THESIS

ASSESSING THE SWIMMING AND JUMPING PERFORMANCE OF WYOMING FISHES WITH IMPLICATIONS FOR FISHWAY DESIGN

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ABSTRACT

ASSESSING THE SWIMMING AND JUMPING PERFORMANCE OF WYOMING FISHES WITH IMPLICATIONS FOR FISHWAY DESIGN

To successfully begin to solve the complex problems facing native fish conservation efforts, we need to seek a deeper understanding of the fish that inhabit the communities that we hope to conserve. With regards to the issue facing the fragmentation of our lotic ecosystems, and the effects that dams and similar structures can have on fish communities, fishways are a common tool used to restore the connectivity of streams by allowing the uninhibited passage of fish. In these experiments we studied the swimming and jumping abilities of Hornyhead Chub (Nocomis biguttatus), Bigmouth Shiner (Notropis dorsalis), Iowa Darter (Etheostoma exile), and Brook Stickleback (Culaea inconstans) in order to provide fisheries managers with criteria for fishway design that will allow the passage of desirable target species, and potentially block the spread of invasive Brook Stickleback. We did this by testing the jumping abilities of each species at various temperatures using artificial waterfalls. After testing groups of fish at various waterfall heights, we used logistic regression to predict the probability of individual fish passage under various conditions. To test the swimming ability of each species, we used swim tunnels to determine the maximum swimming velocity of each species, and estimate their endurance at various swimming velocities.

Our results show that a vertical barrier greater than 15 cm will block the upstream movement of nearly all individual Hornyhead Chub. Heights greater than 8.4 cm will block the upstream passage of Bigmouth Shiner, and barriers taller than 6.0 cm will block the upstream passage of Iowa Darter and Brook Stickleback. Given this information, if vertical drops and pool designs were to be incorporated into fishways designed for these species, drops between fishway pools should remain within these thresholds

if successful passage is to be achieved. The results of the swimming performance experiments show that each species' swimming abilities are unique relative to their raw maximum swimming abilities and overall endurance.

The problem facing engineers and biologists is that many different species that make up these communities are unique, and have characteristics that pose specific challenges or advantages to assisting their movements. Additionally, fisheries scientists must remain cognizant that fishways that allow native fish movement will likely allow the movement of non-target species (including potential invasives) present in the same systems. Managers must balance the trade-offs between restoring native ecosystems and protecting areas that have not been invaded.

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Introduction

Humans have been modifying aquatic ecosystems throughout recorded history for numerous reasons. With a growing global population, modifications of riverine systems for human use have also been expanding. More than half of the world's rivers have been fragmented by anthropogenic activities, and in the United States nearly 85% of all streams are impacted by habitat fragmentation (Wilde and Urbanczyk 2013). One of the most common ways that humans have modified lotic ecosystems is through the construction of water impoundment structures used to divert or store water (Poff et al. 1997; Falke and Gido 2006; Wilde and Urbanczyk 2013; Haworth et al. 2020).

The documented effects that dams and other vertical barriers have created for migrating fish date back hundreds of years in North America. This loss of connectivity across the landscape has contributed to the declines of numerous North American fishes, including many in the Great Plains (Wilde and Urbanczyk 2013). Many fish species native to these ecosystems have evolved life history strategies that exploit different habitat types, and thus require them to move across the landscape (Schlosser and Angermeier 1995). These strategies can include seasonal reproductive migrations when individuals can travel hundreds of kilometers. Other strategies include frequent movement to seek optimal foraging habitat or refuge from stochastic disturbances. Due to these requirements, maintaining longitudinal connectivity of riverine systems for fish movement is critical for the conservation of native fish communities (Fausch and Bestgen 1997). In addition to aiding the movement of native species, inhibiting the movement of invasive species can often be a desired goal of fisheries management. This can be accomplished in a number of ways, such as maintaining vertical barriers like waterfalls and weir structures in areas where invasive species are present downstream.

The existence of dams within a specific system can have impacts beyond the restriction of movement; there can also be population-level effects. The overabundance of dams and similar structures in certain areas can create a scenario where individual river fragment lengths are too short for juvenile fish to hatch from pelagic or semi-pelagic eggs and replenish upstream populations (Wilde and Urbanczyk 2013). These individuals will drift over dams as eggs and larvae, and eventually become trapped downstream of their source populations. This can leave upstream populations imperiled to further decline due to lack of recruitment (Wilde and Urbanczyk 2013). Additionally, dams that fragment longitudinal connectivity could prevent upstream recolonization by many fish species that have adapted to intermittent flow conditions (Fausch and Bestgen 1997).

Fish Passage Structures

Smaller instream structures such as low head dams, structures with a vertical height less than one meter, can still severely impact successful fish movement (Ficke et al. 2011). Past research has shown that an 0.6 m high vertical barrier impeded the upstream movement of many small-bodied fishes, and an 0.1 m high barrier can severely impact the movement of Common Shiner *Luxilus cornutus*, Brassy Minnow *Hybognathus hankinsoni*, and Arkansas Darter *Etheostoma cragini* (Ficke and Myrick 2009; Ficke 2015). Fisheries scientists must work diligently to devise creative, practical solutions to reduce instream fragmentation while retaining the positive benefits of potential barriers to migration. This is especially important if we are to successfully conserve native fish species in the future, where increased demands on aquatic resources are destined to continue.

Fish passage structures, also called fishways, are a possible solution to stream-wide diversions and other barriers to fish movement. Depending on site characteristics and specific stream hydrology, managers can either modify existing instream structures or build completely new structures that allow fish to overcome barriers to fish movement. These structures come in a variety of different designs, featuring different strategies for allowing fish to negotiate the instream obstructions. One of the most well-known types of fishway is the pool and weir structure, which features a series of pools arranged like a small staircase built into the side of a vertical obstacle (Clay 1995). Such fishways were implemented mostly for species that attempt to jump over instream obstacles, such as most salmonids. Fishways that do not force fish to jump, but rather allow them to swim up a specially designed ramp or passageway, are often favored when dealing with fish species that have poor jumping performance or that do not attempt to jump over instream obstacles.

Two popular types of fishways that fall into this latter category are the vertical slot and rock ramp fishways. Vertical slot fishways are a more conventional design featuring a step-like series of connected pools similar to weir type fishways, except fish are not forced to jump between successive steps (Hameed and Hilo 2021). The main current flows down the center of the structure, but each “step” contains velocity refugia on each side of the thalweg that fish can use to rest. The fish is allowed to dart through the opening of each step, gaining vertical height with each pool that fish can access until they reach the top of the structure. Rock ramp fishways are a type of fish passage structure sometimes referred to as nature-like fishways (Richer et al. 2020). These structures simulate more natural conditions and are useful in areas where native fish communities contain small-bodied fishes that require significant assistance to overcome vertical dams and diversion structures (Richer et al. 2020). Rock ramp fishways are typically constructed as a low-gradient ramp structure, commonly embedded with small to medium stones along the surface of the ramp to provide refuge from high water velocities that allow fish to “rest” while ascending the structure. Fish are not required to jump in this type of structure and are only limited by sufficient water depth and water velocity thresholds.

Due to the wide range of swimming and jumping abilities of small-bodied native fishes, it is critical that managers and engineers design fish passage structures thoughtfully, so that target species have the best chance of successfully utilizing them. An ideal fish passage structure not only allows passage of the strongest swimming species, but also facilitate passage of species that might not be the most powerful swimmers and jumpers (Ficke et al. 2011). To achieve this objective, we must understand the way native fishes face and attempt to overcome the challenges posed by vertical barriers.

Quantifying the swimming and jumping performance of fishes that could use the fishways is important because it allows us to develop standards for structure design.

In this study, I evaluated the jumping and swimming performance of four different fish species to predict what conditions might present barriers to upstream fish passage, and to inform fish passage structure design criteria. The target species of this study are Hornyhead Chub *Nocomis biguttatus*, Bigmouth Shiner *Notropis dorsalis*, Iowa Darter *Etheostoma exile*, and Brook Stickleback *Culaea inconstans*. Brook Stickleback are an invasive species in parts of Colorado and Wyoming. The other three species are the focus of this study and are species of conservation need (SGCN) in the state of Wyoming. Managers are eager to gain insight into successful strategies for designing structures that accommodate upstream movement for native fish species, and block movement of invasive species.

Materials and Methods

Study Species

The Hornyhead Chub is a small-bodied (commonly 100 – 150 mm TL, maximum TL 250 mm) North American cyprinid (Miller et al. 2015)Ideal habitat conditions include streams with low to moderate gradient containing a mix of riffle and pools with clean gravel substrate available for nest building (Hickerson and Walters 2019). Hornyhead Chub are considered a cool water species that spawn during spring-summer when water temperatures exceed 16°C (Hickerson and Walters 2019).

The historic native range of Hornyhead Chub extended across North America stretching east-west from New York to Wyoming, and southward to Arkansas (Echelle et al. 2014). Populations in the Platte drainages of Colorado and Wyoming once existed as disjunct populations and were glacial relics existing from Pleistocene refugia (Miller et al. 2015). Populations in Colorado have since been extirpated, and the Wyoming distribution is limited to only the Laramie and Sweetwater River watersheds (Miller et al. 2015; Hickerson and Walters 2019; Whitney et al. 2020). There have been studies assessing the swimming endurance of Hornyhead Chub at high velocity, and it was reported that Hornyhead Chub could swim for nearly one minute at 67 cm/s (Billman and Pyron 2005).

The Iowa Darter is a small-bodied member of the family Percidae (Boczek and Johnson 2014). The historic native range of Iowa Darter in North America spreads west-east from the eastern Rocky Mountains across to New York, and northward into Canada. In Colorado and Wyoming, native populations exist in the Platte River drainages, but there are introduced populations west of the Continental Divide in Colorado (Walford and Bestgen 2008). Prior to this study, Iowa Darter had not been the subject of jumping experiments, but similar species such as Arkansas Darter had been tested (Ficke et al. 2011). This earlier study showed that Arkansas Darters have significant difficulty negotiating vertical barriers 5 cm high. Prior to this study, swimming experiments have been conducted to test the maximum sprinting ability of Iowa Darter, but no work has been conducted to assess their endurance at various water velocities. Past research has shown that Iowa Darter can sprint at velocities up to 72 cm/s (Ficke 2015).

The Bigmouth Shiner is a small-bodied (60-75 mm TL) Cyprinid native to North America. This species inhabits small prairie streams with continuous annual flows and clean sandy substrate (Tompkins. 1987). Prior to my study, there has been little research regarding the swimming or jumping abilities of this species. Some experiments have been conducted assessing the swimming performance of similar species such as Sand Shiner *Notropis stramineus*, and Topeka Shiner *N. topeka*. Past studies have shown that although many of these small-bodied cyprinids share similar maximum sprinting abilities, there is great variability in the swimming endurance of fishes in this family (Billman and Pyron 2005). Jumping performance experiments on Sand Shiner have indicated that they may struggle to overcome vertical barriers of only 3-4 cm high (Prenosil et al. 2016).

Brook Stickleback are a small-bodied fish in the family Gasterosteidae, with adult individuals reaching total lengths of 50-75 mm. Brook Stickleback have a vast native range, extending from the northeastern United States, across the Great Plains and north into Canada, continuing westward into small parts of eastern Wyoming and Colorado. Although research concerning the ecological impacts of this species has been undertaken, no experiments prior to my study have been conducted to date that test the jumping ability of this species (Wieker et al. 2016; Ruthven et al. 2023). There has been limited research into the maximum sprinting abilities of this species, which are reported to reach velocities of nearly 70 cm/s (Ficke 2015).

Fish Collections and Holding

Hornyhead Chub were collected from the Laramie River, Wyoming. Bigmouth Shiner were collected from populations from the Sweetwater River, Wyoming, and the South Platte River in Colorado. Since lotic populations of Iowa Darter are not easily collected in Colorado or Wyoming, I collected fish from Shadow Mountain Reservoir in Grand County, Colorado. Brook Stickleback were also difficult to collect from lotic sources, so I chose to collect fish from a small floodplain pond in Fort Collins, Colorado. Fish were transported in insulated coolers filled with aerated water to which NaCl (5 g/L) was added to reduce osmotic stress during transport to the CSU Foothills Fisheries Laboratory. Temperature was checked at least hourly during transport, and chlorine-free ice was added as needed to maintain constant temperatures during summer.

Upon arrival at the lab, fish were acclimated to seasonally appropriate temperatures determined by the collection site conditions. The fish were transitioned to a 14L:10D light cycle for the duration of the study. This photoperiod was chosen to maintain consistent conditions for all fish being tested throughout the duration of the study. Holding tank temperatures were maintained using computer-controlled solenoid mixing valves to regulate water supply temperatures within 1-2^{o}C of setpoints. In preparation for testing, fish were segregated by species and temperature treatment into separate holding tanks. Afterwards, the temperature of their holding tanks was changed by 1°C/d until their target temperatures were reached for testing. For all experiments, each species group was divided evenly into three water temperature treatments for testing; 10°, 17.5°, and 25°C. Fish were allowed at least one week to acclimate to testing temperatures before the start of trials. All tanks were cleaned daily, and the direction of water flow was reversed weekly. To reduce stress and encourage natural behavior, cover in the form of artificial plastic vegetation, and variable PVC structures was provided inside the tanks. Fish were fed once daily to satiation with either frozen HIKARI^{tm} and San Fransisco Bay^{tm} brand frozen bloodworms, and San Fransisco Bay brand frozen brine shrimp. Aqueon^{tm} flake feeds added were also supplemented during feedings if fish were reluctant to eat frozen feeds upon arrival to the lab.

