RELATIONSHIPS AMONG SWIMMING PERFORMANCE, BEHAVIOR, WATER VELOCITY, TEMPERATURE, AND BODY SIZE FOR SAUGER *SANDER CANADENSIS* AND LONGNOSE DACE *RHINICHTHYS CATARACTAE*

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ABSTRACT

Migration barriers and resulting habitat fragmentation are a major conservation concern for freshwater fishes. Characterizing the swimming abilities of fish is vital for fishway design and identifying potential movement barriers. The objective of this study was to assess the swimming performance of two of the most widely distributed prairie fishes, the large-bodied, large river sauger *Sander Canadensis*, and the small-bodied, small stream longnose dace *Rhinichthys cataractae*. Swimming performance for both species was assessed using a variety of metrics (passage success, maximum ascent distance, maximum sprint speed) in an open channel flume over a range of velocities (sauger, 51, 80, 93 cm/; dace, 39, 64, 78, and 90 cm/s), temperatures (sauger, 10.0, 14.3, 18.3°C; dace, 10.7, 15.3, and 19.3°C) , and body sizes (sauger, 34.0-43.9 cm; dace, 4.6-12.4 cm). Passage success of sauger was surprisingly high (91%) over all test velocities, as was the mean maximum sprint velocity (mean, 219 cm/s). Contrary to expectations, water temperature and body size had little effect on swimming performance. Video observation showed that sauger transitioned from steady sustained swimming (aerobic metabolism) to unsteady, burst-glide or steady burst swimming (anaerobic metabolism) at 97 cm/s. Additional testing of sustained time of burst swimming by sauger in a swim tunnel (critical velocity, U_{sprint}) showed they are capable of short term maximum bursts of 124 cm/s over a 15 second duration before fatigue. Longnose dace had high passage success in the test flume (95%) at test velocities of 39 and 64 cm/s, but success rate dropped markedly at higher velocities (66% at 78 cm/s and 19.7% at 90 cm/s). Dace swam along the bottom of the flume at all test velocities, but increased position-holding as velocity increased. Their maximum sprint velocity (139 cm/s) was about half that of sauger. Dace swimming performance generally increased with water temperature and body size.

CHAPTER 1

INTRODUCTION

Habitat fragmentation in freshwater ecosystems can threaten the viability of freshwater and anadromous fish populations through direct loss of spawning and rearing habitat, loss of gene flow between isolated populations, and prevention of migrations that may be necessary to obtain food, avoid deleterious local conditions, or recolonize vacant habitats (Clapp et al. 1990; Matthews and Marsh-Matthews 2003; Pess et al. 2003; Ficke 2006; Dudley and Platania 2007). These consequences of habitat fragmentation have contributed to freshwater fish having the highest extinction rates among vertebrates worldwide (Dudgeon et al. 2005; Nilsson et al. 2005; Bunn et al. 2010; Burkhead 2012). Dams on large rivers represent complete barriers to fish movements if passage structures are not provided. In the United States alone there are approximately 76,000 large dams (>8 m) and 85% of the large rivers have been fragmented by dams (Larinier 2000; Hughes et al. 2005). Range-wide declines in the abundance and distribution of sauger and other large-bodied fish have been attributed to dams blocking access to spawning tributaries (Hesse 1994; Auer 1996; McMahon and Gardner 2001; Hughes et al. 2005). Culverts, weirs, diversion dams, and other instream structures on lower order streams are even more pervasive, with an estimated 1.4 million instream structures associated with road-crossings in the United States (Hudy, USFS, unpublished data). These structures can act as complete or partial barriers to fish movements if hydraulic conditions exceed physiological or behavioral capabilities of fish. Only recently has it been recognized that barriers to movement may negatively affect the distribution and abundance of small-

bodied fish on lower order streams throughout the arid Great Plains region (Cross et al. 1985; Bestgen and Platania 1991; Winston et al. 1991; Dudley and Platania 2007).

Barrier removal and provision of effective passage structures are among the most effective restoration techniques available to restore small-bodied and large-bodied fish populations in fragmented habitats (Scully et al. 1990; Roni et al. 2002). However, identification of barriers and design of effective passage structures depends on knowledge of swimming abilities and behaviors, which is lacking for many species of concern. The purpose of this study was to provide information on the swimming abilities and behaviors of the large-bodied sauger *Sander canadensis* and small-bodied longnose dace *Rhinichthys cataractae* that can be used by managers to restore and maintain connectivity.

