provided intellectual contributions, co-authored proposal to secure funding, reviewed manuscript.

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Contributions: Helped form conceptual basis of project, co-authored proposal to secure funding, reviewed manuscript.

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Contributions: Helped form conceptual basis of project, co-authored proposal to secure funding, reviewed manuscript, provided fisheries knowledge, completed the Institutional Animal Care and Use Committee (IACUC) protocol.

Co-Author: David Dockery

Contributions: Helped with the statistical analysis and reviewed manuscript.

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Abstract

Yellowstone Cutthroat Trout (*Oncorhynchus virginalis bouvieri*; YCT) inhabit the upper portions of the Yellowstone and Snake River basins of Montana, Wyoming, and Idaho. Although individual populations of YCT remain intact in headwater streams, anthropogenic activities have induced habitat fragmentation which has caused substantial declines in their historic range and core population abundance. We used an open-channel flume to characterize the swimming performance of YCT ranging in total length from 292 to 450 mm; volitional swim performance of 168 healthy hatchery raised YCT were observed. Passage success, maximum distance of ascent, maximum sprint velocities, and gait transitions for sustained, prolonged, burst glide, and burst swim modes were tested against four water velocities (0.61, 0.94, 1.75, and 2.00 $m \cdot s^{-1}$) at two temperatures (8.0 and 12.0°C). Passive integrated transponders (PIT) and an overhead digital video camera were used to evaluate swimming performance. Passage success decreased as water velocities increased, with success of ascending the entire flume ranging from 98% (water velocity of 0.61 $m \cdot s^{-1}$) to 19% (water velocity of 2.00 $m \cdot s^{-1}$). The overall maximum sprinting velocity was 4.59 $m \cdot s^{-1}$, mean maximum swimming velocity of 2.15 $m \cdot s^{-1}$, and gait transitions from sustained to prolonged occurred at water velocities of 0.61 $m \cdot s^{-1}$, from prolonged to unsteady burst glide at 0.94 $m \cdot s^{-1}$, and from unsteady burst glide to steady burst at 1.73 $m \cdot s^{-1}$. Multiple linear regression was performed to evaluate swimming speeds and determined that body size had no significant effect on swimming speeds, however the 12°C treatments produced significant higher swimming speeds (p-value < 0.015) than the 8°C treatments. Kaplin Meier survival curves and log rank tests were used to determine that temperature treatments had no significant effect on passage success or maximum distance of ascent (X^2 ranged from 0.0 to 1.0,

p-value ≥ 0.3, df = 1). The project results provide new information on the swimming abilities of YCT that can be used to support native populations by improving passage evaluations, identifying barriers to movements, and designing effective fish passage structure.

Introduction

The clear, cold, and clean rivers, lakes, and streams of Montana, Idaho, and Wyoming are considered world-class trout fisheries, providing critical habitats for species like the Yellowstone Cutthroat Trout (*Oncorhynchus virginalis bouvieri*; YCT). However, anthropogenic activities such as the construction of dams, weirs, culverts, and other instream structures have the potential to create passage barriers, causing habitat fragmentation and hindering fishes' ability to migrate for spawning, food searching, and temperature regulation (Belford & Gould, 1989; Gresswell, 1995, 2011). Hydraulic structures, such as culverts, can induce insufficient water depths, large outlet drop heights, and excessive water velocities, creating potential physical barriers to upstream fish migration (Blank et al., 2005, 2020). The construction of intentional barriers aims to isolate native fish species upstream of these barriers, preventing hybridization and competition caused by the presence of non-native and invasive species (Blank et al., 2020; Kovach et al., 2011; Rosenthal et al., 2022; Seiler & Keeley, 2007).

To restore river connectivity and enhance the long-term viability of aquatic species, researchers, biologists, and engineers have developed fish passage structures. Initially, fishway designs often lacked sufficient information on fish swimming abilities and design criteria, resulting in many ineffective structures (Katopodis & Williams, 2012). Research has since focused on optimizing passage efficiencies through passage studies and quantifying swimming performances of various species, especially salmonids. However, species like YCT have received minimal attention despite being classified as a “species of special concern” or “vulnerable to global extinction or extirpation in the state” (Gresswell, 2011; MNHP & MFWP, n.d.).

Understanding the swimming performance of individual fish species and how their capabilities apply to fishway designs and passage assessments can restore longitudinal connectivity and protect native fish populations (Blank et al., 2020). Historically, fish swimming performance is often categorized by one of three modes; sustained, prolonged, and burst swim modes. These swimming modes have been developed and tested to relate energy exertion to swimming velocities (Beamish, 1978; Blake, 2004). Sustained swimming is quantified as long periods (>200 minutes) without muscle fatigue, while prolonged swimming can be maintained for 20 seconds to 200 minutes and ends in muscle fatigue. Burst swimming can be maintained for <20 seconds and also ends in muscle fatigue (Beamish, 1978). Additional metrics like critical swimming velocity (U_{crit}) and sprint swimming velocity (U_{sprint}) measure the maximum aerobic and anaerobic capabilities and are typically tested in respirometers or swim chambers (Aedo et al., 2009; Dockery et al., 2017). These metrics are useful for designing fishways and evaluating passage success but are considered to underestimate swimming capabilities observed in natural environments (Castro-Santos, 2004; Castro-Santos et al., 2013; Dockery et al., 2017b; Dow, 1962; Haro et al., 2004; Peake, 2008b, 2008a). Volitional open-channel studies are now preferred for testing swimming abilities and analyzing passage success since enclosed swim chambers restrict the ability of fish to recruit different behavioral strategies (Castro-Santos et al., 2013) and exploit vortices found in turbulent regimes (Liao et al., 2003). Additionally, swimming passage studies that measure the maximum distance of ascent (D_{max}) a species can achieve against different hydraulic conditions can provide useful information for fishway and barrier designs

(Belford & Gould, 1989; Blank et al., 2005; Peterson et al., 2013; Solcz, 2007). Researchers can gain valuable insights into the locomotion capabilities of various fish species by examining metrics such as D_{max} and swimming velocities, which are essential for assessing and designing fish passage.

Yellowstone Cutthroat Trout are a subspecies of native inland Cutthroat Trout (*Oncorhynchus clarkii*), belonging to the salmonid family (*Salmonidae*) (MNHP & MFWP, n.d.). These trout inhabit cold, clear reaches of rivers, lakes, and streams with temperatures ranging from 0°C to 27°C, and optimal temperature of 15°C for their maximum activity and metabolism, as consistently reported in the literature (Dwyer & Kramer, 1975; Gresswell, 2011; McMahon et al., 2008). They inhabit both sides of the continental divide (Thurow & King, 1994), but their current range is now limited to the Yellowstone River, the Clarks Fork of the Yellowstone, the Bighorn River, the Tongue River, and upper portions of the Snake River (MNHP & MFWP, n.d.). Habitat degradation associated with anthropogenic activities has reduced the historic range to 42% and core population to 28% (Gresswell, 2011). Mature YCT, typically 3 to 4 years old, spawn on gravel beds from April to July, following the descending limb of the annual hydrograph (Gresswell, 2011; MNHP & MFWP, n.d.). Additionally, YCT exhibit fluvial or adfluvial life history patterns, further emphasizing the importance of maintaining and restoring longitudinal connectivity within their current habitat (MNHP & MFWP, n.d.). Understanding the swimming abilities of YCT is crucial for their conservation and management, as increasing anthropogenic pressures and habitat alterations persist.

A review of previous YCT swimming performance studies provide interesting insights into the objectives, methodologies, and range of swimming metrics obtained. However, as of this writing, there have been no volitional open-channel swimming studies designed to evaluate the swimming performance of YCT. One study by Seiler and Keeley (2007) evaluated the critical swimming velocity (U_{crit}) of YCT in a swim chamber. Other studies have provided anecdotal swimming information by assessing the success of YCT in overcoming varying velocity challenges in culverts (Belford & Gould, 1989; Blank et al., 2005; Solcz, 2007). These studies can help establish a relationship between the geometry of a structure and the hydraulic conditions within it, establishing "at-least swim speed thresholds" (Blank et al., 2020), as well as maximum distance of ascent (D_{max}) metrics.

Due to the limited number of swimming studies evaluating YCT, a review of previous swimming performance studies for other subspecies of Cutthroat Trout (*Oncorhynchus clarkii*) was performed. Additionally, other relevant open-channel studies using salmonids with similar life histories and body morphologies, were included in the review. Peterson et al. (2013) performed a passage assessment study through a 12.2 m long culvert with wild-caught resident Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) over a wide range of velocities. Researchers have also performed swim chamber studies to evaluate the U_{crit} swimming performance of Cutthroat Trout (Hawkins & Quinn, 1996; MacNutt et al., 2004), and the U_{sprint} abilities of Bonneville Cutthroat Trout (*Oncorhynchus clarkii utah*) (Aedo et al., 2009). Bell (1991) reported the sustained, prolonged, and burst swimming modes for Cutthroat Trout. Volitional open-channel flume methodologies have been used to evaluate the swimming performance of Rainbow Trout (*Oncorhynchus mykiss*) and Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) (Blank et al., 2020), and wild-caught Brown Trout (*Salmo trutta*) and Brook Trout (*Salvelinus fontinalis*) (Castro-Santos et al., 2013). Mesa et al. (2008) also performed an open-channel swimming study with Bull Trout (*Salvelinus confluentus*), but coerced fish to swim. The methodologies, the diversity in fish species and lengths, the number of fish studied, and the swimming information derived from each study varied significantly. However, comparisons between the results from this study and metrics reported in the literature can be used to validate our studies findings and create a robust swimming performance overview for YCT.

In summary, limited published swimming performance information for YCT exists, and studies that evaluate trout species with similar life histories apply a variety of methodologies, producing swimming metrics that are challenging to compare. The primary objective of this project was to characterize the volitional swimming performance, specifically maximum distance of ascent (D_{max}) and swimming velocities, of YCT in an open-channel flume setting. These swimming performance metrics were studied at two different temperature treatments to examine the effects of temperature. Quantifying YCT's swimming abilities will expand our understanding of how these fish interact with their environment and can be applied to design future ecohydraulic structures and passage evaluations, supporting conservation efforts.

Methods and Materials

Test Fish

The YCT swum in this study originated from brood stock at the Yellowstone Cutthroat Trout Hatchery in Big Timber, MT. The embryos were sourced from the hatchery’s spawning operations and then moved to the Bozeman Fish Technology Center (BFTC) where they were incubated and hatched at 12°C and oxygen maintained at 8 $mg \cdot L^{-1}$. Test fish were progressively moved to larger tanks to maintain a density below 0.023 $kg \cdot L^{-1}$ and reared according to standard techniques and parameters described for trout culture in Piper et al. (1982) prior to our study. These YCT had previously swam in 2021 as pilot study fish in determining passage through a scaled Denil fishway (Buller, 2023).

At the beginning of the study, 200 YCT were equally distributed among five 1.83-meter diameter circular holding tanks, with each tank initially containing 40 fish. To control tank temperatures, warm and cold well water was mixed and then entered the tank through a nozzle that was directed at the tank surface. This created circular flow patterns, which exercised the fish, where water velocities ranged from 0.01 to 0.54 $m \cdot s^{-1}$. Each tank had both warm and cold-water pipes equipped with 3.18-cemtimeter ball valves for temperature control. The first hydraulic challenges for the swim trials were performed at 8°C and the second set of trials was at 12°C. While the velocity challenges were randomized during the study, temperature was not; varying temperature changes can be challenging to fish health and so required a non-random approach.

To identify and track the 200 YCT used in this study, 23 mm half duplex (HDX) passive integrated transponders (PIT) tags (OregonRFID, Portland, OR) were surgically inserted into the peritoneal cavity. Fish were lightly anesthetized with tricaine methanesulfonate (MS 222, 25mg/L) during the PIT tagging process. The incision wounds were small and did not require sutures (Gries & Letcher, 2002). Fish were held without food for 24 hours before and after the tagging to ensure they were in a post-absorptive state. After tagging, fish were given a minimum of 28 days to recover before participating in swimming studies.

Experimental Flume

Swimming tests were conducted at an indoor open-channel flume (0.91 m wide x 1.37 m deep x 17.46 m long) at the BFTC. The flume consists of seven fiberglass sections, featuring concrete headwater and tailwater boxes. To ensure a near-flat incline while allowing water to drain, the flume was constructed on a slope of 0.83%.

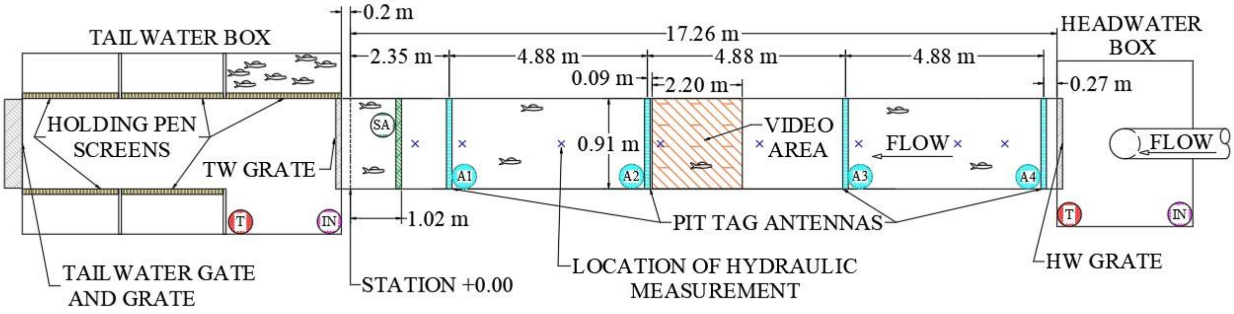

Figure 3.1: The flume setup at the Bozeman Fish Technology Center; PIT antenna system is highlighted in light blue, all grates are light gray, location of temperature measurements are in red, video analysis area is orange. The location of velocity and depth measurements are indicated with a dark blue 'X'. The stationing for antenna, video area, and hydraulic measurements in the flume starts 0.2 m upstream from the tailwater box.