Fish Tagging

Each fish was implanted with a passive integrated transponder (PIT) tag for individual identification during jumping experiments, and general tracking throughout the entire study. Hornyhead

Chub received 9 mm x 2.1 mm full duplex tags (FDX), due to their slightly larger body size, and for use in later experiments that required optimal tag read ranges. Tags larger than 9 mm were not used for Hornyhead Chub to ensure that the adjustable read ranges of RFID antennas used for jumping experiments could be easily configured to ensure consistent levels of detection for all species. Iowa Darters, Bigmouth Shiners, and Brook Sticklebacks were tagged with 8.4 mm x 1.4 mm FDX-B tags. Although previous studies have shown similar species can be successfully tagged with larger tags, we chose 8-mm tags to maximize tag retention and survival of individuals and to minimize the chance of impacting fish swimming performance (Bangs et al. 2013; Pennock 2017). Feed was withheld from fish 24 hours prior to tagging. During the tagging procedure, fish were anesthetized using 50-75 mg/l buffered MS-222 solution. After the fish lost equilibrium, they were removed from the anesthetic bath, weighed and measured (TL, in mm). A small 2-mm incision was made using a scalpel just above the vent or pelvic fins, and slightly off the midline of the fish. The tag was inserted into the body cavity through the incision and gently pushed anteriorly (Schumann et al. 2020; Swarr et al. 2022). After tagging, fish were returned to holding tanks for monitoring. Fish were monitored daily and given a minimum of 72 hours to recover before being used in swimming or jumping experiments. If implantation sites were irritated, or secondary infections occurred, fish were not tested until they were deemed healthy.

Jumping Performance Experiment

Jumping performance experiments were performed in three modified Kondratieff-type artificial waterfalls (as described in (Brandt et al. 2005; Kondratieff and Myrick 2006; Ficke et al. 2011). These devices consist of a two-chambered box that is filled with water, divided in the center by an adjustable-height weir. The weir is raised in specific increments to maintain a higher water level in the upper chamber, so that a simulated waterfall cascades down into the lower plunge pool chamber. Water (72 L/min) is pumped into the upper chamber from an external sump using two Danner MD-18 magnetic drive pumps, and then it flows back to the sump through drains in the lower chamber floor. The lower jumping chamber is approximately 60 cm wide x 48 cm long x 30 cm deep. An adjustable floor was installed in the lower jumping chamber to allow the water depth to be raised or lowered for testing the effects of different pool depth treatments.

In addition to filming all trials to confirm fish passage results with HD webcams, the waterfalls were outfitted with BioMark^{TM} small-scale PIT Tag antenna monitoring systems to record individual fish passage attempts in real time. Coupled with video information, this PIT tag monitoring system allowed me to monitor the activity of fish being tested at any time during the trial, especially when they were attempting to jump or swim over the vertical barrier. One antenna in each waterfall was placed behind the upstream face of the vertical weir, creating a limited tag detection field that recorded when fish breached the water surface in front of the waterfall. This antenna collected data on passage attempts and passage success. A second antenna was positioned horizontally in the upper chamber, located behind the entrance to the upper chamber. Every time a fish attempted to jump the waterfall, it was detected by the first antenna, and if successful, it was detected by the second antenna shortly after entering the upper chamber. We constructed three waterfall units, and the combined six total antennas were connected to a central Biomark^{TM} multiplex ASR650 reader with an attached Bluetooth BLE Data Logger to download and interpret tag data. We used the data from PIT tag antennas and video footage to confirm passage attempts and successful passage of fish during every trial.

At the start of each trial, fish were placed in the lower plunge pool of the waterfall apparatus and allowed to volitionally attempt to jump or swim over the vertical barrier. Due to their conservation status and limited number of Hornyhead Chub available for the project, one individual was used for each jumping trial. For the three remaining species, fish were tested in groups of three. This group size was chosen to balance time constraints, fish holding capabilities, and achieving ideal number of treatment combinations. Each trial group was given 20 hours to attempt to ascend the waterfall, (10 hours light, then 10 hours of dark) as used by (Brandt et al. 2005; Gardunio et al. 2014). The number and identity of individual fish that were successful in overcoming the barrier were recorded for each trial, along with data regarding passage attempts.

For each species, I planned to test each temperature group at four increasing levels of weir height, using increments based on the mean body length of the species being tested, and their relative jumping ability observed during pilot trials (Ficke et al. 2011). Because overall performance in the 10°C groups for each species was very poor at all heights tested, I only tested fish at three weir heights. A control group for each species with a weir height of 0 cm was also used to determine whether fish would swim freely between the chambers if the vertical barrier was removed. Trials for all species began at approximately one body length, equal to the mean total length of each species being tested (Tables 1, 2). If any fish accomplished successful passage in a particular temperature treatment, the height of the weir was increased by one increment and the process repeated until fish were unable to access the upper chamber (Ficke et al. 2011; Prenosil et al. 2016). After five unsuccessful trials at a given weir height and both pool depth treatments (10 trials total/weir height), this was considered the critical weir height for each species. Five additional trials at each pool depth (10 trials total/weir height), were conducted at an additional increased height increment to ensure that no fish could negotiate the barrier, and that the height identified was the maximum weir test height for each species at each water temperature. After identifying the critical weir height and maximum weir test heights, the remaining replicates at lower weir heights were randomly assigned to all fish for the remainder of the experiment. Novel fish were used for every jumping trial.

Swimming Performance Experiments

Fish swimming performance was assessed using two Loligo^{TM} Model 90 recirculating swimming tunnels. Individual fish are placed inside a fixed swimming chamber, and are forced to swim against a constant, directional current at a chosen water velocity. These swim tunnels were upgraded to allow accurate computer control of the water current velocities using Loligo^{TM} AutoResp software. A single HD webcam in front of each swimming chamber allowed the operator to remotely monitor and record observations during the trials. Two main types of tests were conducted to assess the swimming performance of each species, at the same three water temperatures used in the jumping performance trials. Anaerobic swimming performance was tested using constant acceleration trials, and aerobic swimming endurance was measured using fixed velocity trials (Leavy and Bonner 2009; Ficke et al. 2011; Gardunio et al. 2014; Swarr et al. 2022).

Constant Acceleration Trials

Constant acceleration trials were utilized to assess anaerobic swimming performance, and ultimately the maximum sprinting ability of the four fish species being tested, with the caveat that sprinting abilities within a confined flume can underestimate those of fish in a less-restricted setting (Castro-Santos et al. 2013). The information gathered from this type of trial is not only useful for making simple comparisons between species, but also for making suggestions on maximum fishway water velocities that these fishes can tolerate. Fish were given one hour to acclimate and become familiar with the swimming chamber with a 10 cm/s current present for rheotaxis. Pilot trials indicated that Iowa Darter, the species predicted to be the poorest performing swimmers of the group, could hold their position in the swimming chamber indefinitely at this acclimation velocity (>4.5 hours).

Once the trial began, the water velocity inside the swim tunnel was increased by 5 cm/s every ten seconds, until the fish was exhausted and became impinged on the rear screen of the swimming chamber for four seconds (Leavy and Bonner 2009; Swarr et al. 2022). The velocity at exhaustion was defined as the maximum exposure velocity (V_{max}) and was recorded in cm/s and body lengths/second, based upon measurement of the fish's total length.

Fixed Velocity Trials

Fixed velocity trials were used to assess each species' swimming abilities and allowed me to describe their "endurance" at a variety of swimming speeds. Swimming velocity treatments were based on the mean body size and relative maximum swimming abilities of each species observed during constant acceleration trials (Ficke et al. 2011). Once mean V_{max} were established for each species during constant acceleration trials, four swimming velocity treatments tested were chosen based on the maximum abilities of each species, the speeds at which they transitioned swimming gaits, and their relative body size. Bigmouth Shiner were tested at 36, 42, 48, and 60 cm/s for both the 10°C and 17.5°C treatments. Repeated trials in the 25°C treatment showed fish could continue swimming for 200 minutes at 36 cm/s, so test velocities were increased to 42, 48, 60, and 72 cm/s. Hornyhead Chub were tested at 24, 36, 48, and 60 cm/s for each temperature treatment. Iowa Darter swimming performance was tested using final water velocities of 20, 25, 30, and 35 cm/s. Iowa Darter were initially tested at 15 cm/s, but individuals at all temperatures were able to continue for longer than 200 minutes. Brook Stickleback were tested using trial velocities of 15, 20, 25, and 30 cm/s for all temperature treatments. I tested a minimum of 20 individuals at each water velocity for Bigmouth Shiner, Iowa Darter, and Brook Stickleback. Due to the limited availability of Hornyhead Chub, 10 individuals were tested at each water velocity per temperature treatment.

Methods for conducting fixed velocity trials were similar to constant acceleration trials except a single fixed velocity was used. Fish were placed in the swim tunnel for one hour to acclimate prior to testing while exposed to a constant velocity of 10 cm/s. The water velocity was then increased immediately to the test velocity randomly assigned to that trial. Once the fish became impinged on the rear screen of the swim chamber for greater than four seconds, the trial was stopped. The time that the fish was able to maintain swimming inside the chamber was recorded in minutes (time to exhaustion). If a fish could swim for greater than 200 minutes, the trial was ended (Ficke et al. 2011). Any fish that refused or were reluctant to swim for trials are classified as non-performers and were removed from the study. Because of limited available numbers of fish collected, and because overall participation was greater than 50% for nearly all treatment combinations, I did not replace non-performers with additional fish (Table 8). Novel fish were used for all swimming experimental trials.

Data Analysis: Jumping Performance

I used Generalized Linear Models (GLM) with an applied logistic function (family = "binomial") in Program R (version 4.3.2) to predict probabilities of successful individual fish passage for each species based on the approaches of Kondratieff and Myrick (2005) and Ficke et al. (2012). Waterfall height, plunge pool depth, and fish total length were included in each species' global additive model (Table 3). All predictor variables were treated as fixed effects. Model selection was completed using Akaike Information Criteria (AIC) using the MuMin package in Program R. Corrected AIC scores (AICc) were utilized to account for small sample sizes. None of the top candidate models included interactions between independent variables. I stratified my analysis for each species by their three discrete temperature treatments. Modeling each temperature group within each species individually significantly improved model predictions of maximum jumping performance and allowed for more accurate interpretation of the results.

Data Analysis: Swimming Performance

I used data from fixed velocity trials to conduct a survival analysis and estimate median time to exhaustion for each species at various swimming speeds (Peake et al. 1997; Ficke et al. 2011). I used the survival package (version 3.5-7) in program R (version 4.3.2) to conduct a survival analysis for Bigmouth Shiner, Hornyhead Chub, Iowa Darter, and Brook Stickleback using data from fixed velocity trials. A Cox proportional hazard model was fitted to data from each species individually. I then used the "Survfit" function in program R to fit survival curves and estimate median time to exhaustion for each species at specified treatment values. Water velocity, water temperature, and individual total length were included in the analyses as predictor variables. Predictor variables were considered significant at the ($p < 0.05$) level and included in the final model for each species.

I used the predicted median exhaustion values to create performance curves for each species that show the relative range of velocities where species exhibit prolonged and burst swimming capabilities (Peake et al. 1997; Ficke et al. 2011). Additionally, I used these data to create plots recommending combinations of maximum fishway velocity and length criteria that should allow the passage of Hornyhead Chub, Bigmouth Shiner, and Iowa Darter (Peake et al. 1997; Ficke et al. 2011). Conversely, I used the same data to recommend minimum fishway velocity and length combinations that should restrict the passage of Brook Stickleback.

Results

Jumping Performance

Trials for Hornyhead Chub (87-154 mm TL, mean = 121 ± 15.9 mm) were conducted to assess the jumping ability of this species. Hornyhead Chub exhibited two similar strategies for overcoming the waterfall where individual fish would either approach from the side of the waterfall or the bottom of the plunge pool, and then attempt to swim up the descending water column to reach the upper chamber. Jumping performance overall increased with water temperature (Figures 1, 2, and 3).

The top candidate models for all three temperature groups included weir height (WH), while only the 17.5° and 25° groups included both WH and pool depth (PP) terms (Table 3). Individual fish total length (TL) was not included in the top candidate models for any temperature group. Jumping success decreased with increasing weir height and decreased with increasing pool depth for the two warmer temperature groups (Figures 3 and 4). Water temperature also influenced maximum successful passage height observed during trials. The 25° group jumped the highest with a maximum successful passage of 150 mm. The 17.5° group cleared a 125-mm high obstacle, and the 10° group only passed at a maximum height of 75 mm (Table 5 and Figure 2).

Jumping performance trials for Bigmouth Shiner (42-79 mm TL, mean = 62.7 ± 6.1 mm) showed that they used different strategies for attempting to move into the upper chamber. Some fish attempted to swim up the sides of the waterfall column like Hornyhead Chub, while others appeared to use true jumping behavior and left the water during their attempts. Schooling behavior was observed periodically, and multiple fish jumping simultaneously was also observed. The top candidate models for Bigmouth Shiner only included weir height as a significant predictor of jumping success for all three temperature treatments (Table 3). Plunge pool depth and individual total length did not have a significant effect on jumping performance. Jumping success decreased as weir height increased (Figures 4, 5, and 6).

Maximum jumping height increased with increasing water temperature (Table 5). The 10° fish jumped a maximum height of 48 mm, the 17.5° group successfully overcame the waterfall at a maximum height of 72 mm, and the maximum height that the 25° group successfully jumped was 84 mm.

Iowa darter (39-69 mm TL, mean = 49.3 ± 4.7 mm) exhibited the lowest overall jumping performance of all species tested (Table 5). When attempting to negotiate the waterfall, Iowa Darter did not exhibit true jumping behavior. Most individuals approached the waterfall from the sides of the pool, and then attempted to swim up the waterfall. The top model for the 10° and 17.5° C treatments included both waterfall height and plunge pool depth terms as predictor variables. The top model for the 25° treatment only included weir height in the top model. Weir height affected Iowa Darter performance across all temperature treatments similarly, but plunge pool depth affected the two warmer treatments differently (Figure 7, 8, and 9). Predicted jumping success decreased with increasing weir height and pool depth for the 10°C treatment. In the 17.5°C treatment jumping success decreased with increasing weir height but increased with increasing pool depth. Jumping success decreased as weir height increased in the 25°C treatment. The 10°C treatment had a maximum jumping height of 40 mm. The 17.5°C treatment had a maximum jumping height of 50 mm. The 25°C Iowa Darter treatment jumped a maximum height of 60 mm.