Sauger were selected to represent a migratory large river prairie fish. Sauger are the most migratory member of the perch family and have historically been among the most widely distributed fish species in North America (Scott and Crossman 1973; Hesse 1994). However, migratory barriers blocking access to spawning and rearing habitats have contributed to range-wide declines in abundance and distribution (Rawson and Scholl 1978; Hesse 1994; McMahon and Gardner 2001). The highly migratory nature of sauger, their dependence on a wide diversity of physical habitats to complete their life history, and their propensity to travel long distances to spawn in select areas make sauger particularly sensitive to habitat fragmentation (Collette et al. 1977; Leach et al. 1977; Penkal 1992; Hesse 1994, McMahon 1999). A lack of swimming information on sauger inhibits our ability to design effective passage structures for this species.

Longnose dace were selected to represent a small-bodied stream prairie fish. Longnose dace have the widest distribution of any minnow species in North America and field studies have indicated that culverts and other instream barriers may be inhibiting natural movements throughout their range (Gilbert and Shute 1980; Dodd et al. 2003; McLaughlin et al. 2006; Rosenthal 2007). On the small prairie streams of the Great Plains, flooding and desiccation events are common and repeatedly depopulate habitat patches (Fausch and Bestgen 1997; Dodd et al. 2003). Thus, movements to recolonize suitable habitats are a key factor affecting species and population persistence (Schlosser and Angermeier 1995; Labbe and Fausch 2000).

Chapter two focuses on assessing the swimming performance and behavior of sauger. Swimming performance tests were performed in both an open-channel flume and swim chamber and the advantages and disadvantages of each testing apparatus are discussed. Distances of ascent and passage success against a range of water velocities were measured in an open-channel flume. Maximum swimming velocities were also measured in the open-channel flume and swimming endurance at sprinting velocities was measured in a swim chamber. Associations among swimming performance and water velocity, temperature, and body size were examined. Recommendations for barrier identification and design criteria of passage structures are provided.

Chapter three focuses on assessing the swimming performance and behavior of longnose dace. Distances of ascent and passage success against a range of water velocities were measured in an open-channel flume. Predictive models were developed from the results that allow managers and engineers to predict passage success and

distances of ascent against a range of velocities while accounting for the effects of body size and temperature. Recommendations for barrier identification and design criteria of passage structures are provided.

Chapter 4 summarizes the results of the study, provides recommendations for barrier identification and the design of passage structures, compares the results of the longnose dace and sauger experiments, and provides recommendations for the design of future fish swimming studies.

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CHAPTER 2

RELATIONSHIPS AMONG SWIMMING PERFORMANCE, BEHAVIOR, WATER VELOCITY, TEMPERATURE, AND BODY SIZE FOR SAUGER *SANDER CANADENSIS*

Abstract

Range-wide declines in the abundance and distribution of sauger have been attributed to migration barriers that fragment habitat and populations. To assess their swimming performance in relation to potential passage barriers, we estimated passage success, maximum ascent distances, and maximum sprint velocities in an open-channel flume over a range of water velocities (51, 80, and 93 cm/s) and temperatures (10.0, 14.3, and 18.3 °C). Passage success of sauger was surprisingly high (91%) over all test velocities, as was the maximum sprint velocity (mean, 219 cm/s). Contrary to expectations, water temperature and body size had little effect on swimming performance. Video observation showed that sauger transitioned from steady sustained swimming (aerobic metabolism) to unsteady, burst-glide or steady burst swimming (anaerobic metabolism) at 97 cm/s. Additional testing of sustained time of burst swimming by sauger in a swim tunnel showed they are capable of short term maximum bursts of 124 cm/s over 15 second duration before fatigue. Based on these results, passage structures with water velocities less than 97 cm/s should provide high probability of successful passage of adult sauger whereas structures with water velocities exceeding 219 cm/s will be impassable.

Introduction

The widespread construction of dams, weirs, culverts, and other instream structures throughout the 20th and 21st century has led to lotic freshwater systems being among the most modified ecosystems in the world (Arthington and Welcome 1995; Saunders et al. 2002). In the United States alone there are approximately 76,000 large dams (>8 m) and 85% of the large rivers have been fragmented by dams (Larinier 2000; Hughes et al. 2005). Sauger *Sander canadensis* are primarily a large-river fish that have historically been among the most widely distributed of any North American fish (Scott and Crossman 1973; Hesse 1994). However, instream barriers that limit access to spawning and rearing habitats, isolate populations, alter thermal and flow regimes, and reduce suspended sediment loads have contributed to range-wide declines in their abundance and distribution (Rawson and Scholl 1978; Hesse 1994; Pegg et al. 1997; McMahon and Gardner 2001; Amadio et al. 2005; Jaeger et al. 2005; Bellgraph et al. 2008). The highly migratory nature of sauger, their dependence on a wide diversity of physical habitats to complete their life history, and their propensity to travel long distances to spawn in select areas make sauger particularly sensitive to habitat fragmentation (Collette et al. 1977; Leach et al. 1977; Penkal 1992; Hesse 1994, McMahon 1999). Additionally, complete fragmentation results in smaller isolated subpopulations that are more vulnerable to inbreeding depression and extirpation from stochastic environmental events (Winston et al. 1991; Frankham 1995). Providing effective fishways that reconnect habitat and isolated populations is among the most promising management actions for restoring sauger to their historical abundance and

distribution. However, a lack of information on the swimming behavior and abilities of sauger may inhibit the design of effective passage structures for this species.