Water circulation in the flume was maintained by two non-submersible Prime Vertical Axial Pumps: a 40-horsepower and a 20-horsepower pump. Both pumps can operate simultaneously, providing a flow rate from 0.032 to 0.315 $m^3 \cdot s^{-1}$. Water was stored in a 34.07 m^3 sump at the downstream end of the tailwater box and was recirculated to the headwater box through a 25.4 cm diameter schedule 40 polymerized vinyl chloride (PVC) pipe. The headwater box was designed to encourage fish to swim the entire length of the open-channel flume in search of low-velocity refuge areas. At the downstream end of the flume a staging area was constructed in the first 1.22 m which allowed fish to acclimate to the hydraulic challenges before each trial. The staging area featured a metal grate inserted perpendicular to the flow of water at station 1.02 m. An additional permanent metal grate was installed at the downstream end of the staging area, to prevent fish from entering the tailwater box. All metal grates were constructed out of expanded aluminum metal panels, with openings 4.27 cm by 1.70 cm, and cut to fit in the flume. Downstream of the staging area, water descended over a 0.46 m vertical drop into the tailwater box, and eventually returned to the sump. Within the tailwater box, removable screens were used to create five holding pens.

Water utilized in the flume was sourced from on-site warm and cold-water artesian wells. Inflow water temperatures were controlled using visual float valves. The two water temperature streams passed through a packing column before entering the flume to thoroughly mix the water. Freshwater inflows were located at both the headwater and tailwater boxes.

The hydraulic conditions in the flume were controlled by adjusting the pump outflow and by manipulating the height of the steel tailwater gate (Fresno Downward Opening Weir Gate, Selma, CA). A Signet 2540 paddle wheel flow meter (GF Piping Systems, Schlaffhausen, Switzerland) was installed into the recirculation pipe and recorded instantaneous flow rates. The elevation of the steel tailwater gate, functioning as a downstream weir, was adjusted to set the water depth in the flume.

A Multi-Antenna HDX Reader (OregonRFID, Portland, OR) PIT system was used to track individual fish over the duration of a swimming trial. Four stationary PIT antennas were placed within the flume. The antennas were designed to slide into grooves in the flume to minimize flow disruptions and eliminate resting areas for fish. The four PIT antennas release an electrical charge for 50 milliseconds, which is long enough to fully charge a PIT tag in a fish, and then pause for 50 milliseconds to listen for the response of a PIT tag. When a PIT tag passes through an antenna the Multi-Antenna HDX reader box will record the PIT tag number and the time of detection. The first antenna (A1) located at station 2.35 m identified voluntary participants. Antennae placed at station 7.23 m (A2) and station 12.11 m (A3) monitored fish progress, while the most upstream antenna at station 16.99 m (A4) assessed passage success. These antennae measured distances ascended and recorded detection times that could then be used to calculate swimming velocities. Detection probability was tested when tuning the PIT system. The system was calibrated until 100% single tag detection and 85% multi-tag detection rates were achieved (Triano et al., 2022).

A Sony Handicam video camera (Sony Corporation, New York, NY), mounted directly over the flume between stations 7.32 m and 9.52 m, captured fish swimming behavior during the trials. A grid, constructed with yellow electrical tape on the flume bottom at 0.305-meter increments in the longitudinal and transverse directions, served as reference points within the camera's field of view allowing swim position to be quantified. Video footage was recorded from the start of each trial (13:00 Mountain Standard Time (MST)) until dark (around 22:00 MST). The general flume layout, PIT antenna layout, and video camera analysis area are shown in Figure 3.1.

Experimental Treatments

Volitional YCT swimming trials were performed at specific hydraulics challenges (HC) and temperature treatments. Swimming trials were conducted from June 15th to July 18th, 2023, at the BFTC in the experimental flume outlined in Figure 3.1. Combinations of different pumps' flow rates and elevations of the steel tailwater gate, resulted in four different combinations of average water velocities and average water depths. The HC were characterized by average velocities and depths of 0.61 $m{\cdot}s^{-1}$ and 0.31 m (HC1), 0.94 $m{\cdot}s^{-1}$ and 0.37 m (HC2), 1.75 $m{\cdot}s^{-1}$ and 0.18 m (HC3), and 2.00 $m{\cdot}s^{-1}$ and 0.18 m (HC4), respectively. These HC settings were chosen to encompass a range of stable hydraulic conditions achievable in the BFTC open-channel flume system and to match velocities examined in previous open-channel swimming studies (Blank et al., 2020; Castro-Santos, 2004, 2005; Castro-Santos et al., 2013; Dockery et al., 2017b, 2019; Haro et al., 2004). Two temperature treatments, 8°C and 12°C, were examined. Temperatures varied in the flume ± 1.4°C during the 20-hour trial period due to natural fluctuations in source water, air temperatures, and turbulence from water entering the headwater box. To enhance statistical power, each combination of HC and temperature treatment was replicated three times (24 trials in total). All the 8°C treatments were conducted first and then all the 12°C treatments. The order of HC selection for each holding tank of fish was randomized using a random number generator. The experimental treatments tested in this study aimed at characterizing the maximum distance of ascent and swimming velocities of YCT and passage success.

Trial Process

Twenty-four hours before the start of each trial, seven fish were haphazardly netted from a holding tank. Seven fish were used per trial to support statistical analysis and account for possible mortality during trials throughout the study. These fish were scanned with a hand-held PIT tag reader (Model 601, Biomark, Boise, ID) to ensure a functioning PIT tag. Fish were then transported in a rolling cooler with 0.095 to 0.114 m^3 of water matching the holding tanks and trial target temperature. These fish were placed in one of five holding pens in the tailwater box. During the holding period, all fish were provided at least twenty-four hours to acclimatize to the flume environment and food was withheld to ensure a post-absorptive state.

Before the start of the trial, pump flow rates, inflow water ratios, and tailwater gate elevations were manually set to the pre-established values associated with the targeted treatment.

While the hydraulics in the flume stabilized, the PIT array was turned on and the detection rate was determined with a multiple-tag (23 mm HDX) detection test. Once the system reached steady state, a preliminary set of hydraulic and temperature measurements were taken to ensure the test conditions matched that of the targeted treatment conditions.

Thirty minutes before the start of the trial, fish from a holding pen were netted, PIT tag numbers re-scanned, and were placed into the 1.22 m x 0.91 m staging area. This period allowed fish to acclimatize to the hydraulic challenge. At the beginning of the trial (13:00 MST), the staging area upstream grate was removed, enabling fish to volitionally swim up the open-channel flume.

Trials lasted from 13:00 MST to 09:00 MST the following day, to capture peak movement periods at dusk and dawn. At the end of the trial, the PIT array system was turned off and the metal grates for the staging area and headwater box were inserted. Fish were removed from the flume, PIT tag numbers were re-scanned, their final positions in the flume were recorded (staging area, flume, or headwater box), and they were transported to the recovery tanks via a rolling cooler. A secondary, more robust, set of hydraulic and temperature measurements were collected before the pumps were turned off. The six 0.91-meter diameter recovery tanks received water through the hatchery's reuse water system. Recovery tanks-maintained temperatures within ± 0.2°C of the holding tanks. Food was withheld for twenty-four hours after participating in a trial. Once four trials were completed, all fish in the recovery tanks were weighed and total lengths measured. Fish were lightly anesthetized during these measurements using the same process as PIT tagging. Any fish found without PIT tags were re-tagged, and all fish were then returned to their original holding tank. The swim trial process flow diagram depicting how fish were held and moved to and from the flume apparatus is displayed in Figure 3.2.

The 12°C trials began after the completion of the 8°C trials and all holding tanks remained at 8°C. In preparation for a 12°C trial a holding tank was selected and the temperature in the tank was increased by one degree per day over four days; fish reached 12°C and acclimated to the new test temperature for two days (48 hours). Holding tank temperature ramp-ups were coordinated with the date the selected holding tank was needed for experimentation to minimize stress on the fish due to higher water temperatures, thus all fish were held at 8°C until exposed to the same 6-day ramping and holding regime prior to a 12°C test.

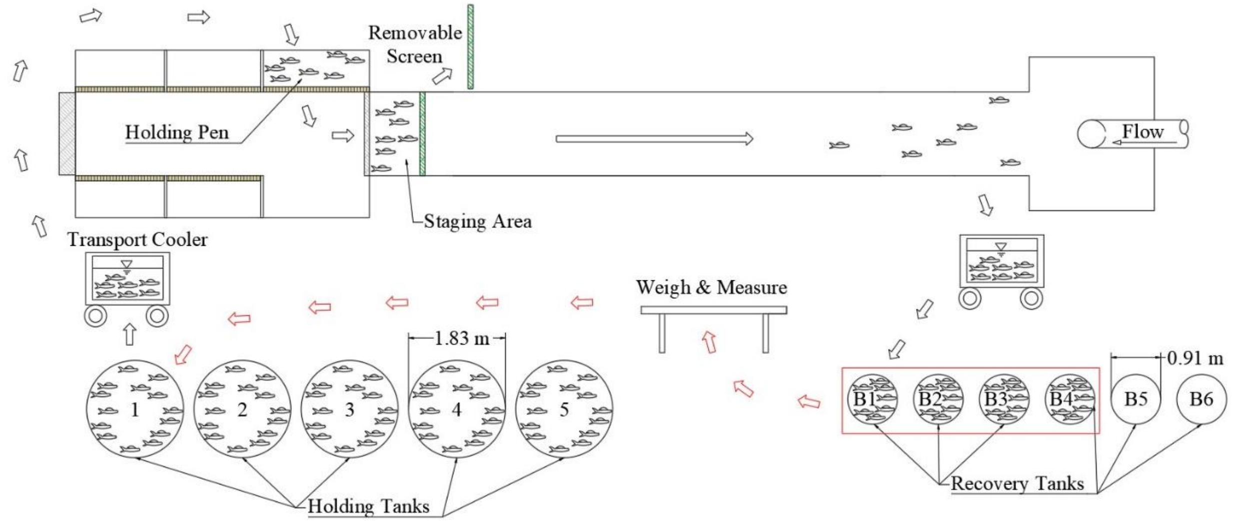

Figure 3.2: The arrows represent the fish handling process starting and returning to the Holding Tanks. Seven fish were haphazardly selected from a Holding Tank, then were transported to the holding pen via a rolling cooler. Fish were then placed in the staging area at the beginning of the trial. After the trial was over, fish were transported to the Recovery Tanks where they waited until four trials worth of fish (28 fish all originating from the same Holding Tank) were in the Recovery Tanks. All fish were weighed and measured, then returned to their original Holding Tank.

Hydraulic Data Collection

Ten locations along the flume's length, station 1.22 m, 2.59 m, 5.03 m, 6.10 m, 7.47 m, 9.91 m, 10.97 m, 12.34 m, 14.78 m, and 15.85 m, were used to measure water depths and velocities. See Figure 3.1 for locations of hydraulics measurements. Velocity measurements were taken at the cross-section midpoint and at 0.4 of the water depth from the bottom of the flume using a Marsh McBirney Flo-Mate velocimeter (Hach Corp., Loveland, CO). Water velocity at 0.4 m of the water depth generally approximates the average velocity in a column of water in an open channel. Water depth measurements were also taken at the cross-section midpoint with a graduated rod. Measurements were recorded at specific stations before and after each trial, to obtain velocity profiles used to calculate fish swimming speeds. Additionally, three cross-section velocity gradient measurements were taken at stations 7.32 m, 8.23 m, and 9.14 m for each HC. These measurement locations were selected to align with the video cameras viewing frame. The hydraulic gradient maps for each station at each HC are displayed in Figure 3.3.

Water and air temperatures were measured with an Ertco-Eutenchnics Model 4400 digital thermometer (Alpha Technics, Oceanside, CA). Water temperatures were measured in the headwater box, tailwater box, freshwater inflow in headwater box, and freshwater inflow in tailwater box pre- and post-trial. Additionally, all holding and recovery tanks temperatures were measured twice per day to monitor for temperature drift. Total flume flow rate was measured by summing the average flow rate in the recirculation pipe and the freshwater inflow rate in the headwater box. A summary of the measured hydraulic and temperature conditions is displayed in Table 3.1.

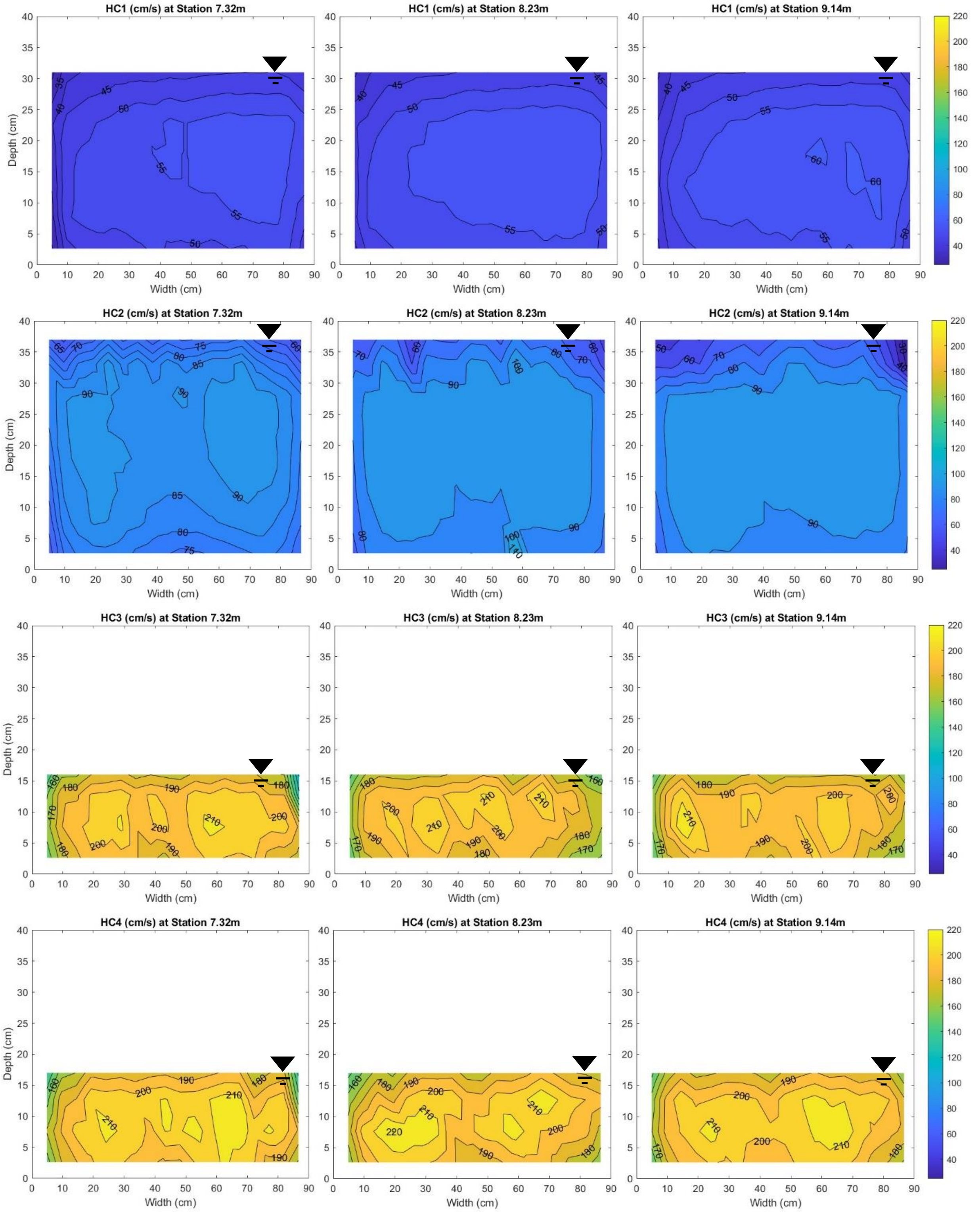

Figure 3.3: Velocity Gradient Maps at station 7.32 m, 8.23 m, 9.14 m in (cm/s) for each hydraulic challenge, oriented left to right looking downstream. Using a three-point fit method to extrapolate water velocities to the measured water surface elevation (Mueller, 2022). At the

boundaries (walls and flume bottom) accurate velocities could not be measured. A no-slip, zero velocity, boundary condition was applied at all walls therefore all velocities at the interface of the wall and flume bottom are considered zero.