Jumping performance trials for Brook Stickleback (39-62 mm TL, mean = 46.7 ± 4.2 mm) showed that the strategy that this species utilized to attempt to overcome the barrier were similar to Iowa Darter. Most individuals approached the weir from the side and attempted to swim up the water column. Several fish were observed swimming under the water column and “resting” on the small horizontal shelf downstream of the weir. The top models for all temperature treatments only included weir height as a significant predictor of jumping success. As weir height increased predicted jumping success decreased for all temperature treatments (Figures 10, 11, and 12). Maximum observed and predicted jumping height during trials and increased with water temperature. The 10°C treatment performed the worst of all species x temperature combinations tested. While no individuals successfully passed the barrier at heights greater than 0 mm, fish did move into the upper chamber at the 0-mm waterfall height treatment. The 17.5°C treatment achieved a maximum jumping height of 50 mm and the 25°C treatment jumped a maximum of 60 mm high.

Swimming Performance

The constant acceleration trials showed that Hornyhead Chub can sprint up to speeds of 120 cm/s inside swim tunnels. Hornyhead Chub exhibited the highest absolute burst swimming velocity of all species and V_{max} increased with water temperature (Figure 13). The 10, 17.5, and 25°C treatments exhibited mean swimming speeds of 85, 100, and 104 cm/s, respectively (Table 6). At speeds below 35 cm/s, most individuals exhibited a stroke-and-glide swimming gait and remained near the back of the swimming chamber. Between 35 and 40 cm/s, most individuals began to exhibit a steady swimming gait. At speeds exceeding 60 cm/s most fish began to exhibit unsteady/burst swimming gaits and were not able to hold a consistent position in the chamber for more than a few seconds. The results of fixed velocity trials for Hornyhead Chub show that water velocity, water temperature, and total length were significant predictors of predicted exhaustion times. Predicted swimming endurance increased with increasing water temperature, but dramatically decreased at water velocities greater than 24 cm/s (Figure 16). At slower velocities, swimming endurance is variable for Hornyhead Chub. At increased water velocities, the difference in endurance predictions between temperature treatments decreased.

Bigmouth Shiner are capable of swimming velocities up to 90 cm/s and their V_{max} increased with water temperature. Mean V_{max} for 10, 17.5, and 25°C treatments were 58, 72, and 78 cm/s, respectively (Table 6). Bigmouth Shiner exhibited the highest relative swimming speeds of all species tested (Figure 14). Results show that Bigmouth Shiner can swim up to a maximum of approximately 17 body lengths per second (Figure 14). At speeds less than 30 cm/s, most individuals exhibited a stroke-and-glide swimming gait. At all temperatures, most individuals exhibited a steady swimming gait at speeds between 30 and 50 cm/s. At speeds above 50 cm/s, most individuals began to exhibit unsteady swimming gaits consistent with burst swimming. During trials most individuals alternated positions throughout the swim chamber, but many individuals spent a majority of the trial near the floor of the swim tunnel. Results from fixed velocity trials show that swimming endurance is also variable for Bigmouth Shiner, especially at slower water velocities. Results from the Cox hazard model indicated that water velocity, water temperature, and fish total length were considered significant predictors of swimming endurance. Overall, endurance increased with water temperature and increasing fish length, but dramatically decreased with increasing water velocity for all temperature treatments (Figure 15).

Iowa Darter exhibited lower sprint swimming capabilities than Bigmouth Shiner and Hornyhead Chub at all temperatures (Figure 13). While a few individuals showed that Iowa Darter can swim up to speeds of 80 cm/s, mean swimming speeds were significantly lower than Bigmouth Shiner and Hornyhead Chub. The mean V_{max} at 10, 17.5, and 25°C treatments were 39, 43, and 45 cm/s respectively, but these values were not significantly different from each other. Iowa Darter exhibited a mixture of swimming and position holding behavior throughout swimming performance trials. At speeds less than 20 cm/s, darters almost exclusively utilized position holding behavior at all temperatures. Infrequently, fish would use bursts of swimming to reposition themselves on the floor of the chamber. At speeds greater than 20 cm/s, individuals began to exhibit a consistent mixture of position holding behavior and burst swimming. Darters would utilize position holding behavior and slowly slide to the rear of the swimming chamber, but before reaching the rear screen, would reposition themselves near the front of the chamber. At speeds greater than 30 cm/s, most individuals tested at all temperatures could no longer exhibit position holding behavior for more than a few seconds, and almost solely relied on burst swimming until exhaustion. The results of fixed velocity trials showed that like other species, swimming endurance was variable at slower water velocities. While water velocity and water temperature were significant predictors of swimming endurance, total length was not. Predicted median exhaustion times increased with water temperature but decreased dramatically with increasing water velocity (Figure 17).

Brook Stickleback showed the lowest burst swimming performance of all species tested during this study. The fastest individuals reached a maximum speed of 60 cm/s. Mean V_{max} for the 10, 17.5, and 25°C treatments were 30, 39, and 43 cm/s respectively. At speeds less than 15 cm/s, individuals exhibited a mixture of pectoral rowing techniques and unsteady swimming gaits. At speeds greater than 15 cm/s, most individuals exhibited burst swimming gaits before exhaustion. The results of fixed velocity trials showed that Brook Stickleback had the lowest swimming endurance relative to the other species tested (Figure 18). Water velocity, water temperature, and total length were significant predictors of predicted time to exhaustion. Exhaustion times increased with water temperature and fish length. Swimming performance was similar at all water temperatures, at speeds greater than 15 cm/s.

Discussion

Jumping Performance

The results for Hornyhead Chub were not surprising, given their strategy for ascending the waterfalls. Because Hornyhead Chub did not exhibit the behavioral ability to jump clear out of the water, trying to swim up the water column probably hindered their ability to pass upstream. The negative effect that downstream pool depth had on jumping performance for the 17.5°C and 25°C groups could be attributed to a number of possibilities. One way to explain this effect is that individuals in both groups were able to push off the floor of the shallow plunge pool while attempting to overcome the waterfall, allowing them to “jump” with more force than fish in the deep pools. A second reason could be that the hydraulics near the surface of the lower plunge pool allowed individuals to take advantage of recirculating hydraulics that were created when the lower pool was set to a depth of 150 mm. This might allow Hornyhead Chub to increase their swimming speed while approaching the waterfall. While there has not been any previous research investigating the jumping abilities of Hornyhead Chub or other *Nocomis* species, there has been research investigating the jumping abilities of other Great Plains fishes. It appears that many of these species attempt to overcome vertical barriers in the same way, by attempting to swim up the water column instead of jumping. Because the Great Plains ecoregion is comprised of mostly low-gradient streams with mobile sediment, the ability to jump might have never been a necessary evolutionary adaptation for these species. Before humans began building stream-wide diversion structures, it is likely that these species had never been regularly threatened by widespread natural vertical barriers in the past.

The results for Bigmouth Shiner were not entirely surprising given their small size, and strategy for overcoming the vertical barrier, similar to Hornyhead Chub. Given their moderate capacity for burst swimming exhibited during constant acceleration trials, it is not surprising that Bigmouth Shiner were able to ascend barriers taller than Iowa Darters, but not quite as high as species like Hornyhead Chub, who can sprint much faster. Additionally, because Bigmouth Shiner evolved to live in small Great Plains streams like Hornyhead Chub, they may not have evolved the need to exhibit jumping behavior when faced with vertical obstacles. Bigmouth Shiner were able to overcome a maximum vertical height of 84 mm, which is slightly higher than similar species tested in the past using similar methods. This is more than 50 mm higher than similar sized Sand Shiner were able to jump (Prenosil et al. 2016).

The results for Iowa Darter were consistent with their swimming performance relative to other species tested in this study. It was surprising that these fish were able to overcome any barrier, given their behavioral propensity to spend most of their time laying stationary on the floor of the lower plunge pool. Past jumping performance research on the related Arkansas Darter also showed that this species struggled to overcome any barrier higher than 0 mm (Ficke et al. 2011). Although is important to note that many individuals attempted to ascend the waterfall, and a few individuals were able to overcome barriers between 50-60 mm in height. This means that although their behavioral propensity to remain stationary on the floor of the lower chamber might contribute to lower overall success compared to other species in this study, many individuals were motivated to move upstream at some point during their individual trials. Given what is known about their life history, which can vary greatly across their native range, their lack of jumping ability is not surprising.

The results for Brook Stickleback were also not surprising, given their relatively weak swimming performance from swimming trials and what is known about their life history. Brook Stickleback performed similarly to Iowa Darter, which is consistent with both species' abilities to exhibit moderate sprinting abilities. Brook Stickleback likely do not invade new habitats by actively jumping over barriers but disperse opportunistically and potentially by taking advantage of marginal habitats to negotiate instream obstacles. Compared to research assessing the swimming performance of a similar species, the Threespine Stickleback *Gasterosteus aculeatus*, our results show that Brook Stickleback exhibited significantly reduced endurance. Threespine Stickleback have the capability to swim for 12-25 minutes at 30 cm/s, while Brook Stickleback from my study are predicted to only swim for less than one minute at a velocity of 30 cm/s (Taylor and McPhail 1986). It should be noted that the mean standard length of fish in that study was approximately 60 mm, while the fish used in our study were approximately 45 mm TL. A nearly 33% increase in body size could be a source of this disparity in swimming performance. They have been observed to move upstream when seasonal flows are high enough to connect new habitats, or heavy precipitation events create pathways for invasion (Ruthven et al. 2023).

Swimming Performance

Hornyhead Chub showed the highest absolute swimming speed of all species being tested. This was not surprising, as these fish were almost twice the length and up to 20 times the body weight of the other fish tested in this study. Higher proportions of musculature would allow fish to produce more power while swimming. Hornyhead Chub endurance was consistent with findings from past research at higher velocities (Billman and Pyron 2005). Billman and Pyron found that juvenile Hornyhead Chub were able to swim for approximately 65 seconds at speeds between 64-67 cm/s. Predicted median exhaustion times for Hornyhead Chub ranged from 0.87 to 2.8 minutes between 10 C° and 25 C°.

Given the known information regarding Hornyhead Chub life history, having the ability to swim for extended periods at high velocities might be unnecessary in their native habitats. Specific habitat requirements such as specific gravel substrate size, refuge complexity, and consistent flows suggest that long distance movement is infrequent (Mills et al. 1993). The riffle-pool habitat reaches of the Laramie River where fish were collected are filled with large cobbles and other complex habitat features that would allow fish to find refuge from strong flows. Hornyhead Chub were able to sprint at the highest speeds of all target species and showed the highest predicted endurance at the fastest speeds tested for most temperature treatments (48-60 cm/s). The combined results of sprinting and endurance swimming data suggests a trade-off between the requirements of nest building and navigating local habitats daily, while maintaining the ability to successfully swim upstream seasonally to reproduce, if Hornyhead Chub do migrate infrequently. This could also be evidence of behavior that correlates with relic habitats of the past that these fish used to occupy in Wyoming and Colorado, where the range was larger and seasonal migrations were possibly more common.

Bigmouth Shiner showed the highest relative swimming speeds, which is similar to the results found in other studies. Sand Shiners are capable of absolute swimming speeds between 62 and 66 cm/s, and relative speeds of 15.7 body lengths per second(Leavy and Bonner 2009; Prenosil et al. 2016). Bigmouth Shiner had the highest absolute endurance of all fishes at slower velocities of 36-42 cm/s. This is not surprising given the environments that Bigmouth Shiner have evolved in. Great Plains streams have flashy hydrographs and are prone to seasonal breaks in longitudinal connectivity (Labbe and Fausch 2000). Fish in these systems likely benefit from enhanced swimming capabilities in order to maintain their position during high flow events and/or make long distance movements to recolonize new habitats quickly after displacement or changes in connectivity. In small Great Plains streams, refugia in the form of complex substrate and wooden structure can sometimes be rare, so fish could be forced to swim for extended periods of time during high flow events.

Iowa Darter exhibited similar behaviors and relative performance as has been reported for other darter species. Rio Grande Darters (*E. grahimi*) can attain a maximum swimming velocity of 40 cm/s, and a relative speed of 11 body lengths per second (Leavy and Bonner 2009). Iowa Darter swimming endurance was also similar to other species being tested. Arkansas Darter were shown to hold position inside swimming tunnels almost indefinitely at speeds less than 15 cm/s (Ficke et al. 2011). Additionally, as speed increased only five cm/s, swimming endurance dramatically decreased at all temperatures, which is a trend that I observed during Iowa Darter trials as well. Their lesser capabilities in terms of maximum swimming speed and endurance are also likely a product of their morphology and evolutionary history. Iowa Darter and other benthic species likely do not subject themselves to constant, laminar flows in order to move upstream. Fishes like Iowa Darter likely need to exploit streambed heterogeneity, stream margins, and boundary layers to move within lotic habitats and fishways that exhibit high average water velocities.

Brook Stickleback were able to sprint at velocities similar to Iowa Darter, but their endurance was dramatically lower than that of the other species in this study. Their body morphology suggests that they are not strong swimmers. They have a very slender caudal peduncle relative to their body compared to other fishes, and they also have a very small caudal fin relative to the size of their body. The lack of red musculature along their spine suggests this species might struggle to swim for extended periods (Ficke 2015). Additionally, their preference for pectoral rowing at low speeds, and burst swimming gaits at high speeds are what one would expect from a species that likes to live in heavily vegetated ponds, backwater areas, and stream margins with low current velocities (Ruthven et al. 2023)(Wieker et al. 2016). Brook Stickleback can utilize pectoral rowing swimming techniques to maximize maneuvering capabilities in heavily vegetated areas, and their burst swimming capabilities could aid them with predator avoidance and prey capture.