In order to be effective, passage structures must compliment the swimming abilities and behaviors of fish. Passage design is commonly based on swimming abilities of fish as determined in laboratory studies (Jones et al. 1974; Powers et al. 1985; Bell 1991; Clay 1995; Peake 2008). However, despite the use of sophisticated modeling, passage predictions based purely on laboratory observations of swimming abilities often differ from field passage assessments (Burford et al. 2009; Neary 2012). Behavioral aspects of swimming also need to be considered as they influence whether a fish can locate the passage entrance and whether hydraulic conditions at the entrance and within the structure will stimulate or deter passage attempts.

Swimming abilities have traditionally been studied in fixed and incremental velocity tests conducted in swim chambers (Katopodis and Gervias 2011). Fixed velocity tests measure the time to fatigue at a fixed velocity. In incremental velocity tests (U_{crit}), velocity is incrementally increased and the time to fatigue at the maximum velocity obtained is measured (Brett 1964). Calculations of the distance a fish could ascend using time to fatigue studies are commonly used to set water velocity criteria for passage structures (Jones et al. 1974; Bell 1991; Clay 1995; Peake 2004). These calculations assume fish swim at a constant velocity and that swimming performance and behavior in the uniform rectilinear flow of swim chambers will be equivalent to that in the complex flow dynamics often found in passage structures (Peake 1997; Peake 2004). Observation of free-swimming fish in more natural settings have not supported these assumptions

(Peake 2004; Peake and Farrell 2004; Peterson et al. 2013) and recent studies have indicated that fatigue tests may substantially underestimate a species' ability to navigate fishways (Mallen-Cooper 1992; Peake 2004; Peake and Farrell 2006; Holthe et al. 2008). Additionally, the forced nature of the test procedures and the artificial settings of swim chambers may further limit the applicability of fatigue testing for assessing swimming performance and associated fishway design.

Recently, swimming performance has been evaluated with the use of open-channel flumes. Flumes have been found to more closely simulate conditions in fishways and therefore may provide more realistic correlates for passage success in natural conditions (Haro et al. 2004). Observations of free-swimming fish in flumes can reveal subtle behaviors such as gait-transitions, holding behavior, optimized ground velocity, path selection and other behavioral traits that can inform passage design and identify incompatibilities between behavior and fishway conditions (Haro et al. 2004; Castro-Santos 2006; Bestgen et al. 2010; Ficke et al. 2011; Peterson et al. 2013). Swimming performance can be quantified in flumes using a variety of metrics that more closely reflect actual passage, such as passage success and distance of maximum ascent over a range of hydraulic conditions. These metrics can be directly applied to fishway design and evaluation. Additionally, flumes provide a relatively controlled environment in which to examine elements that may be important to fish passage, which can be difficult to examine in field studies due to a lack of control of conditions and the simultaneous interaction of multiple variables (Burford 2005; Katopodis and Gervias 2011).

Previous studies have indicated that water velocity, temperature, and body size can affect swimming performance and behavior (Beamish 1978; Hammer 1995; Katopodis and Gervias 2011). Water velocity dictates swimming velocities and energy expenditures necessary to make upstream progress. At low water velocities, fish use low swimming velocities powered by aerobic processes that can be maintained indefinitely without fatigue to progress upstream (Beamish 1978). Upstream passage at high water velocities requires use of fast glycolytic white muscle powered by anaerobic processes, which are sustainable for only short periods (Beamish 1978). Given the variety of water velocities associated with passage structures, examination of swimming abilities over a range of water velocities is necessary to inform passage design. In addition, as thermal conformers, temperature has a profound effect on swimming abilities and behavior of fish (Castro-Santos 2004; Coutant 2006). Given the wide range of seasonal temperatures sauger encounter, examination of swimming abilities over the range of water temperatures associated with sauger movements is needed to properly design and assess passage structures (Hokanson 1977; Hasnain et al. 2010). Swimming performance is also affected by body size (Beamish 1978; Videler 1993). Therefore, consideration of the size of migrating fish is also needed for effective passage design.

In this study, we assessed swimming performance of sauger over a range of velocities and temperatures to provide better estimates of passage success and restriction at current and future fishways. Using an open-channel flume, we estimated passage success, maximum ascent distances, and maximum sprint velocity, and documented

swimming gait transitions in relation to varying hydraulic conditions. We also used a swim chamber to estimate their maximum sprint endurance.