Data and Video Analysis

For each trial, the PIT data collected from the Multi-Antenna HDX Reader was sorted by PIT tag number to establish the location and time of each individual fish throughout the trial period. Detections at the A1 antenna indicated fish participation in the trial, while detections at A4 quantified successful passage. All PIT antennas were utilized to assess the distance of ascent and calculate swimming speeds. However, fish that did not ascend to the second antenna (A2) had no swimming speed data available and were marked as participants without velocity data.

An attempt was defined as all PIT antenna detections from when a fish initially passed through A1, moving upstream, until it returned to A1. Although most fish made multiple attempts to ascend the flume, only the first best attempt (FBA) was used in this analysis. We defined FBA as the first time a maximum distance of ascent was achieved, independent of attempt number. A fish could make several attempts before it achieved their maximum ascent distance and might produce several additional attempts to the same distance. This allowed us to evaluate the swimming velocities that comprise a maximum distance of ascent attempt which would represent the swimming strategy a fish used when attempting to pass a velocity barrier. Within each FBA, the uppermost upstream antenna detection was recorded, along with the time duration between A1 and the uppermost detection (FBA duration), and the starting time of the attempt (FBA time of day). All the data used in the analysis, except for overall maximum sprinting speeds and the video data, was collected and calculated from a fish's FBA. The decision to analyze FBA swimming velocities was based on the study performed by Castro-Santos (2005) which stated, "because most individuals achieve the greatest distance on the first attempt, there is no reason to expect that fish will adopt any strategy other than distance-maximization." Castro-Santos (2005) reported that the best attempt occurred 65 to 95% of the time on a first attempt.

The maximum distance of ascent (D_{max}) was determined by identifying the farthest upstream PIT antenna detection attained by individual fish during the trial. Analysis of D_{max} was conducted using the statistical software R version 4.3.0 (R Core Team, 2023), utilizing the survival package (Therneau, 2024). A Kaplan-Meier survival curve served as the primary analytical tool to evaluate the survival rate across the eight distinct HC and temperature treatment combinations. The Kaplin-Meier survival curve was used to evaluate D_{max} since our data was censored. Fish were capable of successfully passing the flume at the hardest HC; therefore, we cannot conclude how much further our fish could swim upstream before failing. Additionally, survival curves are typically used to describe death as the point of failure. We adapted the survival curve to express failure when the hydraulic conditions prevented passage success. This analysis visually mapped the relationship between distance of ascent on the x-axis and survival rate represented as a percentage on the y-axis. Notably, the non-parametric nature of the Kaplan-Meier survival curve method ensures robustness against assumption violations within the D_{max} data. Furthermore, a log-rank test was utilized to examine differences in D_{max} across the different temperature treatments within each hydraulic challenge. After this analysis, survival curves were generated and graphically depicted for each hydraulic challenge.

Fish total length and weight were determined to be normally distributed based on visual assessment of boxplots, and homogeneity of variance was confirmed, with a Levene's test, across all hydraulic challenges and temperature treatment combinations. The total length ranged from

292 mm to 450 mm, with a mean total length of 381.10 mm (standard deviation (SD) = 27.27 mm) and all fish were of the same age-class. Welch's One-way ANOVA revealed no significant differences in fish total length among hydraulic challenges or temperature treatments (p-value = 0.179, $F_{7,155} = 1.478$). Additionally, Levene's test indicated homogeneity of variance (p-value = 0.454). Fish weight ranged from 257.2 g to 981.4 g, with a mean weight of 569.8 g (SD = 129.10 g). Similarly, Welch's One-way ANOVA showed no significant differences in fish weight among hydraulic challenges or temperature treatments (p-value = 0.389, $F_{7,155} = 1.065$), and Levene's test confirmed homogeneity of variance (p-value = 0.647). Given the high correlation between fish total length and weight, only the total length was utilized for exploratory models of swimming velocities.

The overall maximum sprinting speeds were determined to quantify the upper limits of YCT sprinting abilities. Maximum sprinting speed metrics for every fish within each treatment combination were compiled in Excel. These maximum sprinting speed metrics were not limited to FBAs.

In this study, two types of swimming velocities were analyzed from each participants' FBA: ground speed and swimming speed. Ground speed refers to a fish's velocity in relation to a stationary viewing frame positioned on the bottom of the flume. The calculation of ground speed (V_{GS}) utilized the time difference between detections at consecutive (A1 through A4) and evenly spaced (4.88 m apart) antennas, according to the formula:

$$(1) \qquad V_{GS} = \frac{Distance\ between\ Antenna\ (m)}{Duration\ between\ Detections\ (\mathrm{s})}$$

Swimming speed represents a fish's velocity relative to a viewing frame moving downstream at the velocity of the oncoming water. Therefore, swimming speed (V_{SS}) was determined by adding ground speed (V_{GS}) to the average oncoming water velocity (V_{AV}) between each antenna:

(2) $$V_{SS} = V_{GS} + V_{AV}$$

Average ground and average swimming speeds were calculated from a fish's FBA. Every set of upstream swimming antenna detections that composed a fish's FBA were averaged. For example, if a fish swam in sequential order from A1 to A3 then drifted back to A2 and then swam to A4, there would be four ground velocities to average for this FBA. Only upstream velocities were evaluated in this analysis due to the significance for upstream migration. In addition to the average ground and average swimming speeds, maximum ground and maximum swimming speeds were taken from the series of velocities that composed each fish's FBA. These four swimming velocity metrics were analyzed using R software (R Core Team, 2023).

All fish with detections at A2 or higher provided swimming metrics for analysis, except for those with errors in the PIT data. An error was defined as a missing detection at an antenna as a fish ascended the flume. For instance, if a fish was detected at A1 at the start of an attempt but the next detection in the PIT tag data occurred at A3, it indicated that the fish had swum through A2 but was not recorded in the data. In such cases, swimming metrics between A1 and A2, and between A2 and A3, had to be estimated based on the detection information at A1 and A3. While swimming metrics estimated under constant velocity could potentially be relatively accurate, they also could be incorrect and lead to skewed analysis if the fish utilized different swimming modes. During the FBAs, a total of 12 fish experienced detection errors in their PIT data. The average ground speed and average swimming speed values of these fish were excluded from the analysis. Additionally, if errors occurred at antennas associated with maximum ground speed and maximum swimming speeds, these metrics were excluded from the data analysis. Furthermore, if the first detection (A1) was missing, FBA average swimming metrics were excluded from the analysis. Out of the 12 fish with errors, 7 retained maximum ground speed and maximum swimming speeds metrics for analysis.

All FBA swimming velocity metrics underwent identical analysis procedures. First, the assumptions for Welch's One-way ANOVA test and multiple linear regression models (normality, homogeneity of variance, and independence) were assessed. Swimming velocity metrics were separated into the eight treatment combinations, and boxplots were constructed to evaluate normality. Visual inspection of the boxplots indicated normal distribution for all swimming velocities. Subsequently, Levene's test was used to examine homogeneity of variance. A cutoff p-value > 0.1 signified homogeneity of variance across all treatment combinations. Levene's test yielded p-values > 0.18 for all swimming velocity metrics, confirming homogeneity of variance. The independence assumption was violated in several ways but was eventually deemed satisfied for the purposes of this analysis. Factors that contributed to the lack of independence included individuals participating in multiple trials (19 fish from one holding tank were swam twice, once at 8°C and again at 12°C), and fish-to-fish physical and behavioral interactions within each trial (seven fish per trial). Overall, the assumptions for Welch's One-way ANOVA test and multiple linear regression models were considered met for the purpose of this analysis.

Following this, Welch's One-way ANOVA was conducted. A p-value < 0.05 indicated evidence to reject the null hypothesis (equal means across all treatment combinations). If the null hypothesis was rejected, the swimming velocity metric was analyzed using a multiple linear regression model. Model covariates included water temperature, hydraulic challenge (water velocity and depth), and total fish length, with all two-way and three-way interaction terms initially included in the model. The models were refined using the extra sums of squares (ESS) F-test. Interaction terms with limited statistical support (p-value > 0.05) were eliminated from the model in a stepwise process. Each removal was validated by comparing the previous model to the reduced model, with a p-value > 0.1 indicating the superiority of the reduced model. The most complex term (three-way interaction) was removed first, followed by the elimination of two-way interaction terms with the highest p-values. The final model was selected when all remaining terms yielded p-values < 0.05, indicating significant statistical effects on the response variable. If all explanatory variables were removed from the final model, a Tukey Multiple Comparison ANOVA test would be conducted to identify unequal treatment means.

The video data captured by the overhead camera offered valuable insights into the volitional swimming behavior of YCT. Individual fish were identified upon entering the camera's field of view by correlating their PIT tag detection times at A2 or A3 with the camera's recorded time. The analysis focused on two categories: fish actively swimming upstream and those moving downstream. Swim mode and position proportions were calculated relative to the total number of observations within each treatment. Swim modes were categorized based on the frequency and duration of tail beats, the resulting classifications were sustained (S), sustained/prolonged (S/P), prolonged (P), burst glide (BG), and burst (B) (Beamish, 1978). The proportion of each swim mode utilized in a trial was calculated to evaluate correlations between HCs and temperature treatment.

To quantify fish swimming positions, a grid measuring 0.305 m by 0.305 m fixed to the bottom of the flume and the camera was oriented from left to right, facing downstream. Positions were categorized as left (L), left/middle (L/M), middle (M), right/middle (R/M), right (R), and all over (AO). A fish was assigned a L/M rank if it spent equal amounts of time in the left third and middle third of the flume as it progressed upstream or downstream through the camera's view frame. The R/M assignment used the same methodology as L/M described above. The proportion of each swimming position utilized in a trial was calculated to assess correlations between HCs and temperature treatments.

Results

Test Conditions

Flow in the open-channel flume for all trials was non-uniform (varied) and turbulent. Flow was characterized as subcritical in HC1 and HC2, and mainly supercritical flow was observed in HC3 and HC4. A hydraulic jump occurred at station 3.35 m for HC3 and at station 1.07 m for HC4. In the subcritical challenges, water velocities increased and depths decreased with distance upstream in an approximately linear relationship. As water exited the headwater box and entered the flume contraction losses and recirculating vortices created slightly higher water velocities, not following the linear relationship, which quickly dissipated resulting in relatively steady flow. In the supercritical challenges, upstream of the hydraulic jump, water velocities and depths slightly decreased with distance upstream. Below the hydraulic jump water velocities rapidly decreased and depths rapidly increased. The velocity and depth profiles for each HC are displayed in Figure 3.4, note that the hydraulic jump in HC4 occurred downstream of the first hydraulic measurement and therefore cannot be seen in Figure 3.4. The hydraulics conditions for each treatment combination are displayed in Table 3.1. Both the mean water velocity and mean water depth values have been averaged over the length of the flume and are reported in Table 3.1.

Cross-sectional velocities were generally highest in the center and were lowest along the bottom and sides of the flume. Hydraulic gradient maps for each HC at three different stations within the video area are displayed in Figure 3.3. All HC were in the turbulent regime (Reynolds number (R_e) > 2500) and the R_e increased with average velocity and temperature treatments, ranging from 80,699 for HC1 at 8°C to 203,446 for HC4 at 12°C. The Froude number was calculated with average velocities and average depths for each HC, therefore if a hydraulic jump occurred in the flume the location of the jump would affect the Froude number (hydraulic jumps further upstream would produce lower Froude numbers). Variations in temperature treatment were ≤ 0.92°C for the 8°C temperature treatments and ≤ 0.15°C for the 12°C temperature treatments for all HC. Pre-trial and post-trial temperature measurements were averaged for each trial.

Table 3.1: Summary of test conditions and the results for the eight hydraulic challenges (HC) and temperature (T (°C)) treatment combinations during YCT passage testing in the experimental flume.

HC	T (°C)	Mean Water Velocity ($m\cdot s^{-1}$)	Mean Water Depth (m)	Flow Rate ($m^3\cdot s^{-1}$)	Re	Fr
1	8.12	0.61 ± 0.12	0.31 ± 0.04	0.1553	80699	0.35
	11.87	0.61 ± 0.13	0.31 ± 0.04	0.1565	90626	
2	8.92	0.94 ± 0.14	0.37 ± 0.04	0.3193	138552	0.50
	12.15	0.94 ± 0.15	0.37 ± 0.05	0.3227	155597	
3	8.48	1.73 ± 0.32	0.18 ± 0.05	0.2679	163003	1.31
	11.92	1.76 ± 0.30	0.18 ± 0.05	0.2699	183056	
4	8.73	1.99 ± 0.09	0.17 ± 0.01	0.3191	181169	1.52
	12.15	2.00 ± 0.09	0.18 ± 0.01	0.3213	203456	

Note: The Reynolds number (Re) and the Froude number (Fr) are dimensionless. Mean Water Velocity, and Mean Water Depth are presented as the mean ± 1 standard deviation (SD) and were averaged over the length of the flume.