Considerations For Restoring Connectivity

Unfortunately, there are unintended consequences that can arise from restoring river habitat connectivity. Due to the selective nature of these structures, some native species could be capable of passing, while others are not (Richer et al. 2020). This could have community-level ecological effects in the short or long term that are not greatly understood. Fish can be enticed to enter the fishway, only to find that they are ultimately unable to pass the structure completely. These fish are subjected to the potential for injury or stress in the meantime while in the structure (Mclaughlin et al. 2013). These effects can reduce the fitness of individuals, potentially endangering their future survival. Fish passage structures commonly cause congregations of fish at the bottom plunge pool. These areas could serve as predation hotspots, which could negatively affect conservation efforts if migrating fish experience elevated predation rates at passage structures (Mclaughlin et al. 2013).

Unfortunately, fish passage structures that have been constructed for native species can sometimes also be utilized by non-native species (Pratt et al. 2009; Mclaughlin et al. 2013; Welsh and Loughman 2015). Because restoring habitat connectivity can have unintended consequences, this further reinforces the idea that fish passage structure design must be carefully considered. Specifically, the idea that both non-native and native species likely will utilize fish passage structures should be contemplated (Clay 1995; Welsh and Loughman 2015). This does not necessarily indicate that fish passage structures should not be utilized in areas where invasive species are present, only that the swimming and jumping abilities of non-native species also need to be considered when designing passage structures for natives. This means that if conditions exist where the swimming and/or jumping abilities of desirable species exceeds the capabilities of invasive species in some way, a structure could potentially be designed where selection only for native fishes and exclusion of invasives is possible (Holthe et al. 2005). In situations where this is not the case, then managers need to decide whether the benefit of allowing native fishes to move upstream is outweighed by the risk of also providing access to non-target species.

Recommendations for Fishway Design

The results of swimming and jumping performance experiments for Hornyhead Chub, Bigmouth Shiner, Iowa Darter, and Brook Stickleback clearly highlight the complex problem facing biologists and engineers when designing fishways. Each species tested during this study has shown unique physical and behavioral characteristics that make characterizing their locomotive abilities a challenging task. While each species has exhibited varying levels of swimming and jumping abilities, we believe that designing fish passage structures for Hornyhead Chub, Bigmouth Shiner, and Iowa Darter is possible, and prior studies have identified fishway types that have proved successful for similar taxa (Richer et al. 2020). In the case of Hornyhead Chub, Bigmouth Shiner, and Iowa Darter, managers could choose between multiple fishway types that could accommodate these species. Vertical slot and other baffled type fishways that utilize burst swimming capabilities would be suitable for each species, given that average water velocities do not exceed their maximum burst swimming capabilities (Figure 13). Additionally, fishways that require continuous swimming for extended periods, similar to rock ramp fishways and culverts could also be utilized, so long as maximum fishway and water velocity recommendations are not exceeded (Figure 19).

In the case of Brook Stickleback, designing a structure that will intentionally block their passage might also be possible. If one was not concerned with blocking the upstream passage of natives, and simply wanted to block the passage of all Stickleback, our results suggest that building a vertical barrier seven centimeters high should be sufficient for blocking all movement. This is provided that the barrier consistently maintains the vertical separation between upstream and downstream pools at all flows. This solution becomes an issue when trying to design structures where selective passage of native and non-native fish is desirable. Unfortunately, our results show that utilizing a small vertical barrier to block the upstream movement would also inhibit the passage of native species (e.g., Iowa Darter) so creating a selective passage structure should be considered with caution. Although their sprint swimming capabilities are much lower than Hornyhead Chub or Bigmouth Shiner on average, they were similar to Iowa Darter. This means that a vertical-slot or rock ramp fishway design that allows passage of slower swimming fishes like *Etheostoma sp.* would also allow the passage of Brook Stickleback and other invasive species. Additionally, although their sprinting performance was much less than other species on average, there were a few individuals that exhibited V_{max} up to nearly 70 cm/s. This means that designing a structure that blocks every single individual would be challenging, unless the total exclusion of all fishes were the goal.

Our study was designed to provide criteria for each species individually and we would recommend further multi-species testing with test species-selective fishways under laboratory conditions before any such structure was adopted in the field. Aside from quantifying the locomotive abilities of target species, there are many other factors that must be considered when designing fishways, and considering site-specific requirements are critical. Such variables to consider may include funding availability, construction costs, local hydrology, geology, and climate change. In the end, it is ultimately the manager’s responsibility to choose between the tradeoffs associated with constructing fishways and overall conservation objectives. Whether the goals are successful passage during all seasonal periods, or partial passage during specified time periods, fisheries managers can tailor fishway designs to meet specific conservation goals of native fish restoration projects, such as the restoration of the Sweetwater River in Wyoming.

Tables

Table 1. Summary of mean (± SD) lengths and wet weights of the four species tested during the jumping performance experiments.

Species	Water Temperature	Mean Total Length (mm)	Mean Wet Weight (g)
Hornyhead Chub	10°C	122±14.3	20.2±6.7
	17.5°C	121±15.2	20.3±7.9
	25°C	118±18	18.5±8.4
	Pooled:	121±15.9	19.7±7.7
Bigmouth Shiner	10°C	62.0±7.6	1.9±0.6
	17.5°C	62.1±6.5	1.9±0.6
	25°C	63.8±4.2	1.9±0.3
	Pooled:	62.7±6.1	1.9±0.5
Iowa Darter	10°C	48.0±5	1.0±0.4
	17.5°C	51.1±4.9	1.3±0.4
	25°C	48.7±4.3	1.0±0.3
	Pooled:	49.3±4.7	1.1±0.4
Brook Stickleback	10°C	44.0±3.1	0.8±0.1
	17.5°C	46.9±4.8	0.9±0.3
	25°C	49.4±4.8	1.1±0.3
	Pooled:	46.7±4.2	0.9±0.3

Table 2. Waterfall height levels (mm) tested for each water temperature group (°C). No fish from the 10°C groups successfully jumped at H_2 or H_3, so H_4 trials were not conducted. Each waterfall height was tested with shallow (150-mm deep) and deep (300-mm deep) plunge pools. There were five replicate trials for each treatment combination.

Species	Water Temperature	Waterfall Height				
		H_0 (mm)	H_1 (mm)	H_2 (mm)	H_3 (mm)	H_4 (mm)
Hornyhead Chub	10°C	0	75	100	125	-
	17.5°C	0	100	125	150	175
	25°C	0	125	150	175	200
Bigmouth Shiner	10°C	0	48	60	72	-
	17.5°C	0	60	72	84	96
	25°C	0	72	84	96	108
Iowa Darter	10°C	0	40	50	60	-
	17.5°C	0	40	50	60	70
	25°C	0	50	60	70	80
Brook Stickleback	10°C	0	40	50	60	-
	17.5°C	0	40	50	60	70
	25°C	0	50	60	70	80

Table 3. Set of top candidate models estimating successful fish passage probabilities for Hornyhead Chub, Bigmouth Shiner, Iowa Darter, and Brook Stickleback. Waterfall height (WH), plunge pool depth (PP), and fish total length (TL) were included as predictor variables of successful fish passage in global models. Models highlighted in bold were selected as the best candidate model and used for predictions. Corrected AIC values (AICc) and ΔAICc scores are included for each model. McFadden's R^2 values are included for each top model selection.

Species	Water Temperature	Predictor Variables	AICc	ΔAICc	McFadden's R^2
Hornyhead Chub	10°C	**WH**	**14.33**	**0**	**0.81**
		WH+TL	16.43	2.09	
	17.5°C	**WH+PP**	**19.29**	**0**	**0.77**
		WH+PP+ TL	21.37	2.08	
	25°C	**WH+PP**	**18.12**	**0**	**0.79**
		WH	18.46	0.35	
Bigmouth Shiner	10°C	**WH**	**40.49**	**0**	**0.71**
		WH+PP	41.79	1.3	
	17.5°C	**WH**	**81.06**	**0**	**0.56**
		WH+TL	82.38	1.32	
	25°C	**WH**	**60.64**	**0**	**0.69**
		WH+TL	62.14	1.49	
Iowa Darter	10°C	**WH+PP**	**50.0**	**0**	**0.60**
		WH	51.8	1.32	
	17.5°C	**WH+PP**	**77.42**	**0**	**0.61**
		WH+PP+ TL	79.54	2.11	
	25°C	**WH**	**90.8**	**0**	**0.74**
		WH+TL	91.8	.21	
Brook Stickleback	10°C	**WH**	**18.8**	**0**	**0.88**
		WH+TL	19.21	0.41	
	17.5°C	**WH**	**44.08**	**0**	**0.76**
		WH+TL	44.95	0.88	
	25°C	**WH**	**56.39**	**0**	**0.68**
		WH+TL	58.45	2.06	

Table 4. Summary of top candidate jumping performance models for Hornyhead Chub, Bigmouth Shiner, Iowa Darter, and Brook Stickleback. Top candidate models included independent variables waterfall height (WH) and pool depth (PP). Log odds equation coefficients are included for use in estimating variable parameters (waterfall heights) that correspond to specified desired levels of successful passage.

Species	Water Temperature	Predictor Variables	Equation Coefficients	Standard Error
Hornyhead Chub	10°C	WH	**Intercept: 65.6**	**1290**
			Waterfall: -0.86	172
	17.5°C	WH+PP	**Intercept: 12.6**	6.54
			Waterfall: -0.08	**0.04**
			Pool Depth: -0.03	0.02
	25°C	WH+PP	**Intercept: 11.1**	6.81
			Waterfall: -0.07	**0.03**
			Pool Depth: -0.02	0.02
Bigmouth Shiner	10°C	WH	**Intercept: 1.62**	**0.49**
			Waterfall: -0.11	0.02
	17.5°C	WH	**Intercept: 3.46**	**0.94**
			Waterfall: -0.08	0.01
	25°C	WH	**Intercept: 16.8**	**4.67**
			Waterfall: -0.23	0.06
Iowa Darter	10°C	WH+PP	**Intercept: 2.92**	**1.37**
			Waterfall: -0.12	0.03
			Pool Depth: -0.01	0.01
	17.5°C	WH+PP	**Intercept: 1.19**	**1.40**
			Waterfall: -0.13	0.03
			Pool Depth: 0.02	0.01
	25°C	WH	**Intercept: 1.62**	**0.48**
			Waterfall: -0.07	0.01
Brook Stickleback	10°C	WH	**Intercept: 2.64**	**0.73**
			Waterfall: -0.59	101
	17.5°C	WH	**Intercept: 5.37**	**2.11**
			Waterfall: -0.17	0.05
	25°C	WH	**Intercept: 3.68**	**1.09**
			Waterfall: -0.11	0.02

Table 5. Summary statistics for jumping performance experiment. Column headings include the proportion of fish that attempted to jump during trials for each temperature group, and the maximum height observed during trials that each group successfully jumped.

Species	Water Temperature	Proportion Attempted	Observed Maximum Height Jumped (mm)
Hornyhead Chub	10°C	**0.98**	**75**
	17.5°C	**0.83**	**125**
	25°C	**0.93**	**150**
Bigmouth Shiner	10°C	**0.55**	**48**
	17.5°C	**0.69**	**72**
	25°C	**0.69**	**84**
Iowa Darter	10°C	**0.32**	**40**
	17.5°C	**0.61**	**50**
	25°C	**0.43**	**60**
Brook Stickleback	10°C	**0.79**	**0**
	17.5°C	**0.86**	**50**
	25°C	**0.63**	**60**

Table 6. Summary results of constant acceleration trials for Hornyhead Chub (HHC), Bigmouth Shiner (BMS), Iowa Darter (IOD), and Brook Stickleback (BST). Both absolute (cm/s) and relative (body lengths/s) are shown with 95% confidence intervals.

Species	Water Temperature (°C)	Mean Critical Swim Speed (cm/s)	95% Confidence Interval (cm/s)	Mean Critical Swim Speed (bl/s)	95% Confidence Interval (bl/s)
HHC	10	85.3	81.8 - 88.9	7.1	6.8 - 7.5
	17.5	100.7	95.9 – 105	8.1	7.5 - 8.8
	25	104.0	98.1 – 110	8.8	8.0 - 9.7
BMS	10	57.9	53.9 - 61.7	9.4	8.8 - 10.0
	17.5	71.8	69.2 - 74.5	12.0	11.2 - 12.7
	25	78.1	73.4 - 82.7	13.3	12.4 - 14.2
IOD	10	39.3	33.1 - 45.4	8.3	7.0 - 9.5
	17.5	43.4	38.2 - 48.6	8.1	7.2 - 9.1
	25	45.0	39.8 - 50.2	9.0	7.8 - 10.1
BST	10	30.4	23.1 - 37.6	7.2	5.3 - 9.0
	17.5	38.9	35.5 - 42.3	7.5	6.6 - 8.3
	25	43.2	41.0 - 45.5	7.8	7.3 - 8.4

Table 7. Summary table of Cox proportional hazard model equation outputs for each species used for survival analysis. Columns include predictor variables and equation coefficients. 95% confidence intervals and p-values are provided for each independent variable.

Species	Predictor Variables	Equation Coefficients	95% Confidence Interval	p-value
Bigmouth Shiner	Water Velocity	0.137	0.113-0.157	2.00E-16
	Water Temperature	-0.113	(-0.15) - (-0.08)	5.5E-12
	Total Length	-0.042	(-0.072) - (-0.012)	0.004
Hornyhead Chub	Water Velocity	0.074	0.053 - 0.094	8.37E-13
	Water Temperature	-0.091	(-0.131) - (-0.051)	7.49E-06
	Total Length	-0.014	(-0.028) - (-0.009)	0.037
Iowa Darter	Water Velocity	0.156	0.11 - 0.19	2.00E-16
	Water Temperature	-0.044	(-0.077) - (-0.009)	0.013
Brook Stickleback	Water Velocity	0.148	0.112 - 0.183	2.00E-16
	Water Temperature	-0.057	(-0.087) - (-0.028)	1.88E-04
	Total Length	-0.044	(-0.081) - (-0.005)	2.51E-02

Table 8. Results of trial participation analysis for endurance swimming assessment. Column values represent the number of successful trials (performers) conducted for each treatment combination during fixed velocity trials.

Species	Water velocity (cm/s)	Number of Successful Trials (n)		
		10°C	17.5°C	25°C
BMS	36	17	14	-
	42	13	15	15
	48	18	20	14
	60	17	18	15
	72	-	-	18
HHC	24	10	8	6
	36	7	10	10
	48	6	10	9
	60	7	10	10
IOD	20	11	20	20
	25	8	11	9
	30	12	17	8
	35	15	13	6
BST	15	15	16	10
	20	13	15	11
	25	18	12	9
	30	18	15	10

Table 10. Results of survival analysis used for endurance swimming assessment. Predicted median exhaustion times with 95% confidence intervals are provided for test velocities used for each temperature treatment. Upper limits with values of "NA" could not be returned by the model due to their predicted values exceeding 200 minutes.

Species	Water Velocity (cm/s)	Predicted Median Exhaustion Time (min)		
		10°C	17.5°C	25°C
BMS	36	14.6 (5.3 - 59)	111 (52.1 - NA)	-
	42	2.93 (2.2 – 4.7)	7.9 (5.0 – 35)	91 (29.5 – NA)
	48	1.58 (1.4 - 2.2)	2.42 (2.1 – 3.3)	5.32 (4.8 – 58.6)
	60	0.75 (0.60 - 0.77)	1.0 (0.80 - 1.15)	1.42 (1.2 – 1.8)
	72	-	-	0.67 (0.6 - 0.75)
HHC	24	31 (15 -47)	56 (38 - 116)	142 (79.7 - NA)
	36	4.7 (2.8 - 17)	19 (14- 33)	44 (32 - 87)
	48	1.8 (0.92 - 3.6)	3.9 (2.4 - 8.5)	16(5.4 - 31)
	60	0.87 (0.55 - 1.6)	1.4(0.9 - 2.4)	2.8 (1.8 - 8.8)
IOD	20	25 (9.5 - 87)	55 (25 - 180)	153 (40 - NA)
	25	2.9 (1.1 - 9.6)	6.5 (3.8 - 16)	16 (6.5 - 55)
	30	0.61 (0.53 - 1.0)	0.97 (0.63 - 1.9)	2.2 (0.97 - 6.5)
	35	0.45 (0.38 - 0.53)	0.5 (0.43 - 0.6)	0.57 (0.5 - 1.1)
BST	15	2.4 (1.6 - 4.0)	3.8 (2.6 - 5.2)	5.5 (4.1 - 11)
	20	1.3 (0.93 - 1.6)	1.6 (1.4 - 2.4)	2.0 (1.9 - 4.2)
	25	0.73 (0.65 - 0.88)	0.93 (0.78 -1.2)	1.3(1.1 - 2.1)
	30	0.5 (0.42 - 0.65)	0.65 (0.58 - 0.75)	0.76 (0.67 - 1.1)

Figures

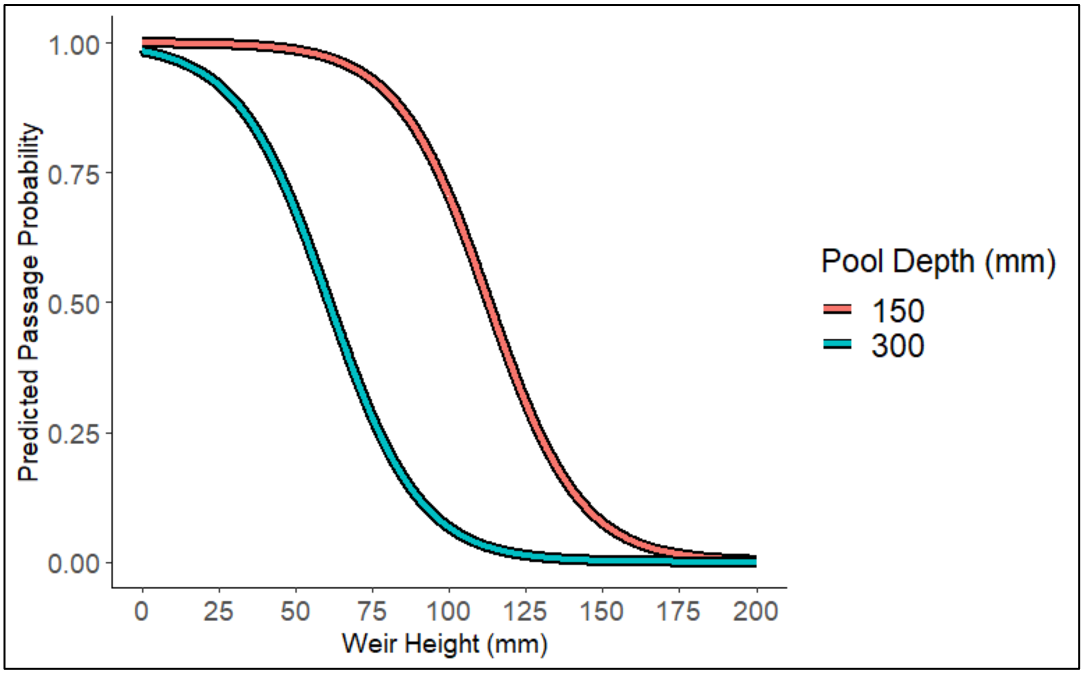

Figure 1. Predicted passage probabilities for Hornyhead Chub at 25°C as a function of weir height and plunge pool depth.

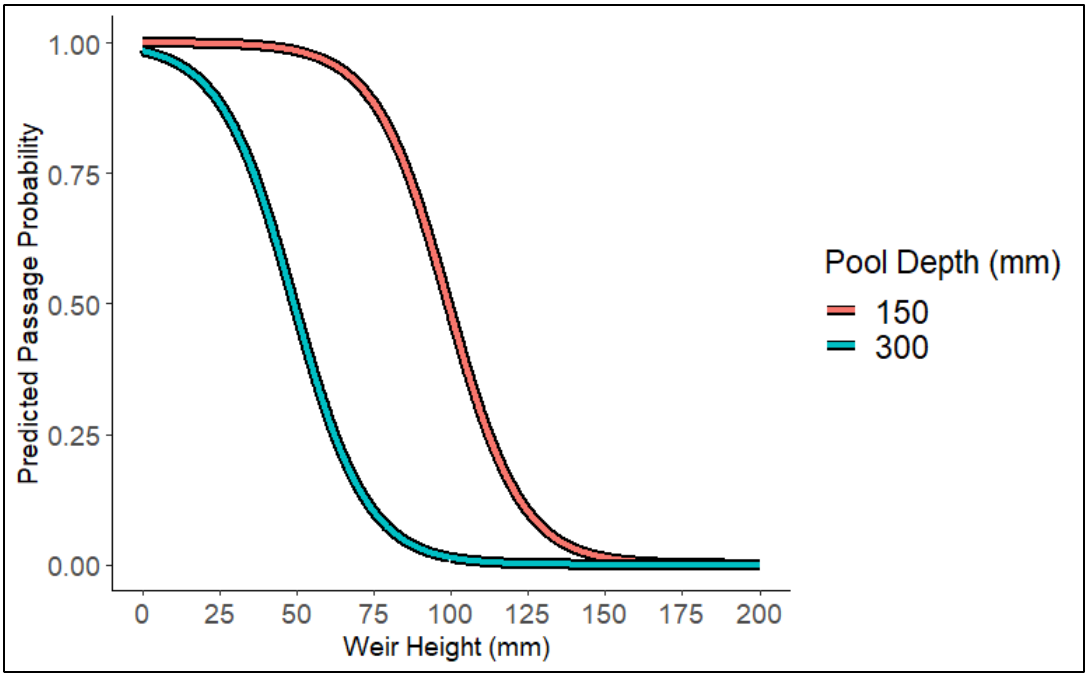

Figure 2. Predicted passage probabilities for Hornyhead Chub at 17.5°C as a function of weir height and plunge pool depth.

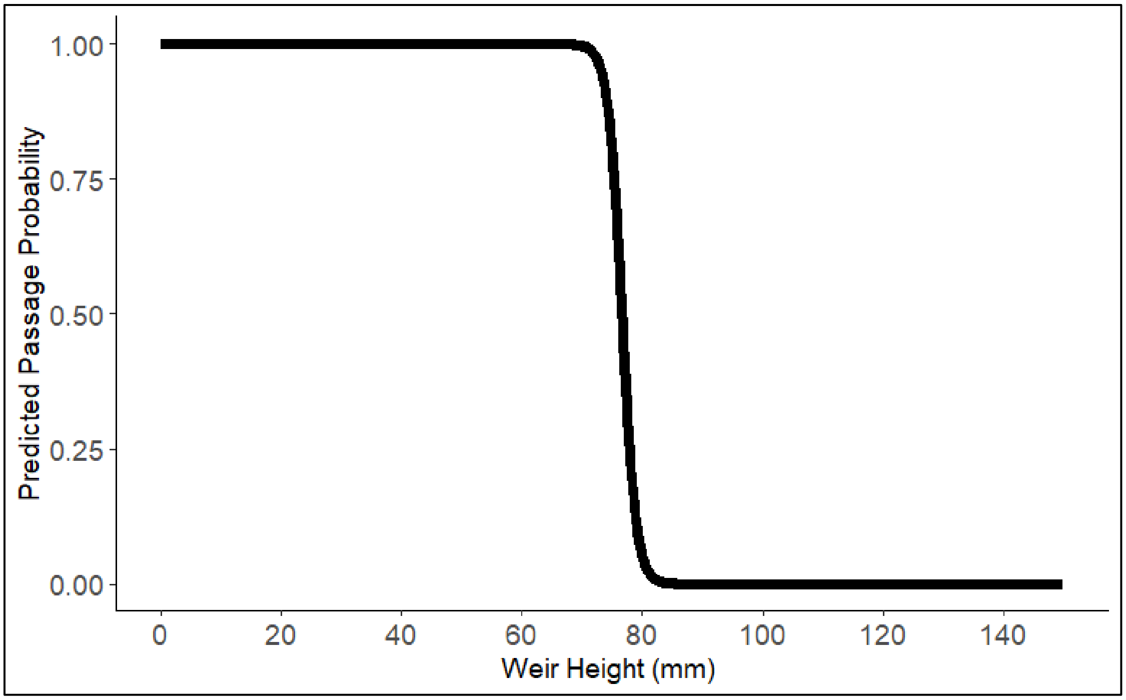

Figure 3. Predicted passage probabilities for Hornyhead Chub at 10°C as a function of weir height.

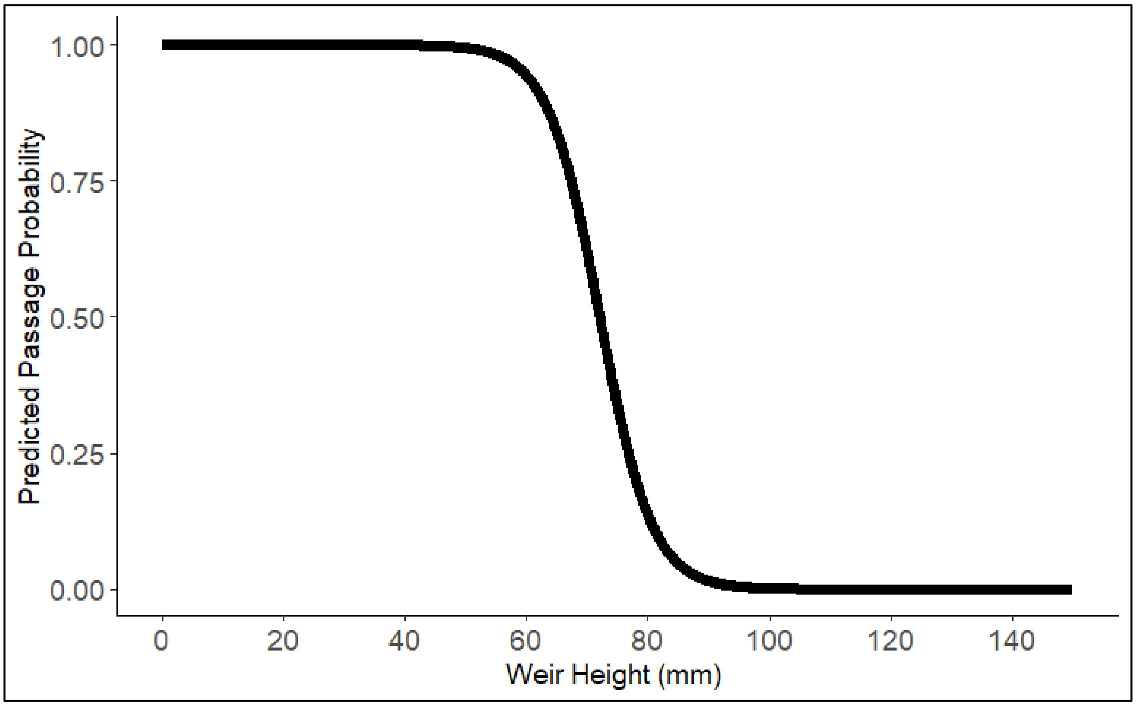

Figure 4. Predicted passage probabilities for Bigmouth Shiner at 25°C as a function of weir height.