A total of 149 unique fish were tested in 24 trials involving four HC's, with two temperature treatments (8°C and 12°C); three trial replicates were performed for each of the eight treatment combinations (HC1-8°, HC1-12°, HC2-8°, HC2-12°, etc.). Note that in Table 3.11 trial 6 has been removed due to the PIT tag data ending mid trial (battery failure). Additionally, 19 of the unique fish swam twice, participating in both the first and last sets of four trials, bringing the total number of fish used in trials to 168. Of the total fish used, 163 fish were identified as participants and provided data for the analysis of swim speeds and distance of ascent. Participation rates were 100% for all trials except HC4, where rates dropped to 86% for the 8°C treatment and 90% for the 12°C treatment. Overall participation rate for all trials was 97% and the overall passage rate was 56%.

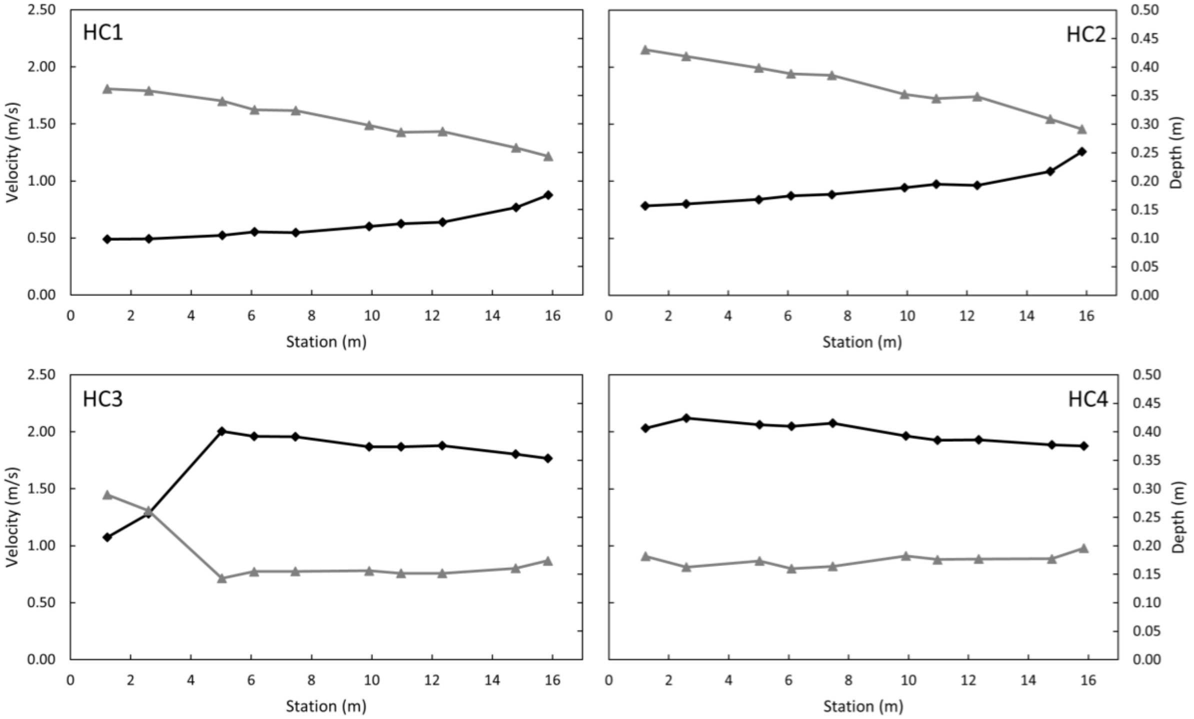

Figure 3.4: The hydraulic profiles for each of the four HCs, measured along the midline of the flumes cross-section for the entire length of the flume. The black line with solid black diamonds represent the HC's water velocity ($m \cdot s^{-1}$), and the gray line with solid gray triangles display the water depths (m).

Maximum Distance of Ascent

Yellowstone Cutthroat Trout displayed high motivation to swim upstream in the flume, with most trial participants exhibiting burst swimming mode once the staging area grate was removed. When fish successfully ascended the flume, they rarely held position in the headwater box for the remainder of the trial. Fish would drift or actively swim downstream to make additional attempts or hold position somewhere within the flume. Multiple attempts to pass the flume occurred in all trials, but as water velocities increased the average number of attempts per trial tended to decrease. A total of ten fish only made one attempt, yet only four of these fish had detections above A1 and none successfully passed the flume. Passage rates among the four HC ranged from 22% to 95% for the 8°C treatments and from 16% to 100% for the 12°C treatments. Passage rates decreased as water velocity increased for all temperature treatments, see Table 3.2 for further detail.

Maximum distance of ascent (D_{max}) followed the same trend as passage rate, D_{max} decreased as water velocity increased. The overall log-rank test confirmed that the mean D_{max} for all HC treatment were not equal ($X^2 = 70.1$, p-value < 0.0001, degrees of freedom (df) =3). Therefore, survival curves were built to compare the effects of temperature within each HC. Log-rank tests for each HC indicated that temperature had no significant statistical effect on mean D_{max} values (X^2 ranged from 0.0 to 1.0, p-value ≥ 0.3, df = 1). The survival curves for each HC can be seen in Figure 3.5. Although the mean D_{max}, presented in Table 3.2, are generally higher in the 12°C treatments compared to the 8°C treatments, no statistical statements can be concluded.

Table 3.2: Summary of D_{max} and first best attempt (FBA) for the eight hydraulic challenges (HC) and temperature (T (°C)) treatment combinations during YCT passage testing in the experimental flume.

HC	T (°C)	Participation Rate	Passage Rate	Mean D_{max} (m)	Ave. # of Attempts	FBA on First Attempt %	Median FBA Time of Day	Median FBA Duration (sec)
1	8.12	1.00	0.95	16.51 ± 2.13	12.0	23.81	17:42	143.2
	11.87	1.00	1.00	16.98 ± 0.00	24.3	80.95	13:00	276.2
2	8.92	1.00	0.76	15.82 ± 2.13	21.3	28.57	15:18	87.5
	12.15	1.00	0.81	15.58 ± 3.14	30.8	57.14	13:00	502.8
3	8.48	1.00	0.33	12.33 ± 4.75	9.3	52.38	15:42	433.6
	11.92	1.00	0.29	12.80 ± 3.19	14.2	66.67	14:00	39.5
4	8.73	0.86	0.22	10.47 ± 4.73	6.3	55.56	18:36	175.2
	12.15	0.90	0.16	11.59 ± 3.60	8.7	52.63	16:00	89.7

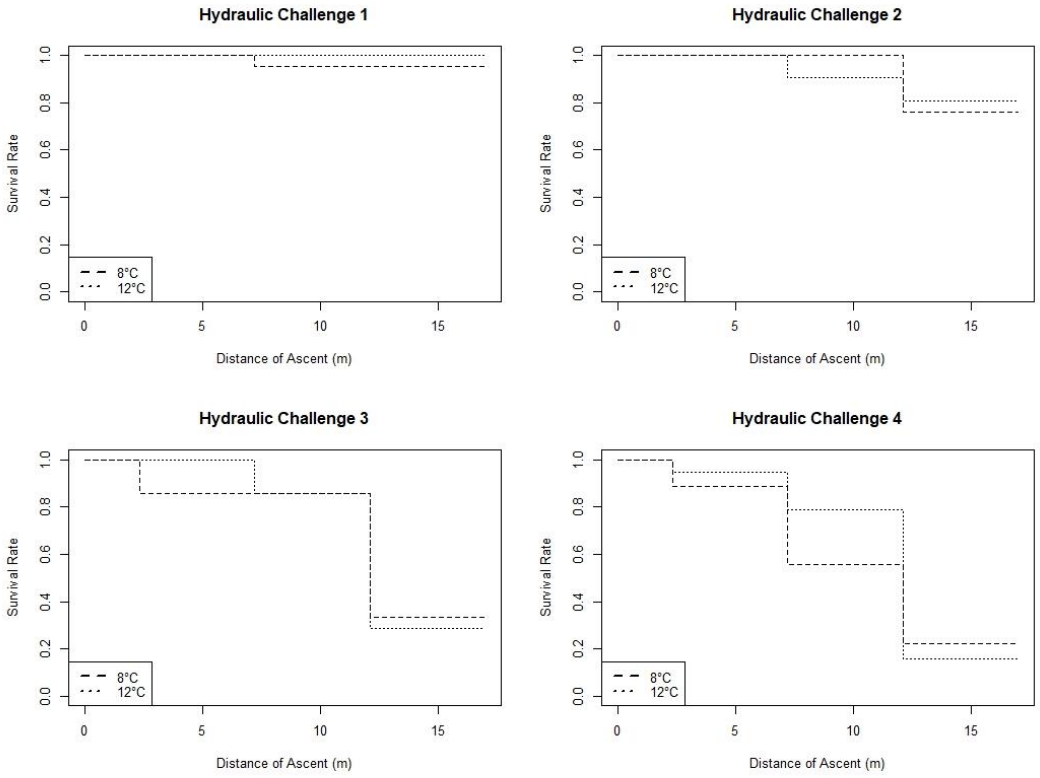

Figure 3.5: Survival curves for each of the four HCs with temperature treatments displayed as long dashed line (8°C) and short dashed line (12°C). The survival curves were created with a Kaplan-Meier survival analysis in R Studio.

Yellowstone Cutthroat Trout obtained D_{max} on the first attempt for > 50% of fish in all temperature treatments and HC's, except for HC1 and HC2 at 8°C where < 30% of fish obtained D_{max} on their first attempt. The average time of day, in hours, of FBA across all treatment combinations occurred at hour 16:11 MST with a standard deviation of 4.22 hours. Furthermore 85% of FBA times occurred before 21:00 MST (9 hours) from the start of the trial (13:00 MST). The time of FBA was not affected by HC or temperature treatment. FBA times were concentrated in the afternoon until dusk (dusk occurred from 21:30 to 22:00 MST) and dawn (dawn occurred from 05:00 to 05:30 MST) which can be seen in Figure 3.6. No clear trends were observed for duration of FBA, but fish that selected a constant distance maximizing velocity typically obtained a higher D_{max}. To determine if fish were utilizing a constant distance maximizing velocity, the FBA average ground speeds were compared to the FBA maximum ground speeds. If these two metrics differed significantly it was determined that a fish was not using a constant distance maximizing velocity.

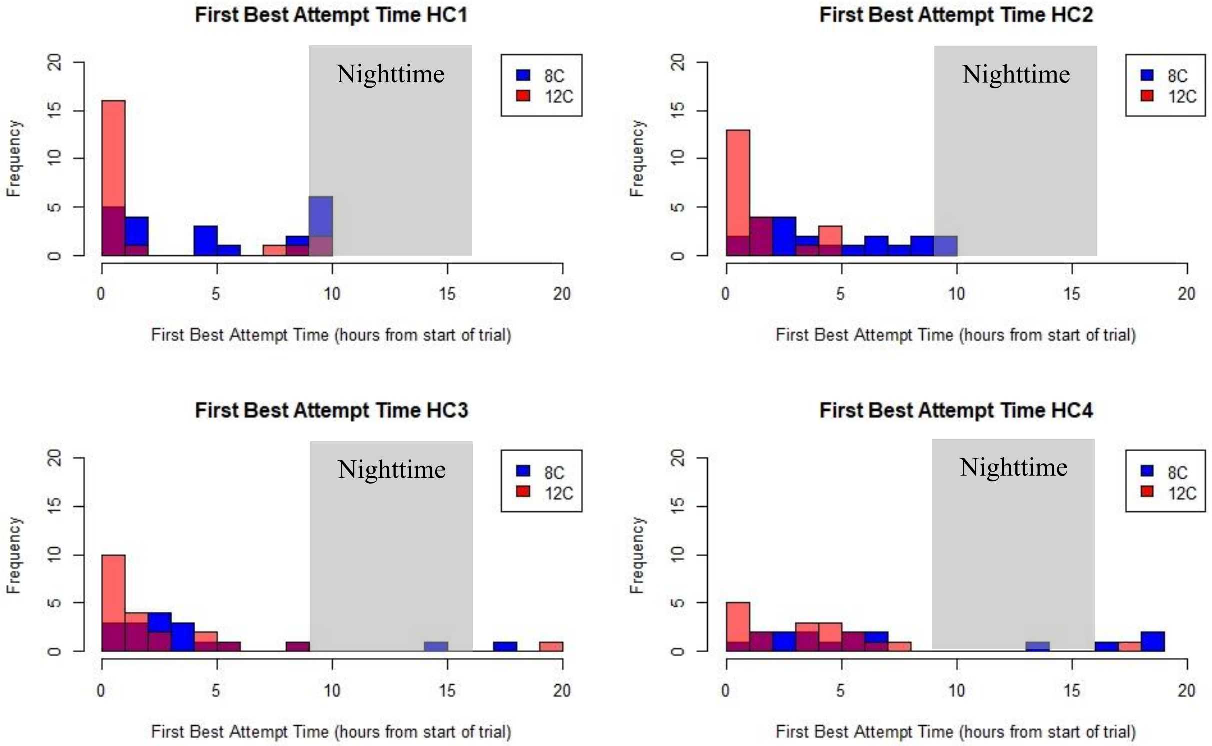

Figure 3.6: Time of FBA for each HC and temperature treatment. The time of FBA was recorded when a fish was detected at A1, these times were then grouped by hour starting at 13:00 MST (start of trial) until 09:00 MST the next day for a total trial duration of 20 hours. Blue data represents 8°C treatments and red data represents 12°C treatments. The gray transparent rectangle represents the nighttime from 22:00 MST to 05:00 MST the next day.

Overall Maximum Sprinting Speeds

All swimming speed data from every trial was compiled, regardless of treatment combination or FBA. The overall maximum sprinting speed observed in any trial was 4.59 $m \cdot s^{-1}$. This velocity occurred between A1 and A2 during HC1 at 12°C treatment combination and was not associated with an FBA. The D_{max} for this specific attempt was A2, station 7.23 m, and based on the resulting velocity it suggests that the fish was using a burst swimming mode. The mean maximum swimming speed for all HC's and temperature treatments was 2.15 $m \cdot s^{-1}$.