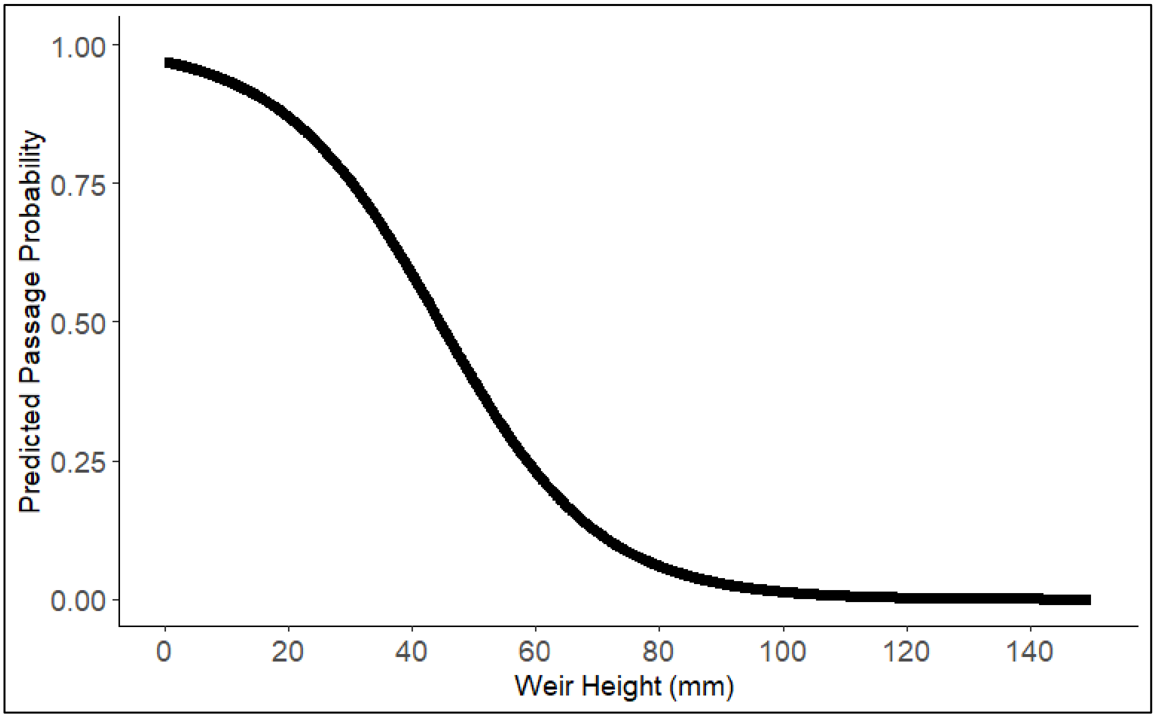

Figure 5. Predicted passage probabilities for Bigmouth Shiner at 17.5°C as a function of weir height.

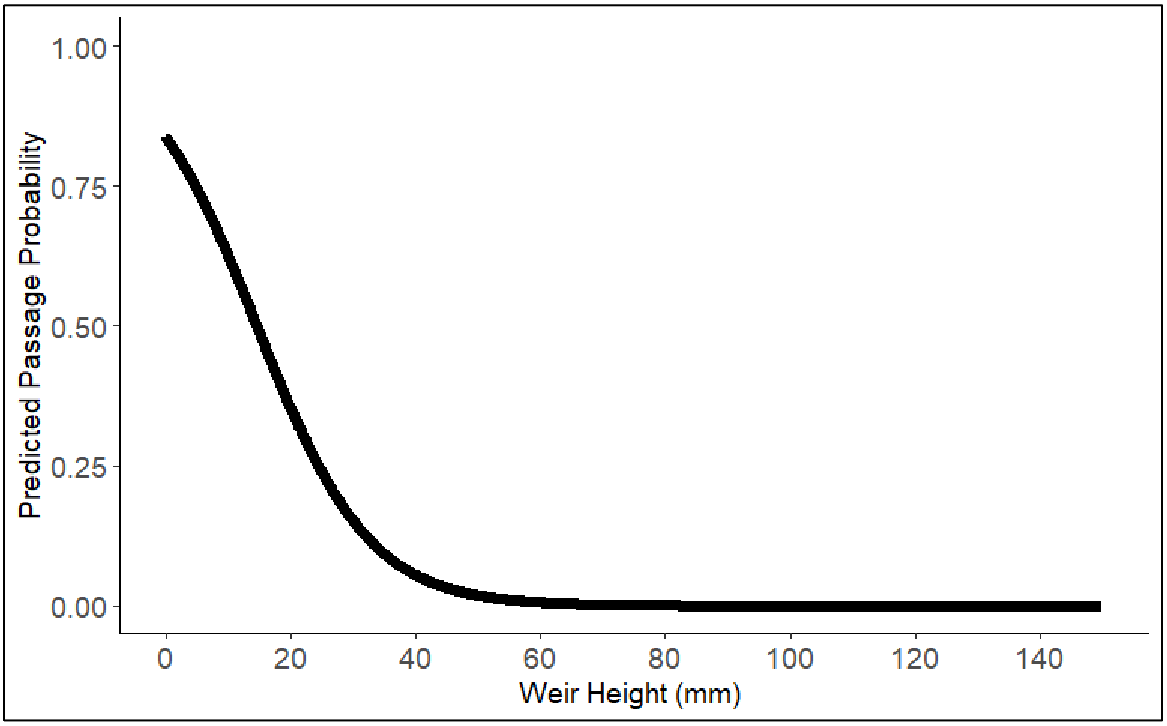

Figure 6. Predicted passage probabilities for Bigmouth Shiner at 10°C as a function of weir height.

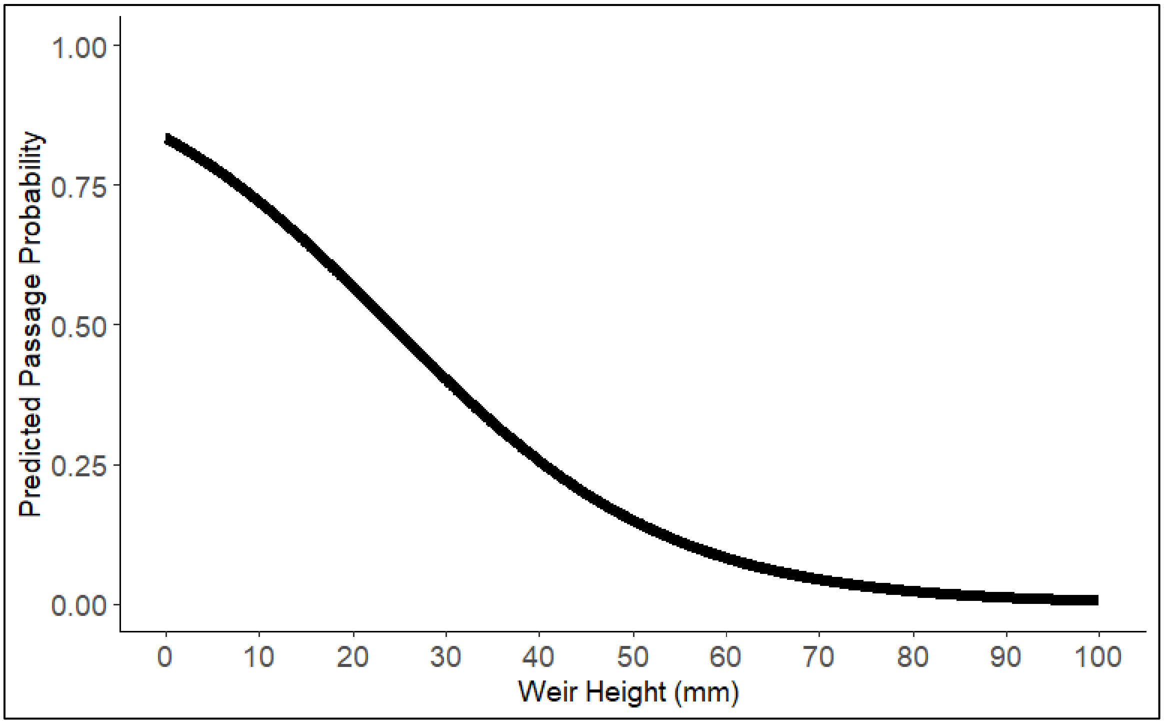

Figure 7. Predicted passage probabilities for Iowa Darter at 25°C as a function of weir height.

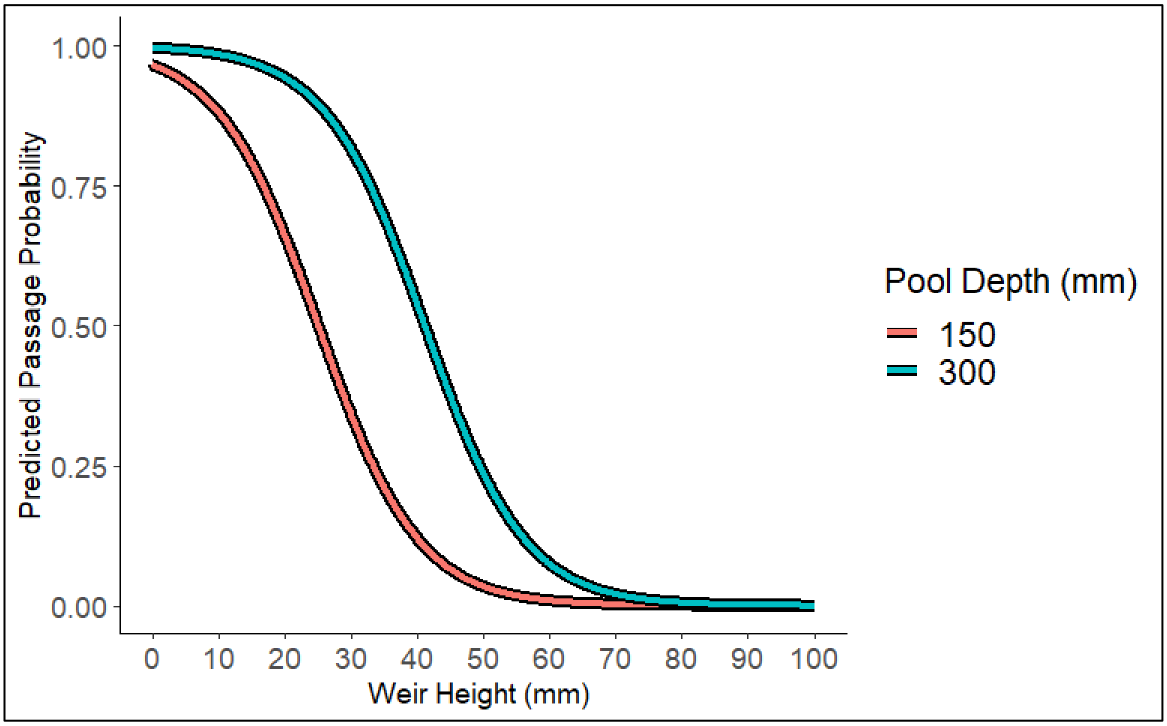

Figure 8. Predicted passage probabilities for Iowa Darter at 17.5°C as a function of weir height and plunge pool depth.

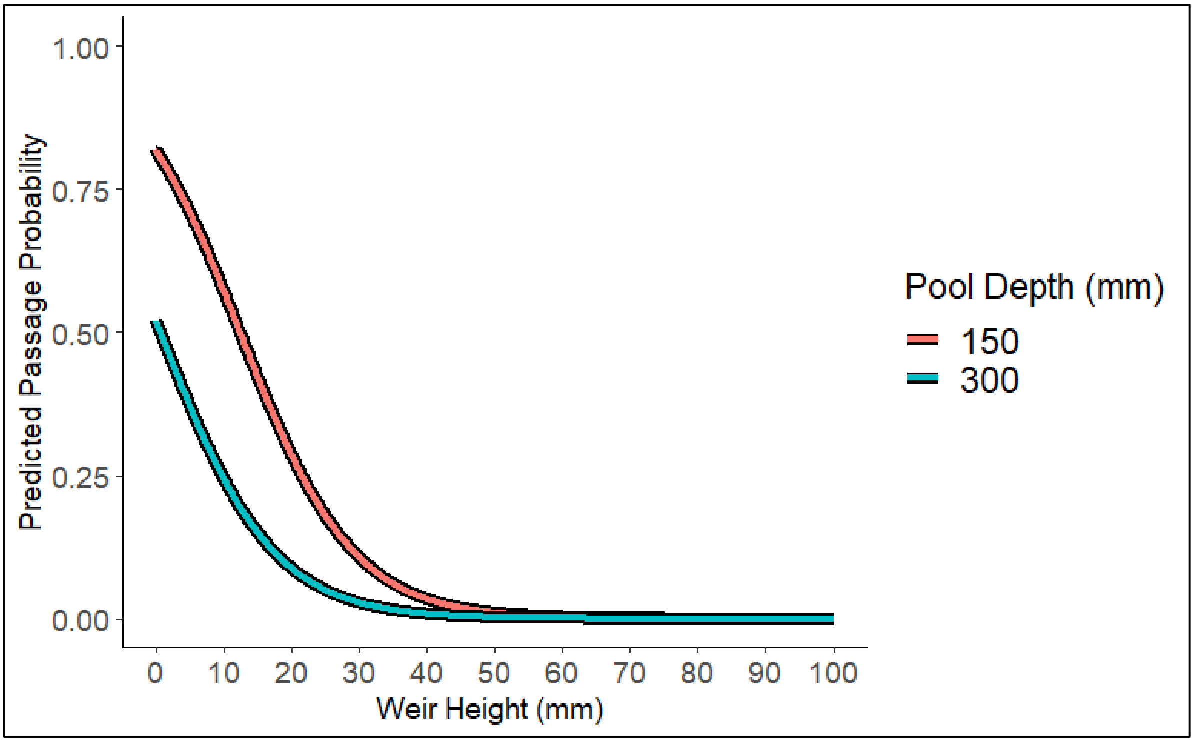

Figure 9. Predicted passage probabilities for Iowa Darter at 10°C as a function of weir height and plunge pool depth.