FBA Average Swimming Metrics

Average swimming metrics calculated for a fish's FBA included average ground speed (AGS) and average swimming speed (ASS). The data for AGS and ASS met the assumptions for Welch's One-way ANOVA test, and both produced p-value < 0.05 indicating evidence to reject the null hypothesis that all treatment means were equal. Therefore, linear regression for both AGS and ASS were conducted.

Table 3.3: Summary table of first best attempt (FBA) average swimming metrics for the eight hydraulic challenges (HC) and temperature (T (°C)) treatment combinations during YCT passage testing in the experimental flume.

HC	T (°C)	Mean Total Length (mm)	FBA Average Ground Speed ($m \cdot s^{-1}$)	AGS Range ($m \cdot s^{-1}$)	FBA Average Swim Speed ($m \cdot s^{-1}$)	ASS Range ($m \cdot s^{-1}$)
1	8.12 ± 0.55	392 ± 19.7	0.26 ± 0.15	(0.07, 0.58)	0.89 ± 0.15	(0.70, 1.20)
	11.87 ± 0.42	383 ± 25.6	0.36 ± 0.21	(0.05, 0.78)	0.99 ± 0.21	(0.69, 1.42)
2	8.92 ± 0.56	389 ± 26.5	0.26 ± 0.14	(0.09, 0.63)	1.20 ± 0.15	(0.98, 1.59)
	12.15 ± 0.40	378 ± 23.0	0.34 ± 0.24	(0.04, 0.90)	1.29 ± 0.25	(0.95, 1.87)
3	8.40 ± 0.45	373 ± 27.1	0.29 ± 0.13	(0.12, 0.58)	2.12 ± 0.13	(1.95, 2.41)
	11.92 ± 0.41	375 ± 33.0	0.40 ± 0.18	(0.16, 0.79)	2.25 ± 0.19	(1.98, 2.65)
4	8.73 ± 0.62	374 ± 33.2	0.33 ± 0.29	(0.01, 1.08)	2.37 ± 0.27	(2.09, 3.06)
	12.15 ± 0.39	385 ± 25.8	0.52 ± 0.24	(0.21, 1.11)	2.55 ± 0.25	(2.23, 3.13)

Note: Mean total length, FBA average ground speed (AGS), and FBA average swim speed (ASS) are presented as mean ± 1 standard deviation. Range metrics are reported as (overall minimum, overall maximum) observed for a specific treatment combination.

Water velocity and temperature treatments influenced average ground speeds. A linear regression model was used to test if the covariant total length, HC, and temperature treatments significantly predicted AGS for YCT. Total length had no statistical significance when predicting AGS, therefore the linear regression model was reduced to (AGS ~ HC + Temperature) ($R^2 = 0.14$). The coefficients used in this model are reported in Table 3.4. There was very strong evidence for a difference in AGS between the 8°C and 12°C treatments (p-value = 0.0006) with AGS estimated to be 0.117 $m \cdot s^{-1}$ faster (95% CI = (0.23 $m \cdot s^{-1}$, 0.51 $m \cdot s^{-1}$)) in the 12°C treatments than the 8°C treatments. The effects of each HC were compared to the differences in AGS, there was moderate evidence to support that the water velocities in the HC4 treatments had a significant statistical effect on the AGS (p-value = 0.019). The AGS was estimated to be 0.116 $m{\cdot}s^{-1}$ faster (95% CI = (0.20 $m{\cdot}s^{-1}$, 0.54 $m{\cdot}s^{-1}$)) in the HC4 treatments than in the HC1 treatments. However, there was no evidence for a difference in AGS between HC2 and HC1, or between HC3 and HC1 (p-value = 0.78 and p-value = 0.46). The mean AGS excluding the effects induced by temperature treatments were as follows; HC1 = 0.31 $m{\cdot}s^{-1}$, HC2 = 0.30 $m{\cdot}s^{-1}$, HC3 = 0.35 $m{\cdot}s^{-1}$, and HC4 = 0.43 $m{\cdot}s^{-1}$. Therefore, YCT experienced no significant difference in AGS through the first three HCs, but HC4 as well as the two temperature treatments caused significant statistical differences. Metrics for mean AGS, standard deviations, and ranges for each treatment combination can be viewed in Table 3.3. The low R^2 value reported above indicates that this model does not fit the data closely, therefore predicting AGS with this model may not produce accurate results.

Table 3.4: Coefficients for the reduced first best attempt (FBA) average ground speed linear regression model during YCT passage testing in the experimental flume.

	Coefficients	Standard Error	P-value	Lower 95%	Upper 95%
Intercept	0.252	0.037	< 0.0001	0.18	0.33
HC2	-0.013	0.047	0.7759	-0.11	0.08
HC3	0.035	0.048	0.4574	-0.06	0.13
HC4	0.116	0.049	0.0185	0.02	0.21
Temp12	0.117	0.033	0.0006	0.05	0.18

Water velocity and temperature treatments influenced ASS. A linear regression was used to test if the covariant total length, HC, and temperature treatments significantly predicted ASS for YCT. Total length had no statistical significance when predicting ASS, therefore the linear regression model was reduced to (ASS ~ HC + Temperature) ($R^2 = 0.91$). The coefficients used in this model are reported in Table 3.5. There was very strong evidence for a difference in ASS between the 8°C and 12°C treatments (p-value = 0.0003) with ASS estimated to be 0.124 $m{\cdot}s^{-1}$ faster (95% Confidence Interval (CI) = (0.06 $m{\cdot}s^{-1}$, 0.19 $m{\cdot}s^{-1}$)) in the 12°C treatments than the 8°C treatments. There was also very strong evidence for differences in ASS among all HC's (p-value < 0.0001; Table 3.4). The mean ASS increased as the water velocity in HC's increased; HC1 was 0.94 $m{\cdot}s^{-1}$, HC2 was 1.24 $m{\cdot}s^{-1}$, HC3 was 2.18 $m{\cdot}s^{-1}$, and HC4 was 2.46 $m{\cdot}s^{-1}$. Metrics for mean ASS, standard deviations, and ranges for each treatment combination can be viewed in Table 3.3.

Table 3.5: Coefficients for the reduced first best attempt (FBA) average swim speed linear regression model during YCT passage testing in the experimental flume.

	Coefficients	Standard Error	P-value	Lower 95%	Upper 95%
Intercept	0.876	0.038	< 0.0001	0.80	0.95
HC2	0.304	0.047	< 0.0001	0.21	0.40
HC3	1.246	0.048	< 0.0001	1.15	1.34
HC4	1.520	0.049	< 0.0001	1.42	1.62
Temp12	0.124	0.034	0.0003	0.06	0.19

FBA Maximum Swimming Metrics

Maximum swimming metrics calculated for a fish's FBA included mean maximum ground speed (MGS) and mean maximum swimming speed (MSS). These metrics can only be calculated between PIT antennas and are therefore average swimming velocities over a 4.88 m length of flume (e.g. between A1 and A2). The data for MGS and MSS met the assumptions for Welch's One-way ANOVA test, and both produced p-value < 0.05 indicating evidence to reject the null hypothesis that all treatment means were equal. Therefore, linear regression for both MGS and MSS was conducted.

Table 3.6: Summary of first best attempt (FBA) maximum swimming metrics for the eight hydraulic challenges (HC) and temperature (T (°C)) treatment combinations during YCT passage testing in the experimental flume.

HC	T (°C)	Mean Total Length (mm)	FBA Max Ground Speed ($m \cdot s^{-1}$)	MGS Range ($m \cdot s^{-1}$)	FBA Max Swim Speed ($m \cdot s^{-1}$)	MSS Range ($m \cdot s^{-1}$)	Max Trial Swim Speed on FBA (%)
1	8.12	392 ± 19.7	0.37 ± 0.26	(0.06, 0.79)	1.04 ± 0.20	(0.81, 1.41)	37.3
	11.87	383 ± 25.6	0.53 ± 0.31	(0.06, 1.08)	1.21 ± 0.29	(0.81, 1.84)	19.0
2	8.92	389 ± 26.5	0.34 ± 0.27	(0.10, 0.99)	1.37 ± 0.26	(1.04, 2.02)	19.0
	12.15	378 ± 23.0	0.46 ± 0.37	(0.06, 1.47)	1.44 ± 0.33	(1.04, 2.33)	25.4
3	8.48	373 ± 27.1	0.47 ± 0.23	(0.08, 0.99)	2.34 ± 0.22	(1.96, 2.80)	38.9
	11.92	375 ± 33.0	0.55 ± 0.30	(0.16, 1.38)	2.42 ± 0.29	(1.98, 3.19)	28.6
4	8.73	374 ± 33.2	0.53 ± 0.57	(0.01, 2.30)	2.53 ± 0.54	(2.09, 4.27)	50.0
	12.15	385 ± 25.8	0.69 ± 0.27	(0.28, 1.47)	2.71 ± 0.27	(2.35, 3.44)	35.6

Note: Mean total length, FBA maximum ground speed (MGS), and FBA maximum swim speed (MSS) are presented as mean ± 1 standard deviation. Range metrics are reported as (overall minimum, overall maximum) observed for a specific treatment combination.

Table 3.7: Coefficients for the reduced first best attempt (FBA) maximum ground speed linear regression model during YCT passage testing in the experimental flume.

	Coefficients	Standard Error	P-value	Lower 95%	Upper 95%
Intercept	0.384	0.059	< 0.0001	0.27	0.50
HC2	-0.050	0.073	0.4954	-0.19	0.09
HC3	0.057	0.074	0.4458	-0.09	0.20
HC4	0.160	0.077	0.0396	0.01	0.31
Temp12	0.131	0.053	0.0149	0.03	0.24

Table 3.8: Coefficients for the reduced first best attempt (FBA) maximum swim speed linear regression model during YCT passage testing in the experimental flume.

	Coefficients	Standard Error	P-value	Lower 95%	Upper 95%
Intercept	1.063	0.055	< 0.0001	0.95	1.17
HC2	0.279	0.068	< 0.0001	0.14	0.41
HC3	1.255	0.070	< 0.0001	1.12	1.39
HC4	1.498	0.072	< 0.0001	1.36	1.64
Temp12	0.123	0.050	0.0147	0.02	0.22

Linear regressions were performed for both MGS and MSS. The final reduced models for MGS were nearly identical to the regression models for AGS. The same trend was observed for the MSS and the ASS regression models. Additionally, each treatment combination induces the same effects on average and maximum swimming metrics for ground speed and swim speed respectively. The regression coefficients for MGS are reported in Table 3.7 and MSS are reported in Table 3.8. Maximum ground speeds revealed slight increases in velocities as water velocities increased (except during HC2, which resulted in a decreased MGS) and significant increases in MGS as temperature increased. Maximum swim speeds showed significant increases in velocities as both water velocities and temperature increased. Again, these were the same trends that the AGS and ASS linear regressions revealed. All maximum swimming metrics are reported in Table 3.6.

Video Data

The video data was qualitatively assessed to examine relations between treatment combinations (water velocity and temperature) and swimming mode as well as preferred swimming position in the water column. Temperature treatments had no significant effect on swim mode and swim position, each treatment combination for swim mode and position data can be viewed in Table 3.9 and Table 3.10. Water velocity influenced the upstream swim mode used to ascend the flume but had limited effects on downstream swim mode. When moving upstream, fish primarily used an S swim mode in HC1 (S = 0.376 proportion of the total fish observed in a trial). Fish transitioned to the utilization of P and BG swim modes when swimming upstream in HC2 (P = 0.433, BG = 0.398). During HC3 and HC4 B swim mode was used almost exclusively

(B = 0.785 at HC3, and B = 0.893 at HC4). When fish exhibited downstream movement, sustained, and prolonged swim modes were primarily observed among all hydraulic challenges.

Table 3.9: Proportion of swim mode utilization for upstream and downstream movement recorded by an overhead video camera for the eight hydraulic condition (HC) and temperature (T (°C)) treatment combinations during YCT passage testing in the experimental flume.

			Upstream Swimming Mode					Downstream Swimming Mode				
HC	T (°C)	Ave. No. of Fish	S	S/P	P	BG	B	S	S/P	P	BG	B
1	8.12	35.7	0.58	0.01	0.26	0.08	0.08	0.90	0.00	0.02	0.00	0.08
	11.87	139.0	0.18	0.00	0.52	0.26	0.04	0.95	0.00	0.04	0.00	0.01
2	8.92	79.3	0.02	0.00	0.30	0.47	0.21	0.94	0.01	0.05	0.01	0.00
	12.15	172.7	0.00	0.00	0.56	0.32	0.11	0.90	0.01	0.09	0.00	0.00
3	8.48	47.7	0.00	0.00	0.03	0.02	0.95	0.78	0.00	0.18	0.04	0.00
	11.92	32.3	0.00	0.00	0.00	0.38	0.62	0.48	0.00	0.48	0.05	0.00
4	8.73	42.0	0.00	0.00	0.00	0.00	1.00	0.66	0.00	0.34	0.00	0.00
	12.15	28.3	0.00	0.00	0.00	0.21	0.79	0.29	0.00	0.62	0.09	0.00

Note: Sustained (S), sustained/prolonged (S/P), prolonged (P), burst glide (BG), and burst (B).

Fish generally preferred to swim against the left wall, camera orientation was left to right facing downstream, throughout all HCs regardless of the direction of travel. However, as the oncoming water velocity increased, fish began utilizing the low velocity areas against the right wall, this trend began in HC3 and continued into HC4. Fish utilized a larger portion of the flume (L/M, M, R/M, and AO) when swimming upstream, but preferred to drift downstream along the walls rather than in the middle of the flume.

Table 3.10: Proportion of swim position utilization for upstream and downstream movement recorded by an overhead video camera for the eight hydraulic condition (HC) and temperature (T (°C)) treatment combinations during YCT passage testing in the experimental flume.

			Upstream Swim Position						Downstream Swim Position					
HC	T (°C)	Ave. No. of Fish	L	L/M	M	R/M	R	AO	L	L/M	M	R/M	R	AO
1	8.12	35.7	0.57	0.22	0.00	0.05	0.01	0.15	0.45	0.11	0.06	0.01	0.23	0.13
	11.87	139.0	0.51	0.09	0.01	0.02	0.23	0.16	0.50	0.09	0.04	0.07	0.17	0.13
2	8.92	79.3	0.59	0.19	0.03	0.01	0.03	0.16	0.65	0.03	0.03	0.02	0.21	0.06
	12.15	172.7	0.42	0.22	0.08	0.12	0.01	0.16	0.59	0.13	0.14	0.05	0.04	0.05
3	8.48	47.7	0.35	0.16	0.08	0.06	0.17	0.20	0.37	0.00	0.06	0.00	0.52	0.05
	11.92	32.3	0.41	0.04	0.00	0.09	0.25	0.21	0.53	0.02	0.04	0.00	0.36	0.05
4	8.73	42.0	0.40	0.05	0.03	0.02	0.47	0.03	0.31	0.08	0.02	0.00	0.46	0.13
	12.15	28.3	0.27	0.18	0.05	0.03	0.41	0.06	0.45	0.01	0.00	0.04	0.41	0.09

Note: Left (L), left/middle (L/M), middle (M), right/middle (R/M), right (R), and all over (AO).

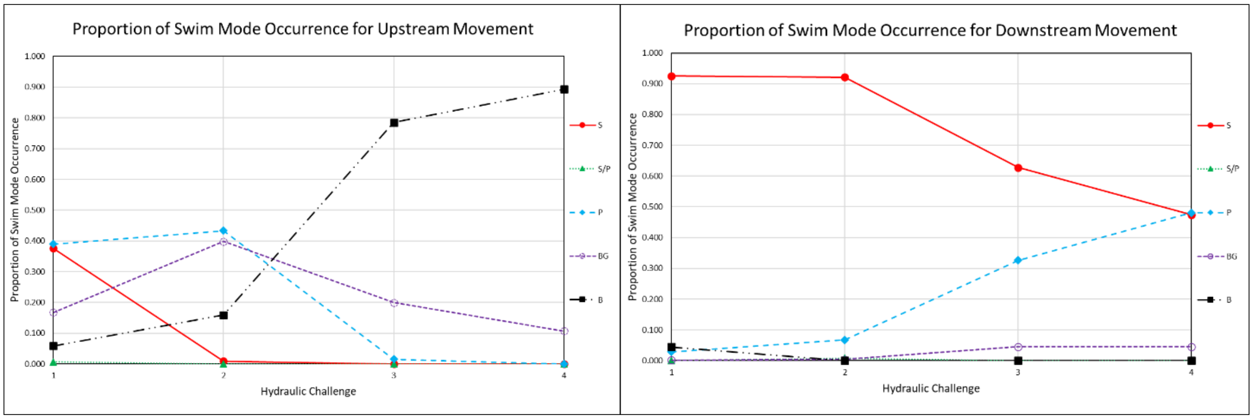

Figure 3.7: Proportion of swimming mode utilization for upstream and downstream movement. Swimming modes have been divided into five categories to quantify what type of swim mode fish select at different on coming water velocities in a rectangular open-channel flume. The categorical swim modes are defined as; S = sustained, S/P = mix of sustained and prolonged, P = prolonged, BG = burst glide, and B = strictly burst.

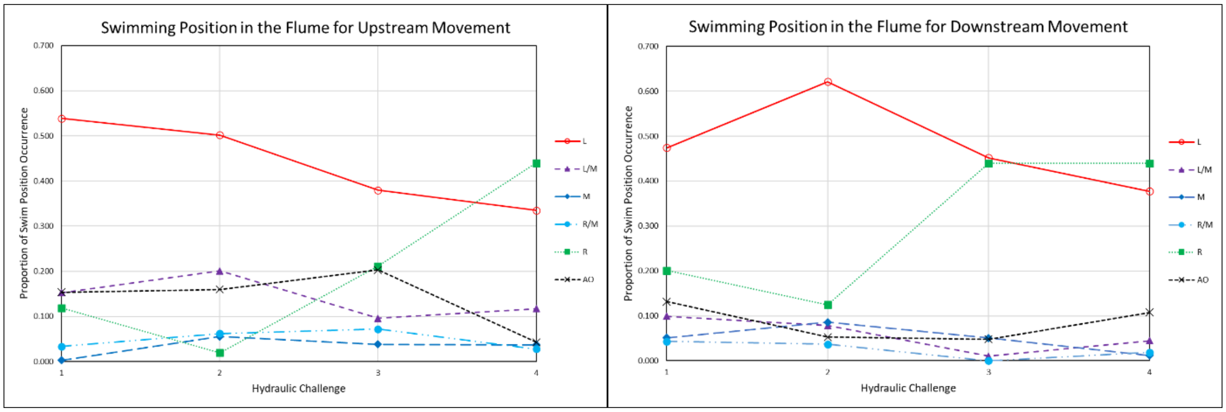

Figure 3.8: Proportion of position utilized for upstream and downstream movement. Swimming positions have been divided into six categories to quantify where fish prefer to swim in a rectangular open-channel flume. The categorical positions in the flume orientated left to right pointed downstream; L = left, L/M = left and middle, M = middle, R/M = right and middle, R = right, and AO = all over the flume cross-section.

Discussion

The goal of this study was to assess the swimming capabilities of YCT using an open-channel flume. Fishway geometries compared to a fish's swimming abilities and behavior ultimately determine the success of a fishway. Specifically, the length of a fishway and the water velocities it generates should not exceed a species' maximum endurance and swimming velocities (Dockery et al., 2017b). Furthermore, hydraulic features such as weirs, drops, bends, obstructions, and baffles, which are used to control water velocities in a fishway, should not impede upstream passage attempts (Castro-Santos, 2004; Dockery et al., 2017b; Peake, 2008a).

In this study, YCT voluntarily swam against four increasingly challenging hydraulic conditions under two temperature regimes (cold and warm) to determine the maximum distance of ascent and passage success. Additionally, the average and maximum swimming velocities associated with the FBA maximum distance of ascent at each treatment combination were calculated to identify potential barriers to migration. Video recordings were used to quantify the swimming behavior strategies employed by YCT when moving upstream and downstream.

Although our research studied the swimming abilities of hatchery raised YCT, it has been determined that healthy continuously exercised hatchery fish exhibit analogous swimming performance to their wild counterparts. This has been found in several studies several studies that examined wild and hatchery raised Arctic Grayling (Cahoon et al., 2018; Dockery et al., 2019; Plymesser et al., 2022; Triano et al., 2022). Therefore, the metrics reported in this study can be valuable for researchers, biologists, and engineers when improving fishway designs and evaluating YCT passage success in existing structures. The overall application of the metrics we report can be used to restore fragmented habitats and enhance longitudinal connectivity.

Maximum Distance of Ascent

The results of the open-channel swimming study showed that passage structures equal to or less than 17.26 m in length, with hydraulic conditions similar to those in our study, should not hinder the passage success of Yellowstone Cutthroat Trout (YCT) (total length: 292 mm to 450 mm) at temperatures between 8°C and 12°C, with mean water velocities less than 0.94 $m \cdot s^{-1}$. Passage success rates for HCs with water velocities equal to or less than 0.94 $m \cdot s^{-1}$ ranged from 76% to 100% of all trial participants. As water velocities increased in each hydraulic challenge, the overall D_{max} decreased. Multiple successful passage attempts were observed in all treatment combinations, leading to the conclusion that the hydraulic conditions tested in HC4 limited passage success but did not prevent it entirely. Therefore, to promote successful passage for YCT we suggest that within a structure sustained water velocities should be less than 0.94 $m \cdot s^{-1}$, water depths greater than 0.17 m, and less than 17.26 m in total length. This recommendation was based on our HC2 where passage success was 79%.

Culvert passage studies can provide valuable insights regarding the abilities of YCT in natural settings. A culvert passage study conducted by Solcz (2007) in a spawning tributary of the Yellowstone River, Montana, examined how existing culverts impacted the passage success of YCT. This study compared the measured passage success using a PIT tag system against the predicted "passability" produced by FishXing software. FishXing is public-domain software that uses 1-D hydraulic calculations to compare known fish swimming velocities to the estimated water depths and velocities within a culvert (Blank et al., 2005; Solcz, 2007). Factors contributing to a barrier becoming impassable for both FishXing and physical systems include excess leap height, insufficient water depth, water velocities exceeding fish swimming abilities, and required burst duration exceeding burst endurance time inducing exhaustion (Blank et al., 2005). Solcz (2007) reported that YCT with a mean total length of 341.5 mm had passage success of 90% through a 9.1 m long culverts and 78% through a 11.4 m long culvert. Mean water velocities were up to 2.8 $m \cdot s^{-1}$. This is a higher swimming performance than we saw in our trials which showed a D_{max} of 11.6 m at water velocities of 2.00 $m \cdot s^{-1}$ with a 19% passage rate, which suggests that YCT can achieve higher swimming performance than we saw in this study. In practical applications, such as passing a culvert, fish can utilize unsteady turbulent flow regimes to their advantage (Haro et al., 2004; J. Liao et al., 2003) Therefore, it is not uncommon to observe increased swimming performance in natural systems.

Another comparable culvert study was performed by Belford & Gould (1989) to evaluate the passage success of wild spawning YCT with total lengths of 224 to 426 mm. The two side-by-side culverts on Cedar Creek, a tributary to the Yellowstone River, in Montana, were 45 m long and 1.9 m in diameter, with a 4.4% slope. Before improvements to the culverts were made, no YCT were able to pass either culvert, but after rest sites (two large rocks placed at 15 and 30 m from the upstream inlet) were created, 8 YCT were able to ascend the culvert (Belford & Gould, 1989). Water velocities and flow rates within the culvert were not reported, but a minimum water depth of 4 cm created impassable conditions for YCT. The D_{max} for our study varied across treatment combination with the shortest D_{max} of 10.47 m in HC4-8°C and the longest D_{max} of 16.98 m in HC1-12°C. Based on the rest site spacing of 15 m and the resulting passage success reported by Belford and Gould (1989) it can be concluded that rest sites should be installed every 15 m or less to promote passage success for YCT.

Peterson et al. (2013) evaluated the passage success of wild Coastal Cutthroat Trout in a 12.2 m long experimental culvert test bed at water temperatures ranging from 9°C to 13.5°C. Passage success rates for Coastal Cutthroat Trout with median fork lengths of 114 mm (range: 85 to 207 mm) ranged from 86% to 31%, with corresponding water velocities of 0.6 to 2.4 $m{\cdot}s^{-1}$ and water depths of 0.12 to 0.28 m (Peterson et al., 2013). The passage success results reported by Peterson et al. (2013) for oncoming water velocity challenges, water depths, and distance of ascent are similar to the passage success results observed in our study. The passage success rate in our study was 97.5% in HC1 (water velocity 0.61 ± 0.13 $m{\cdot}s^{-1}$) and 19% in HC4 (water velocity 2.00 ± 0.09 $m{\cdot}s^{-1}$). Peterson et al. (2013) had a higher passage success rate at higher water velocities compared to our study. This could be caused by the difference in fish length and fish species as well as the difference in hydraulic conditions in a culvert compared to a smooth flume. Peterson et al. (2013) studied smaller fish than our study. It is generally accepted that swimming performance increases with fish length (Fry & Cox, 1970), but in some hydraulics conditions, smaller fish could potentially be better adapted to exploit small flow variations and micro vortices in a water column. This could result in higher D_{max} for smaller fish in fishways with reduced flow rates.

Finally, extrapolation of D_{max} metrics reported in this study is not recommended, as the hydraulic challenges tested in this study did not induce passage failure for all participants (censored data). Therefore, the true maximum distance of ascent in relation to varying oncoming water velocities is still unknown.

Attempt Rate

On average, YCT made more attempts against lower velocities (≤ 0.94 $m \cdot s^{-1}$) in HC1 and HC2 than against higher velocities (≥ 1.73 $m \cdot s^{-1}$) in HC3 and HC4. The reduced number of attempts observed during higher flow conditions could be attributed to the increased energy required to hold position and stage additional attempts. Castro-Santos et al. (2013) reported a similar trend of a reduced attempt rate as water velocities increased for Brown Trout. In another comparable study, Castro-Santos (2005) observed that most individuals achieve the greatest distance on their first attempt. Our study found that YCT achieved their maximum distance of ascent (D_{max}) on their first attempt approximately 52% of the time, which was slightly below the 65 to 95% rate that Castro-Santos (2005) observed for American Shad (*Alosa sapidissima*), Alewife (*Alosa pseudoharengus*), Blueback Herring (*Alosa aestivalis*), Striped Bass (*Morone saxatilis*), Walleye (*Sander vitreus*), and White Suckers (*Catostomus commersonii*).

Furthermore, YCT performed their FBA at a median time of 15:24 MST (directly after the start of a trial at 13:00 MST). The median FBA time of day was not affected by treatment combinations. Additional attempts that achieved D_{max} were concentrated in the morning (before a trial was ended at 09:00 MST). However, since this analysis focused on FBAs, these D_{max} attempts do not appear in Figure 6. However, several YCT did not achieve an FBA until the following morning. This delay could be caused by a lack of motivation or reduced fitness for a particular individual.

The FBA durations, the time it took a fish to reach its D_{max}, showed high variability across all treatment combinations. Median FBA durations ranged from 39.5 seconds to 502.8 seconds (see Table 3.2) and no trends were found between median FBA duration and HC or water temperature. The wide distribution of FBA durations is a result of some YCT holding position in the flume during their FBA which produced long durations, whereas YCT that maintained positive upstream movement produced shorter durations. Fish employ many different behavioral strategies when faced with a velocity barrier; therefore, fish swimming abilities are a measurement of behavioral motivation rather than explicitly physiological stamina (Haro et al., 2004).

Overall Maximum Sprinting Speeds

As of March 20th, 2024, no published studies have examined the swimming abilities of YCT in an open-channel flume. To validate the swimming metrics from our study, methodologies and metrics were compared to studies using other salmonid species. We observed a maximum swim speed of 4.59 $m \cdot s^{-1}$ for a YCT with a total length of 382 mm. This metric was faster than any previously reported swimming metrics for Cutthroat Trout. Blank et al. (2020) conducted a comparable study that evaluated the volitional swimming abilities of wild Westslope Cutthroat Trout in an open-channel flume. They reported a maximum swim speed of 3.55 $m \cdot s^{-1}$

(fork length (FL): 150 mm to 290 mm). Westslope Cutthroat Trout and YCT are subspecies of Cutthroat Trout, so it is unlikely that the difference in overall maximum swim speed is due to morphological differences and may be due to length differences. However, our linear regressions determined that total length variable had no effects on swimming velocities. Therefore, a broader range of fish lengths should be studied to determine how fish lengths affect swimming velocities.