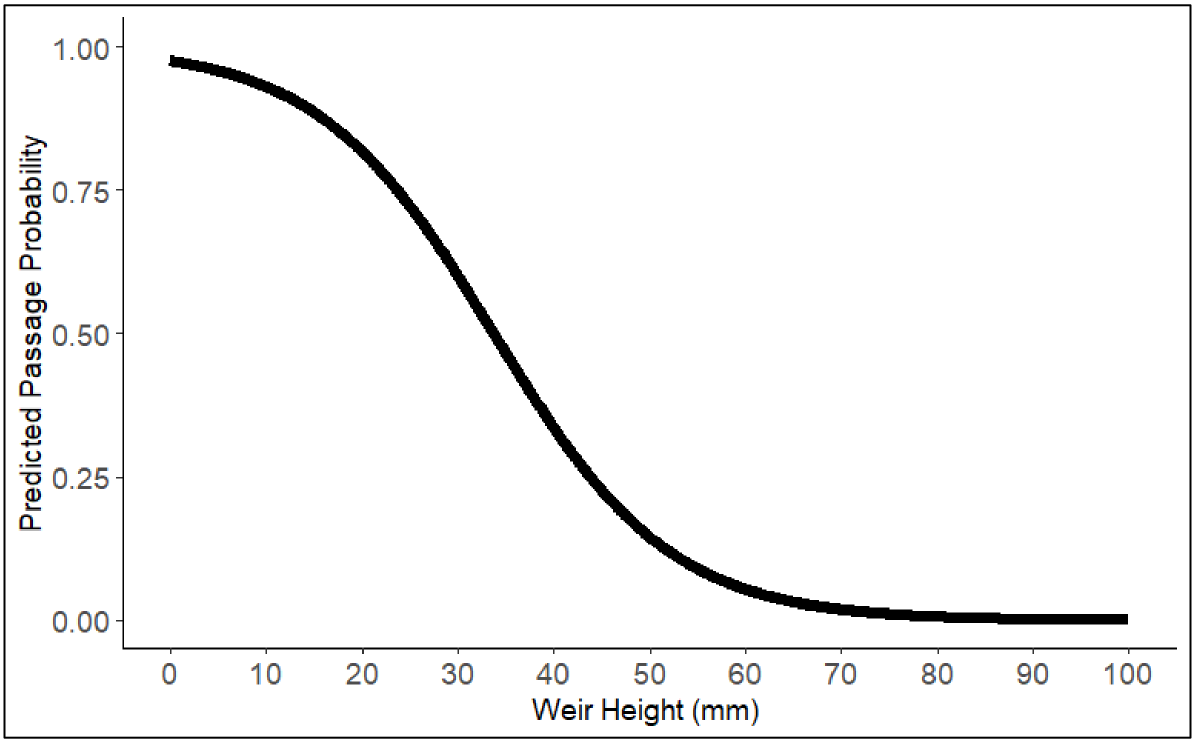

Figure 10. Predicted passage probabilities for Brook Stickleback at 25°C as a function of weir height.

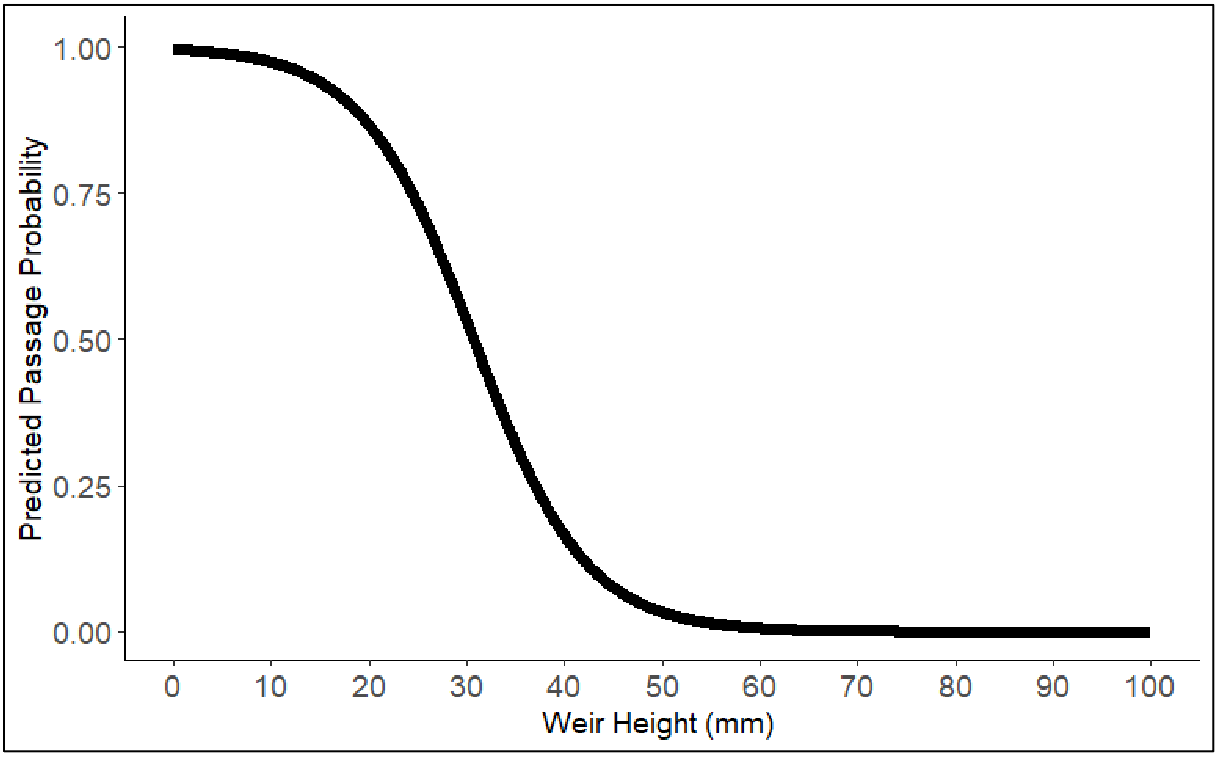

Figure 11. Predicted passage probabilities for Brook Stickleback at 17.5°C as a function of weir height.

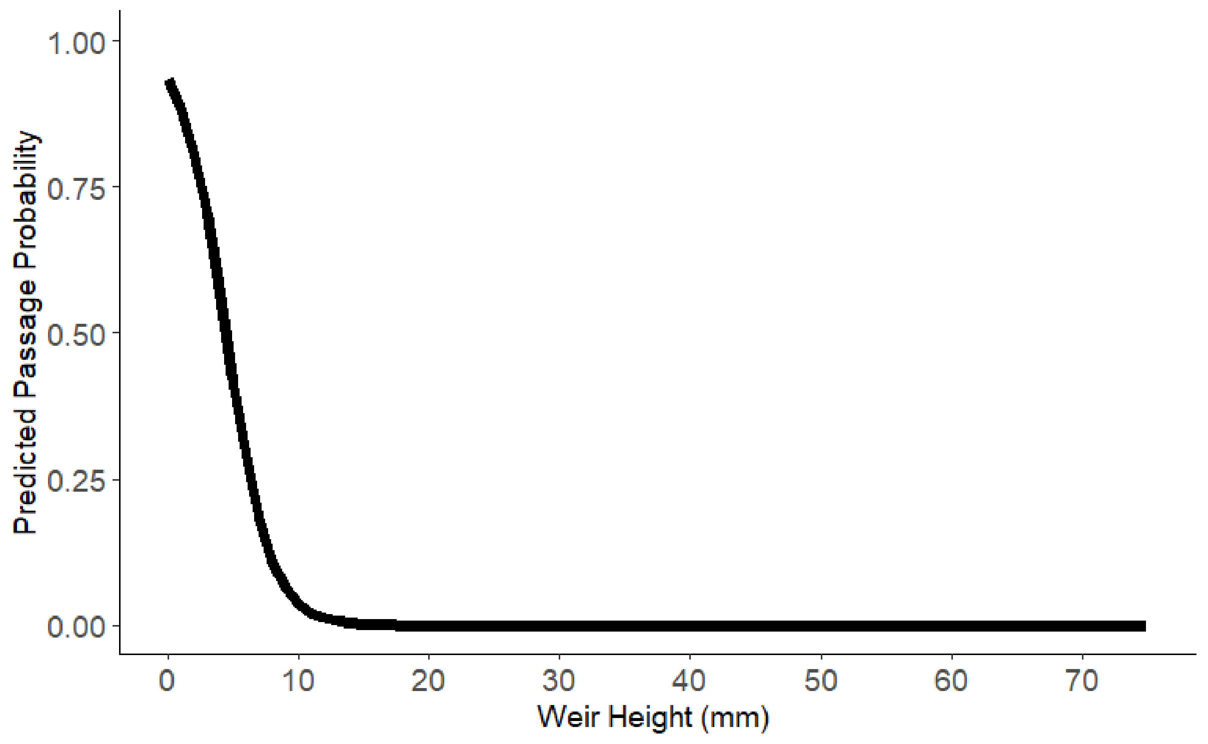

Figure 12. Predicted passage probabilities for Brook Stickleback at 10°C as a function of weir height.

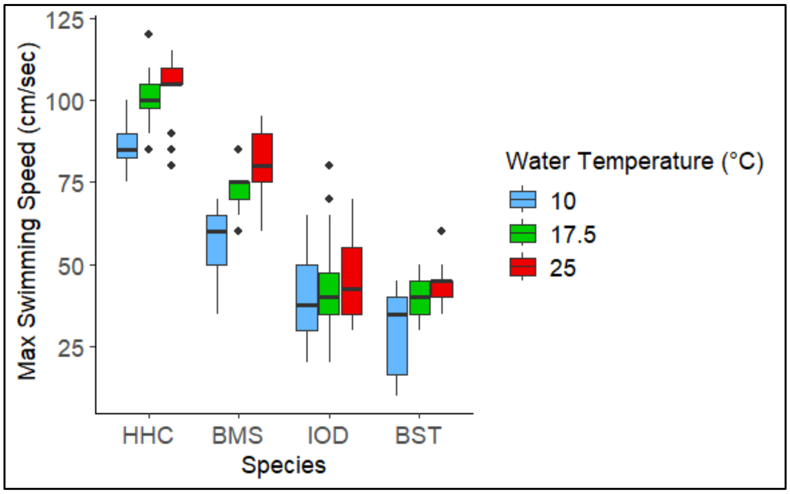

Figure 13. Summary of results of swimming performance trials showing the effects of water temperature (°C) on the constant acceleration performance (V_{max}; cm/s) of Hornyhead Chub (HHC), Bigmouth Shiner (BMS), Iowa Darter (IOD), and Brook Stickleback (BST).

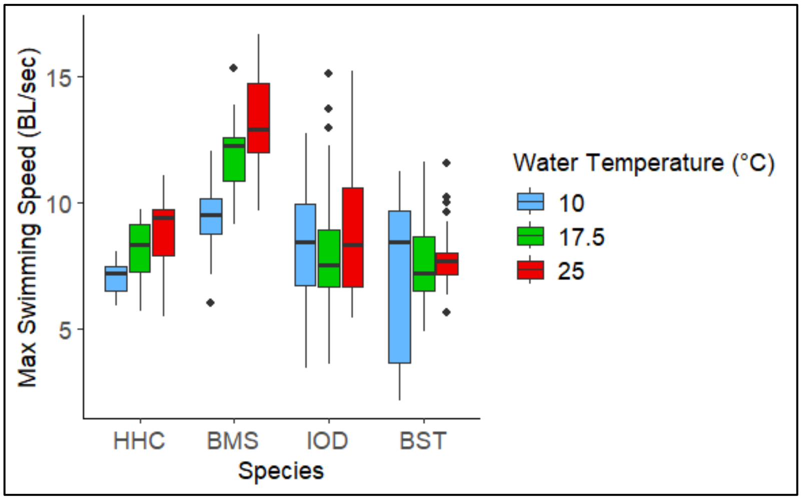

Figure 14. Summary of results of swimming performance trials showing the effects of water temperature (°C) on the relative constant acceleration performance (V_{max}; body lengths/s) of Hornyhead Chub (HHC), Bigmouth Shiner (BMS), Iowa Darter (IOD), and Brook Stickleback (BST).

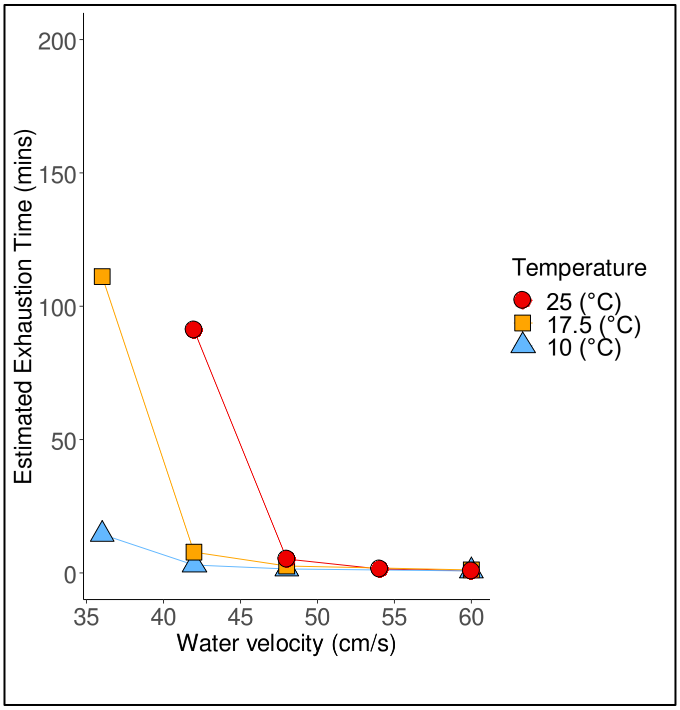

Figure 15. Effects of water temperature on the predicted swimming performance curves for a 62-mm TL Bigmouth Shiner based on a survival analysis.