Our results for overall maximum sprinting speed were significantly faster than other open-channel studies that evaluated maximum swim speeds for salmonids with similar morphologies to YCT. Blank et al. (2020) also reported that the maximum swim speeds of wild Rainbow Trout were 2.73 m·s^{-1} (FL: 150 to 305 mm). The sprint swimming speeds of both wild Brown Trout and wild Brook Trout (Brook Trout FL: 140 ± 27 mm, Brown Trout FL: 155 ± 34 mm) were > 25 body lengths per second (BL·s^{-1}) (Castro-Santos et al., 2013). In absolute terms, the sprint swimming speeds were 3.50 m·s^{-1} for Brook Trout and 3.88 m·s^{-1} for Brown Trout. Castro-Santos et al. (2013) also demonstrated that Brook Trout exhibit two distinct modes of sprint swimming and that it occurs at speeds > 2.66 m·s^{-1}. The velocity challenges examined by Castro-Santos et al. (2013) were at 1.6 and 2.5 m·s^{-1}, which were comparable to the HC velocities used in our study. Finally, Mesa et al. (2008) determined the sprint swimming speeds of Bull Trout (FL: 100 to 310 mm) ranged from 1.3 to 2.3 m·s^{-1}. This study used a similar methodology to our experiment, but coerced fish to swim rather than allowing volitional attempts. Mesa et al. (2008) also reported that these sprint swimming speeds were usually achieved within 0.8 to 1.0 seconds and were independent of fish size.

Swimming metrics can be categorized into sustained, prolonged, and burst swim modes, which relate fish energy exertion to swimming velocities (Beamish, 1978; Blake, 2004). Bell

(1991) reported sustained swim speeds of approximately 0.91 $m \cdot s^{-1}$, prolonged swim speeds of about 1.83 $m \cdot s^{-1}$ and burst swim speeds of around 4.12 $m \cdot s^{-1}$ for adult Cutthroat Trout. However, specific lengths, subspecies, and study procedures were not reported. These metrics describe the upper limit of each progressively more energy-expensive swim mode. The overall maximum sprinting speeds for YCT in our study (4.59 $m \cdot s^{-1}$) were comparable to the burst swim mode metrics provided by Bell (1991). Overall, the maximum sprinting speeds of YCT were significantly faster than the reported values for other maximum swimming performance open-channel salmonid studies. The metrics we report for overall maximum sprinting speeds describe the upper limits of YCT burst swimming abilities.

FBA Gait Transitions

The FBA average swimming speeds for each treatment combination, as provided in Table 3.3, can be anecdotally matched to the swim mode metrics that Bell (1991) reported. To evaluate the water velocities that caused gait transitions, we used the video data to quantify the swim mode YCT utilized in different HCs and compared that to the mean water velocities in each HC. Additionally, we matched the FBA ASS in the HCs that were estimated to cause gait transitions. This allowed us to predict the upper limits of each swim mode.

During HC1, the FBA ASS was 0.89 ± 0.15 $m \cdot s^{-1}$ for 8°C and 0.99 ± 0.21 $m \cdot s^{-1}$ for 12°C, and the majority of upstream swim mode utilization fell into the sustained and prolonged categories (0.376 sustained and 0.390 prolonged). We predicted that the upper limit for sustained swimming was 0.94 $m \cdot s^{-1}$ reported in terms of ASS. The data produced in HC1 of our study supports Bell's (1991) quantification of the maximum sustained swim mode velocity (0.91 $m \cdot s^{-1}$), as YCT appears to exhibit a gait transition when faced with oncoming water velocities of 0.61

$m \cdot s^{-1}$. The average swimming velocities for Westslope Cutthroat Trout reported by Blank et al. (2020) were 0.78 to 0.9 $m \cdot s^{-1}$, suggesting that the fish were utilizing a sustained swim mode. This conclusion can be justified as the water velocities tested ranged from 0.43 to 0.49 $m \cdot s^{-1}$, which was slower than HC1 in our study, inducing a gait transition from sustained to prolonged swim modes.

During HC2, the FBA average swim speed was 1.20 ± 0.15 $m \cdot s^{-1}$ for 8°C and 1.29 ± 0.25 $m \cdot s^{-1}$ for 12°C, and the majority of upstream swim mode utilization fell into the prolonged and burst glide category (0.433 prolonged and 0.398 burst glide). The video data suggests that YCT were exhibiting the next gait transition from a prolonged swim mode to an unsteady burst glide mode when water velocities reached 0.94 $m \cdot s^{-1}$. We predicted that the upper limit for prolonged swimming was 1.25 $m \cdot s^{-1}$ reported in terms of ASS. The FBA ASS was lower than the maximum prolonged swim mode velocity (1.83 $m \cdot s^{-1}$) that Bell (1991) reported. This suggests that YCT's maximum prolonged swim mode velocity could potentially be lower than previously reported by Bell (1991) based on our data. In contrast, Solcz (2007) reported that a YCT (total length: 380 mm) held position for 18.4 minutes in mean water velocity of 2.24 $m \cdot s^{-1}$. This is faster than any of the velocity challenges this study was able to examine, suggesting that either the prolonged swimming mode speed is faster than previously reported or that the fish was utilizing a low-velocity zone or some type of hydraulic condition to its advantage. Overall, it is challenging to quantify velocities that define swim modes in an open-channel flume because swim mode categorization directly relates to the activity levels of fish (Blake, 2004). Fish with different levels of fitness will therefore produce different metrics in each swim mode category.

The gait transition from a prolonged swim mode to a burst swim mode is defined as the point when respiration switches from aerobic to anaerobic (Beamish, 1978; Dockery et al., 2019; Peake, 2008b). Therefore, the maximum prolonged swim mode velocity is also the maximum aerobic capacity of an individual fish (Peake, 2008b). Maximum aerobic capacity is typically tested in a swim chamber or swim tunnel respirometer and uses a step endurance methodology to determine the highest sustainable velocity for a 5-to-10-minute interval, which is defined as the critical swimming velocity (U_{crit}) (Aedo et al., 2009; Brett, 1964; Peake, 2008b; Underwood et al., 2014).

Although the swimming abilities of YCT are relatively undefined in the literature, there has been one YCT U_{crit} study and several others for other subspecies of Cutthroat Trout. Seiler and Keeley (2007) performed a swim chamber study and reported the U_{crit} of YCT (total length: 78 to 98 mm) was 7.7 $BL \cdot s^{-1}$. In absolute terms, U_{crit} ranged from 0.6 to 0.75 $m \cdot s^{-1}$ for YCT tested in this study. Hawkins & Quinn (1996) also performed a swim chamber study to examine the U_{crit} of two hatchery stocks of Coastal Cutthroat Trout. U_{crit} values of 5.58 ± 0.15 $BL \cdot s^{-1}$ (total length: 89.6 ± 12.0 mm) for Shelton Cutthroat Trout and 6.69 ± 0.23 $BL \cdot s^{-1}$ (total length: 88.6 ± 7.7 mm) for Aberdeen Cutthroat Trout were reported. The converted U_{crit} values reported in absolute terms were approximately 0.50 $m \cdot s^{-1}$ for Shelton Cutthroat Trout and 0.59 $m \cdot s^{-1}$ for Aberdeen Cutthroat Trout. MacNutt et al. (2004) also studied Coastal Cutthroat Trout in a swim chamber and reported U_{crit} values of 1.23 $m \cdot s^{-1}$ for fish with fork lengths of 304 mm ±16 mm. Aedo et al. (2009) used a Blazka-type swim chamber, employing the same methodology as a U_{crit} study, to test the mean prolonged swim speed of Bonneville Cutthroat Trout and reported that fish (standard length ± standard error: 54.7 ± 1.26 mm) produced velocities of 0.39 $m \cdot s^{-1}$. All U_{crit}

values reported for Cutthroat Trout were below the maximum prolonged swim mode velocity (1.83 $m \cdot s^{-1}$) reported by Bell (1991), but the U_{crit} value (1.23 $m \cdot s^{-1}$) reported by MacNutt et al. (2004) was nearly identical to the maximum prolonged swim mode velocity we observed in the open-channel flume.

In HC3 and HC4, the FBA average swim speed was 2.19 $m \cdot s^{-1}$ for HC3 and 2.46 $m \cdot s^{-1}$ for HC4, and the majority of upstream swim mode utilization fell into the burst category (HC3: 0.785 burst, HC4: 0.893 burst). The video data indicated the majority of YCT utilized a strictly burst mode to overcome the 1.73 $m \cdot s^{-1}$ velocity. Therefore, we predict that water velocities less than 1.73 $m \cdot s^{-1}$ will induce a gait transition from burst glide to burst swim mode, and that the upper limit for a burst glide swim mode was less than 2.19 $m \cdot s^{-1}$ reported in terms of ASS.

Finally, we quantified the upper limit for YCTs burst swim mode with the overall maximum sprinting velocity which was 4.59 $m \cdot s^{-1}$. However, the FBA ASS that was observed in HC3 (2.19 $m \cdot s^{-1}$) and HC4 (2.46 $m \cdot s^{-1}$) when fish were using a burst swim mode was well below the maximum burst swim mode velocity (4.12 $m \cdot s^{-1}$) reported by Bell (1991). The large difference between burst velocities in HC3 and HC4 compared to our overall maximum sprinting speed lead us to believe that burst swimming can vary significantly. If a fish is attempting to ascend a long distance against a high velocity, such as a culvert, they will select a slower burst swimming velocity. In contrast if a fish is attempting to ascend a short distance at significantly higher water velocity, such as a weir, they will select a burst velocity at the upper limit of their physical capabilities. However, the duration this velocity can be sustained will dramatically decrease with increased effort. This suggests that the HCs in this study did not induce conditions that tested YCTs maximum physical swimming capabilities. Justifying the need for further investigation of their swimming abilities at higher velocities over shorter longitudinal distances.

Another study performed by Aedo et al. (2009) tested the mean burst velocity of Bonneville Cutthroat Trout (standard length ± standard error: 54.7 ± 1.26 mm) using simulated predator attack methodology. He reported a mean burst velocity of 1.21 $m{\cdot}s^{-1}$ which was significantly slower than the burst velocities observed in our study and the study by Bell (1991). Comparisons between swimming metrics are difficult to quantify as fish species, fish size, experimental apparatus, and experiment methodology vary throughout the published literature. Additionally, the study performed by Aedo et al. (2009) confirms the idea that swim chamber studies can underestimate swim speeds relative to open-channel studies (Dow, 1962; Haro et al., 2004).

FBA Ground Speeds

Throughout the published literature, the idea that fish will select a constant distance-maximizing speed to pass a velocity barrier is commonly discussed, yet it is rarely observed in open-channel swimming studies (Castro-Santos, 2005; Castro-Santos et al., 2013). Fish can maximize the distance of ascent and reduce energy costs by selecting a constant ground speed in relation to varying water velocities (Dockery et al., 2017b). Furthermore, a single constant swimming velocity metric is typically applied when designing fishways and evaluating passage success (Bell, 1991; Castro-Santos, 2006; Dockery et al., 2017b).

In our study, linear regressions for FBA average ground speed and FBA maximum ground speed determined there was no statistically significant difference in velocities in HC1, HC2, and HC3 (p-value > 0.4458). The FBA average and FBA maximum ground speeds in HC4 were significantly different ($p\text{-value} < 0.0396$) than FBA average and FBA maximum ground speeds in HC1. These results indicate that once water velocities exceed 1.77 $m \cdot s^{-1}$, YCT utilizes a significantly faster ground speed. Similar patterns were observed by Dockery et al. (2017b), Peake & Farrell (2004), and Castro-Santos (2005; et al. 2013) for Sauger (*Sander canadensis*), Smallmouth Bass (*Micropterus dolomieu*), American Shad, Alewife, Blueback Herring, Brook Trout (*Salvelinus fontinalis*), and Brown Trout (*Salmo trutta*) in flume experiments.

Additionally, FBA average ground speeds were compared to the FBA maximum ground speeds in each treatment combination to evaluate how ground speeds varied over the duration of an FBA. The differences between these metrics were small, mean difference in velocity was 0.15 $m \cdot s^{-1}$ (range: 0.03 to 0.41 $m \cdot s^{-1}$) for all treatment combinations. This result supports the idea that YCT utilizes a relatively constant ground speed when faced with a velocity challenge, even though previous studies have rejected this idea (Castro-Santos, 2005; Castro-Santos et al., 2013; Dockery et al., 2017b). To further investigate if YCT utilizes a constant distance-maximizing speed, a flume experiment that allows for relatively instantaneous variations in velocities would be required. These experiments could be used to evaluate if fish change their swimming speeds to maintain a constant ground speed.

Temperature

Two temperature treatments, 8°C and 12°C, were tested to evaluate their effects on YCT swimming abilities. Maximum distance of ascent was analyzed with log-rank tests for each HC, indicating that temperature had no significant statistical effect on mean D_{max} values (X^2 ranged from 0.0 to 1.0, $p\text{-value} \geq 0.3$, $df = 1$). However, temperature treatments had a statistically significant effect on all swimming metrics (ASS, AGS, MSS, and MGS). Linear regressions for the four-swimming metrics indicated that YCT tested in the 12°C treatments swam significantly faster compared to those in the 8°C treatments (p-value < 0.0149). Regression coefficients for each swim metric are displayed in Tables 4, 6, 8, and 9 for AGS, ASS, MGS, and MSS, respectively. The mortality rate decreased from ten fish (11.9% mortality) in the 8°C treatments to five fish (6.0% mortality) in the 12°C treatments. Additionally, four fish were found dead in the recovery tanks post-trial in the 8°C treatments, bringing the total mortality to 16.7%. The higher mortality rate in the 8°C treatments indicates that some YCT were forced to swim beyond their physical limits and could not recover. It should be noted that 19 fish from the 8°C trials were re-swum in the 12°C trials, which could have unintentionally induced a natural selection process resulting in a higher quantity of fit fish participating in the 12°C trials. Overall, YCT achieved higher swimming metrics in the 12°C trials compared to the 8°C trials. Dwyer & Kramer (1975) reported the scope for activity and active metabolism of cutthroat trout was greatest at 15°C. McMahon et al. (2008) reported a preferred temperature of 14.9°C for Westslope Cutthroat Trout. These thermal evaluations of Cutthroat Trout support our findings that YCT exhibit improved swimming capabilities at 12°C compared to 8°C, as 12°C is closer to their thermal optimum.