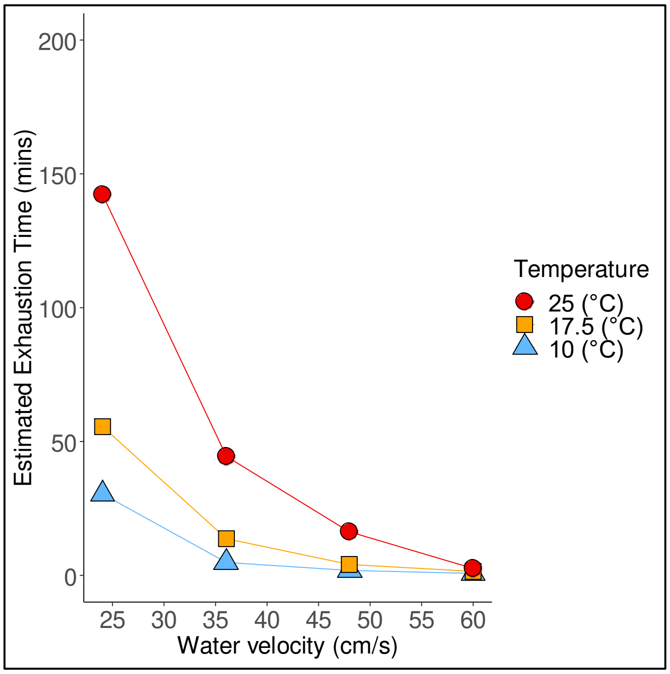

Figure 16. Effects of water temperature on the predicted swimming performance curves for a 118-mm TL Hornyhead Chub based on a survival analysis.

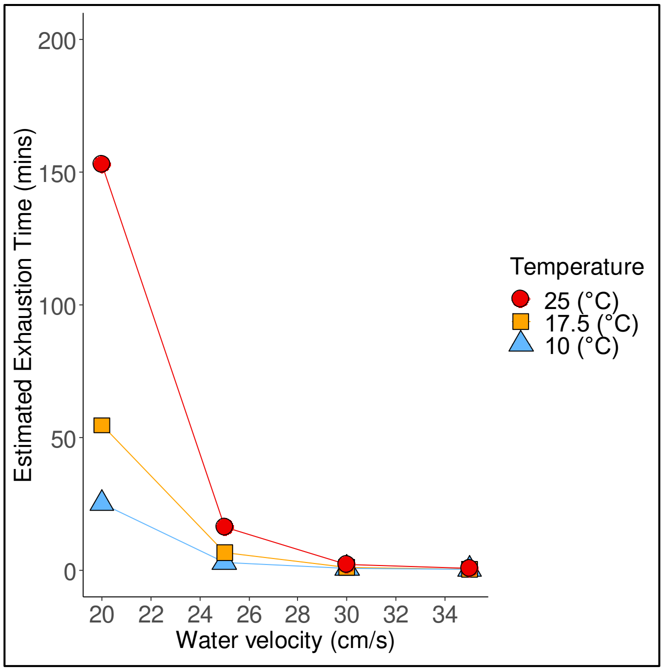

Figure 17. Effects of water temperature on the predicted swimming performance curves for Iowa Darter based on a survival analysis.

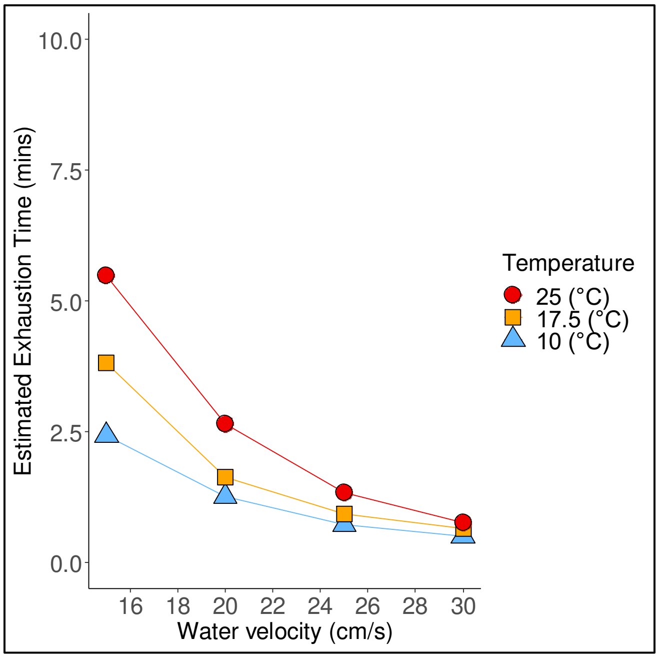

Figure 18. Effects of water temperature on the predicted swimming performance curves for 45-mm TL Brook Stickleback based on a survival analysis.

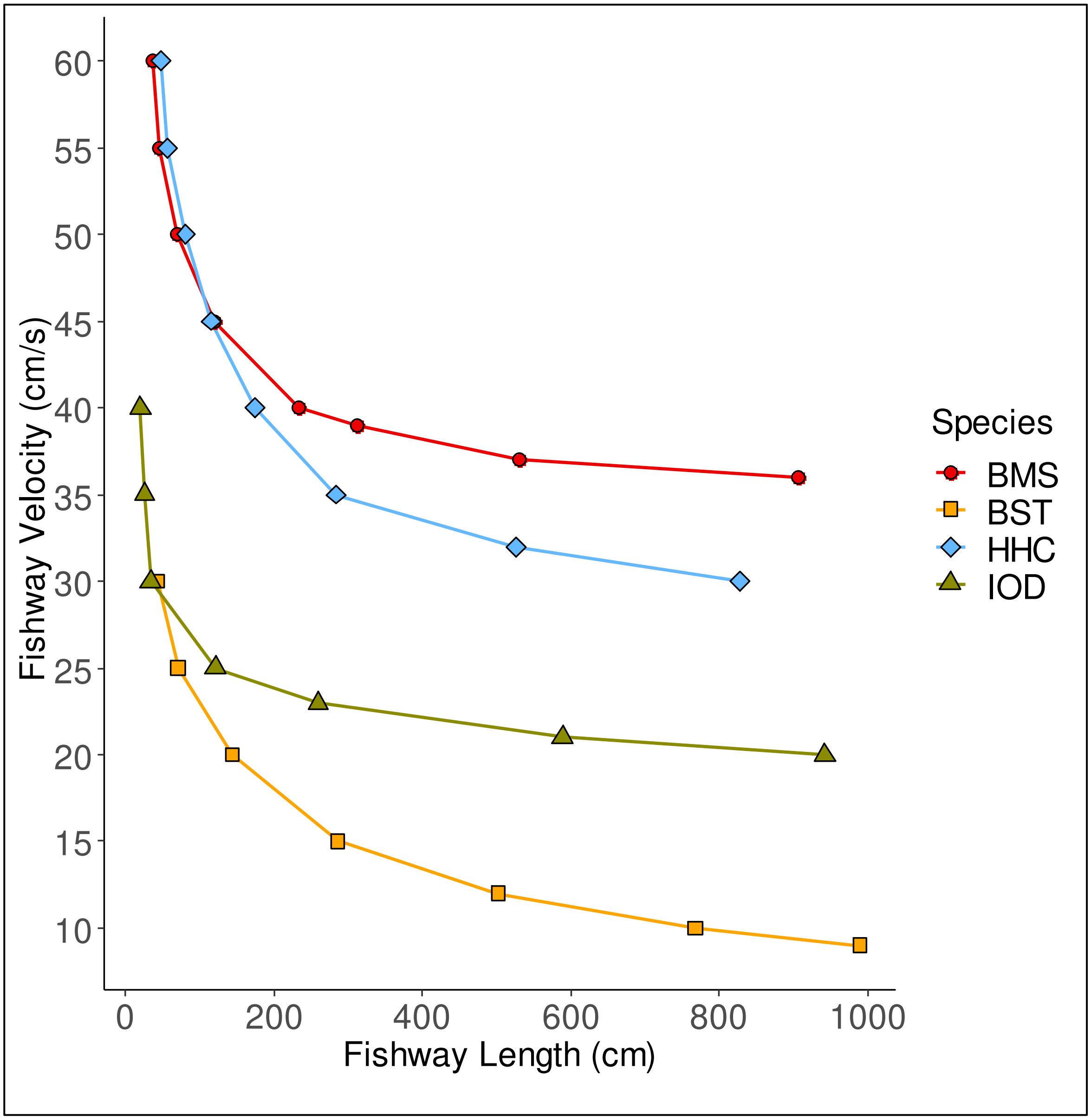

Figure 19. Predicted maximum fishway velocity and distance combinations that will allow the passage of Hornyhead Chub (HHC), Bigmouth Shiner (BMS), Iowa Darter (IOD), and Brook Stickleback (BST). Data for Hornyhead Chub, Bigmouth Shiner, and Iowa Darter were derived from predicted endurance values for individuals acclimated at 10°C. Fishway curve for Brook Stickleback was estimated for individuals acclimated at 25°C. Plots were created using estimated median swimming endurance values from the survival analysis, and fishway length and velocity values derived using Peake's equation (Peake et al. 1997; Ficke et al. 2011). Endurance values assume a constant positive ground speed of 1 cm/s relative to chosen fishway velocities. Values for HHC, BMS, and IOD were chosen from predictions of 10°C to ensure that recommendations are inclusive of native species when swimming performance is predicted to be the lowest relative to other water temperatures. Values for Brook Stickleback acclimated at 25°C were chosen to ensure recommendations for blocking upstream passage matches temperature conditions when Brook Stickleback are predicted to exhibit their highest swimming performance.

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Appendix

Due to Hornyhead Chub's conservation status in the state of Wyoming, this species was the focus of my research. In efforts to provide managers with the best possible information for completing conservation objectives for Hornyhead Chub, I tested the passage performance of fish used previously in swimming and jumping performance experiments in a separate study using a full-scale simulated rock ramp fishway at 17.5°C. The goal of this test was to allow me to provide more granular recommendations on rock ramp fishway design with respect to slope and to gain some appreciation for the difference between performance predictions from the swimming study and actual fish performance in a rock ramp fishway with complex flows.

The rock ramp fishway is the same apparatus described in Swarr et al. 2023 with the modifications developed by (Brittain 2022). I tested the Hornyhead Chub at slopes of 4, 6, and 8%, which correspond to mean flume water column velocities of 67.5, 72.4, and 93.0 cm/s respectively. I tested 30 fish per slope, divided into groups of ten fish per replicate group. Each replicate group of ten fish was given two separate 20-hour trials to ascend the fishway. The fish performed well, with >50% successful passage in the full 6.1-meter long fishway at all tested slopes. Observed passage percentages across the 6.1-meter long fishway were 93%, 83%, and 72% respectively at 4, 6, and 8% slopes.

Hornyhead Chub performance exceeded our model-derived predictions of fishway length and water velocity combinations, possibly because those are based on a continuous ramp design with no roughness elements, surface texture, or velocity refugia (Figure A1). Nevertheless, if predicting fishway performance based on sprint swimming capabilities, the performance of Hornyhead Chub in our simulated fishway are consistent with the results of constant acceleration trials. Mean maximum swimming speed of Hornyhead Chub in the 17.5°C treatments was approximately 100 cm/s during constant acceleration trials. Given these results, it appears that individuals ascending the fishway were utilizing mainly burst swimming capabilities to ascend the fishway, using the large roughness elements inside the rock ramp to rest in between bursts. We feel that these additional results provide a good indication of HHC performance under field passage conditions and would recommend utilizing similar designs for future fishways. While these results exceeded our predictions, we believe our previous recommendations for fishway length and velocities combinations for Hornyhead Chub are still valid. While our predictions of swimming performance based on swim tunnel tests might be conservative, we believe our recommendations will be effective, because conservative estimates will be inclusive of more individuals (e.g., juvenile HHC) in a target species than if we provided estimates that over-estimated the abilities of the fish studied in this project.

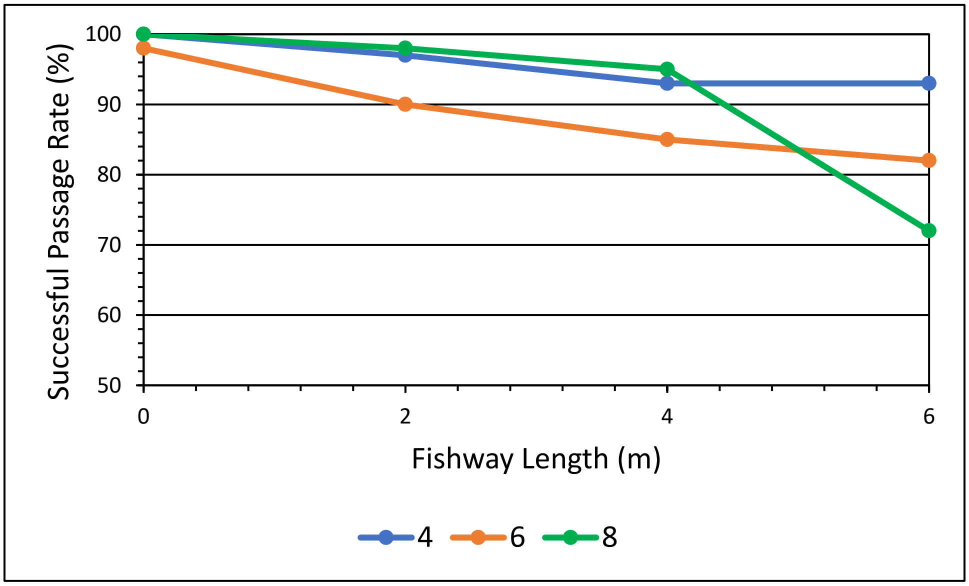

Figure A1. Observed passage success rates (%) of Hornyhead Chub as a function of rock ramp fishway length (m) and slope (4, 6, or 8%) when tested in a 6.1-m long rock ramp fishway with large roughness elements and a cobble substrate. Successful swimming distance (fishway length, meters) was determined by passage over PIT tag antennas located at 2-m intervals under the floor of the fishway.