Video Data

The open-channel experimental flume used in this study was designed to simulate uniform flow, thus minimizing areas of low velocity. However, truly uniform flow is not achievable in a relatively short open-channel flume, resulting in variations in depths and velocities longitudinally. Figure 3.4 displays the hydraulic conditions for each HC. Additionally, velocities varied within the flume's cross-section, as shown in Figure 3.3, which displays the water velocity gradients for each HC. Despite researchers' best efforts to test homogeneous hydraulic conditions, fish were able to find and exploit areas of lower velocities. YCT were observed utilizing the low velocity regions (against the wall and on the bottom of the flume) on average 0.636 of the total proportion of observations when moving upstream and 0.782 when moving downstream during all treatment combinations. This result provides insight into the keen abilities of YCT to find and utilize low velocity regions, even when these areas are subtle.

Shifting Hydraulics

The PIT data and video camera recordings provided accurate metrics for assessing the swimming abilities of YCT in this study. All variables were controlled to evaluate the effects of different hydraulic conditions and water temperatures. However, one unforeseen variable could have affected the results for maximum distance of ascent and swim velocity metrics. If a fish swam to fatigue in a trial, it would eventually pin on the downstream metal grate, which prevented fish from escaping into the tailwater box. This caused changes in hydraulic conditions, as the impinged fish would create a blockage in flow by pinning perpendicular to the oncoming water, increasing water depth, and causing the hydraulic jump to move upstream.

A total of 15 fish became impinged in HC3 and HC4, with no trial having more than two fish impinge. The hydraulic test conditions for HC3 and HC4 were primarily supercritical flow, with hydraulic jumps near the downstream end of the flume at station 3.51 m for HC3 and at station 1.07 m for HC4. For example, in trial 9 (HC3, 8°C), two fish became impinged, causing the hydraulic jump to shift upstream into the camera's view frame around station 7.23 m. This resulted in a 3.72 m shift in the location of the hydraulic jump, changing the water velocities and depths that fish were subjected to.

Since the analysis primarily used data from a YCT's FBA, a hydraulic shift that occurred after all fish completed their FBAs would have minimal impact on swimming data. However, determining exactly when a hydraulic shift occurred was nearly impossible. For instance, in trial 9, the fish that impinged had its last PIT detection at 15:56:10, but the hydraulic jump was not observed in the camera's view frame until roughly 18:15:00, resulting in a 2 hour and 20-minute gap.

Overall, shifting hydraulic jumps potentially changed the hydraulic conditions for the FBAs of 23.8% of participants in HC3 and 76% of participants in HC4. It is recommended that changes in the flume geometry should be incorporated in future studies to eliminate shifting hydraulic jumps caused by impinging fish and ensure more consistent hydraulic conditions for accurate data collection.

Application to Ecohydraulics

In conclusion the swimming metrics derived from this study provide valuable information regarding the overall swimming abilities of YCT. These swimming metrics can be applied to ecohydraulic designs projects for YCT. Passage structures aim to provide longitudinal connectivity that adfluvial YCT require for successful reproduction, food searching, and temperature regulation. Design manuals provide general guidelines for the geometries and resulting hydraulic conditions for designing a fish passage structure, such as technical fish passes (D'Enno et al., 2002), close-to-nature types of fish passes (rock-ramps) (Mooney et al., 2007), and culvert fish passes (Barnard et al., 2013). Based on the design manual guidelines as well as other constraints such as geographic and river morphologies, a fishway type and geometry can be selected. The hydraulic conditions for a specific geometry should then be analyzed using physical or numerical model (Tonina & Jorde, 2013). These models are then used to assess theoretical fish passage success based on the swimming ability of all species in the ecosystem. Water velocities in a fishway should not exceed the maximum swimming speeds and durations of any fish species. Fishway designs should incorporate features such as, adequate resting areas before and after high velocity regions (D'Enno et al., 2002), fishway entrances positioned to facilitate attraction (Williams et al., 2012), minimized leaping heights in or out of the fishway (Blank et al., 2005), and sufficient water depths (fish should be completely submerged in the water column) throughout the length of the fishway. Theoretical models to evaluate fish passage provide engineers insights to the effectiveness of a design before it is constructed. Furthermore, in situ passage studies should be conducted after construction is completed to evaluate the effectiveness of a design as fish swimming abilities in natural systems may vary significantly from metrics reported in laboratory studies (Castro-Santos, 2004; Castro-Santos et al., 2013; Dockery et al., 2017; Dow, 1962; Haro et al., 2004; Peake, 2008b, 2008a). Passage studies can also be used to validate and improve design metrics.

This study has focused on providing swimming metrics for YCT to promote longitudinal connectivity via fishway designs. However, in some cases the best management strategy for preserving and protecting genetically pure populations of YCT is to isolate them above a barrier. For example, YCT and Rainbow Trout exhibit very similar swimming and leaping abilities and therefore hydraulic structures cannot be designed to pass only YCT while excluding Rainbow Trout. This has led to the design and installation of fish migration barriers. In Montana, the design criteria for barriers requires a 1.07 m weir drop onto a 4.88 m long apron (16H:1V slop) which created shallow supercritical flow and a 0.31 m drop from the apron to the maximum design tailwater elevation. Additionally, the structure should be designed to exclude fish passage up to the 50-year flow and structurally withstand a 100-year flow event (Austiguy & White, 2014).

Future studies aimed at improving our understanding of fish swimming abilities, particularly for species like the YCT, could benefit from several approaches. First, there is a need for more volitional open-channel swimming studies, as such studies provide a more natural setting for fish to exhibit their swimming behaviors compared to enclosed swim chambers. Second, researchers could focus on standardizing methodologies across studies to ensure that swimming metrics are comparable between different studies and species. This standardization could include consistent reporting of swim modes (sustained, prolonged, burst), swimming velocities (U_{crit}, U_{sprint}), and experimental conditions (water temperature, fish size). Third, incorporating advanced technologies like underwater video analysis and telemetry systems could provide more detailed and accurate data on fish swimming behaviors and performance. Finally, future studies could explore the effects of environmental factors such as water temperature, flow velocity, and habitat structure on fish swimming abilities, as these factors can significantly influence fish passage success in rivers and streams. By addressing these areas, future research can contribute a more robust understanding of fish swimming abilities and inform the design of more effective passage structures.

Overall, we recommend that sustained water velocities in a fishway should not exceed $0.94\ m{\cdot}s^{-1}$ for YCT. This is the water velocity that we predicted that YCT perform a gait transition from a prolonged to a burst glide swim mode. This transition is also commonly defined as the point when fish switch from aerobic to anaerobic respiration and results in a significant decrease in swimming duration. Additionally, local velocities maximums should not exceed 1.73 m·s^{-1} and should be less than 6.90 m in longitudinal length. We have recommended metrics that significantly underestimate the findings in our study to ensure passage success for a wide range of fish sizes, life stages, and physical conditions.

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CHAPTER FOUR

CONCLUSION

Yellowstone Cutthroat Trout (Oncorhynchus clarkii bouvieri; YCT) inhabit the upper portions of the Yellowstone and Snake River basins of Montana, Wyoming, and Idaho. They are an important native species, but their populations have been significantly impacted by anthropogenic activities, leading to declines in their historic range and core population abundance. To aid in YCT restoration and conservation efforts, we conducted comprehensive studies on their swimming performance.

The open-channel flume study revealed important information about YCT's swimming behavior in response to varying water velocities and temperatures. We found that passage success decreased with increasing water velocities, ranging from 98% at 0.61 $m \cdot s^{-1}$ to 19% at 2.00 $m \cdot s^{-1}$. The overall maximum sprinting velocity was 4.59 $m \cdot s^{-1}$, mean maximum swimming velocity was 2.15 $m \cdot s^{-1}$, and gait transitions for sustained, prolonged, burst glide, and burst swim modes were observed at specific water velocities. Multiple linear regression showed that body size had no significant effect on swimming speeds, but the 12°C treatments produced significantly higher swimming speeds (p-value < 0.015) than the 8°C treatments. Gait transitions from sustained to prolonged occurred at water velocities of 0.61 $m \cdot s^{-1}$, from prolonged to unsteady burst glide at 0.94 $m \cdot s^{-1}$, and from unsteady burst glide to steady burst at 1.73 $m \cdot s^{-1}$. Kaplan-Meier survival curves and log-rank tests showed that temperature treatments had no significant effect on passage success or maximum distance of ascent (X^2 ranged from 0.0 to 1.0, p-value ≥ 0.3, degrees of freedom = 1).

Additionally, our study on the U_{sprint} swimming mode of YCT using a swim chamber provided further insights into their maximum anaerobic sprinting velocity and gait transitions. The mean U_{sprint} relative swimming speed was 3.91 body $lengths \cdot s^{-1}$ (standard deviation (SD) ± 0.56), equivalent to a swimming velocity of 1.48 $m \cdot s^{-1}$ (SD ± 0.18), with velocities ranging from 0.86 $m \cdot s^{-1}$ to 1.85 $m \cdot s^{-1}$ for YCT with total lengths of 314 mm to 456 mm. Gait transitions were observed from sustained-prolonged to burst-glide swim mode at a mean water velocity of 0.88 $m \cdot s^{-1}$ (SD ± 0.15) and from burst-glide to strictly burst at 1.13 $m \cdot s^{-1}$ (SD ± 0.18).

These comprehensive findings provide valuable information for assessing passage success probability and guiding the design of fish passage structures, which are essential for the restoration and conservation of YCT populations in the Yellowstone and Snake River basins. By understanding how YCT respond to different flow conditions and temperatures, we can better protect and restore their habitats, ensuring the long-term viability of YCT populations.

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APPENDIX

SUMMARY OF SWIMMING TRIALS FROM THE OPEN-CHANNEL FLUME STUDY

Table 3.11: Summary table of all swimming trials.

Treatment Combination	Trial	Water Temp (°C)	Mean Fish Total Length (mm)	Mean Fish Weight (g)	N	Participation Rate	Passage Rate	Ave. # of Attempts	Mean FBA	Median FBA Time of Day (hr)	Standard Deviation of FBA Time (hr)	Mean FBA Duration (sec)
1	3	8.2	381 ± 13.11	564 ± 86.22	7.00	1.00	1.00	13.57	3.14	9	3.4	146.84 ± 102.62
	7	8.0	395 ± 24.45	637 ± 123.02	7.00	1.00	1.00	8.00	2.00	2	3.3	162.06 ± 130.80
	11	8.2	400 ± 17.49	605 ± 83.85	7.00	1.00	0.86	14.43	3.86	6	4.2	219.99 ± 163.13
2	1	8.7	382 ± 21.88	600 ± 142.79	7.00	1.00	1.00	18.00	2.14	3	3.2	85.21 ± 35.00
	5	8.8	390 ± 38.84	609 ± 195.62	7.00	1.00	0.71	17.14	2.14	4	1.2	82.39 ± 24.93
	13	9.4	395 ± 15.43	605 ± 96.95	7.00	1.00	0.57	28.71	3.71	3	3.6	91.56 ± 34.64
3	4	8.2	363 ± 24.18	487 ± 96.32	7.00	1.00	0.00	8.57	1.57	3	1.3	140.87 ± 134.89
	9	8.9	380 ± 16.12	574 ± 71.67	7.00	1.00	0.57	10.00	3.86	5	6.3	1736.15 ± 2556.47
	12	8.5	375 ± 37.97	599 ± 187.49	7.00	1.00	0.43	9.43	2.57	3	5.2	2334.49 ± 3711.08
4	2	8.5	382 ± 25.65	585 ± 104.46	6.00	0.86	0.33	11.83	6.33	6	6.2	89.95 ± 83.93
	8	8.9	390 ± 24.63	646 ± 156.54	6.00	0.86	0.33	13.50	6.40	5	7.3	1012.86 ± 1546.98
	10	8.9	350 ± 37.48	448 ± 127.66	6.00	0.86	0.00	4.50	1.17	3	6.2	1381.01 ± 2749.85
5	16	12.0	380 ± 27.62	573 ± 119.67	7.00	1.00	1.00	34.00	1.29	1	0.0	351.07 ± 575.74
	18	12.1	380 ± 30.64	578 ± 163.82	7.00	1.00	1.00	18.57	1.29	1	3.9	158.02 ± 135.16
	23	11.6	388 ± 20.86	613 ± 95.94	7.00	1.00	1.00	20.43	1.57	1	4.1	94.93 ± 117.81
6	17	12.5	368 ± 13.90	513 ± 71.63	7.00	1.00	0.86	18.71	2.57	1	1.7	570.23 ± 800.60
	20	12.2	393 ± 29.63	607 ± 184.70	7.00	1.00	0.57	38.14	1.71	1	1.5	238.33 ± 460.88
	24	11.9	373 ± 17.23	520 ± 79.66	7.00	1.00	1.00	35.57	2.43	1	1.5	151.92 ± 247.04
7	15	12.0	388 ± 29.42	571 ± 105.26	7.00	1.00	0.29	15.71	1.14	2	2.9	26.87 ± 10.35
	21	12.3	370 ± 30.48	494 ± 136.57	7.00	1.00	0.14	17.71	4.57	3	6.7	75.09 ± 64.87
	22	11.5	368 ± 39.72	500 ± 145.81	7.00	1.00	0.43	9.14	1.43	1	0.4	296.05 ± 697.30
8	14	12.3	387 ± 31.91	581 ± 154.39	7.00	1.00	0.29	8.86	3.43	3	2.6	217.53 ± 193.22
	19	12.4	384 ± 28.24	562 ± 108.10	7.00	1.00	0.00	8.14	2.86	5	5.7	438.29 ± 1016.41
	25	11.8	384 ± 16.23	609 ± 133.66	5.00	0.71	0.20	9.20	1.60	4	2.3	37.87 ± 31.07