Methods

Study Design

Tests to characterize the swimming abilities and behavior of sauger were conducted in an open-channel flume (passage and sprint test) and swim chamber (U_{sprint} test) located at the Bozeman Fish Technology Center (BFTC; Bozeman, MT). In the passage test, fish were tested at all combinations of three velocity treatments (nominally 51, 80, and 93 cm/s) and three temperature treatments (nominally 10.0, 14.3, and 18.3 °C) for a total of nine unique treatments. Nominal velocities and temperature represent mean velocities and temperatures, respectively. Temperatures were selected to approximate the seasonal range of temperatures sauger experience in the wild. The lowest test temperature represents temperatures encountered during spring spawning migrations (10.3 °C), the 14.3 °C treatment approximates the isotherm that defines the northern distribution of sauger (15.6 °C), and the highest test temperature approximates their temperature growth optimum (19.6 °C; Hokanson 1977; Hasnain et al. 2010). The velocity treatments were selected to represent a range of velocities likely encountered within fishways that may be potential barriers to movement. Upper temperature and velocity limits were the maximum that could be tested at the BFTC.

Because sauger are listed as a species of concern in Wyoming and Montana (Carlson 2003, Keinath et al. 2003), only a limited number of sauger could be obtained for testing. This necessitated the use of a crossover experimental design wherein all

study fish were subjected to repeated testing across all treatments. Due to the changing seasonal availability of different temperatures of well water and the time involved to adjust test velocity (via changing the flume slope), a sequential rather than random test design was used. Temperature treatments were ordered from 10.0, to 14.3, to 18.3 °C, and the full set of velocity treatments were run sequentially at each test temperature. Velocity treatments were run in an ascending order (i.e. 51, 80, and 93 cm/s) at 10.0 °C, descending order at 14.3 °C, and ascending order at 18.3 °C. Insufficient flow to the flume in the first passage test (51 cm/s at 10.0 °C) warranted retesting after the completion of all other passage tests.

In the sprint test, individual fish were tested at a single velocity (46 cm/s) that provided sufficient current to trigger positive rheotaxis yet prevented excessive energy expenditure. Maximum swimming velocity (V_{max}) was evaluated at three temperatures similar to those used in the passage test (11.5, 14.4, and 17.9 °C). The order of temperature treatments progressed from 17.9, to 11.5, to 14.4 °C. All sprint trials within a temperature treatment were conducted in the same day.

In the U_{sprint} test, time to fatigue of burst swimming was evaluated over seven temperature treatments in a swim chamber. Temperature treatments were ordered as follows: 18.1, 22.3, 20.2, 16.3, 14.0, 12.0, and 10.0 °C, with the order selected to minimize large temperature changes in holding tanks that might induce physiological stress. All available fish were randomly assigned to one of two groups that were tested in two different temperature series (group one: 20.2, 18.1, 16.3, and 12.0 °C; group two: 22.3, 14.0, and 10.0 °C). Fish were split into groups to more closely examine

temperature effects on maximum swimming velocities while increasing the number of rest days between consecutive tests and minimizing the number of trials for each fish. All U_{sprint} trials within a temperature treatment were conducted in the same day.

Trials for all treatments were completed over a 113 day period between June and September of 2012. All passage tests except for the retested treatment combination (51 cm/s at 10.0 °C) were conducted first with a minimum of two days rest (mean=4, range=2-7) between tests. Fish were given a 28 day rest period before beginning the sprint and U_{sprint} tests. Sprint and U_{sprint} tests were conducted simultaneously, with a minimum of 2 days rest (mean=7, range=2-33) between trials. The 51 cm/s at 10.0 °C passage treatment occurred two days after the sprint test at 11.5 °C, 48 days after the last passage tests, in order to take advantage of seasonally available cold water.

Test Fish

Fifteen adult sauger were collected via electrofishing from the Bighorn River near Basin, Wyoming on May 11, 2012. Fish were transported in an aerated tank to the BFTC and transferred to a 4.27 x 1.22 x 1.22 m rectangular holding tank that mimicked river temperature at the time of collection (10.0 ± 2.0 °C). A salt treatment (5 ppm) was applied to alleviate osmotic stress associated with transport. Fish were weighed to the nearest 0.1 g, fork length (FL) was measured to the nearest 0.1 cm, and morphological differences were used to determine sex. A PIT tag (22 x 3 mm) was implanted in the peritoneal cavity through a small incision (no sutures needed) located just anterior of the anal fin to identify individuals. All test fish were males (mean FL=39.3 cm; range=34.0-43.9 cm). The five female sauger collected did not adjust to captivity, had high mortality,

and were omitted from testing. Holding tanks were stocked with two to three-hundred 2.5-7.6 cm hatchery rainbow trout that were restocked when depleted (~every 3-4 weeks). Prior to testing, holding tank temperatures were adjusted at a maximum rate of 1 °C per 8 hours until the desired test temperature was reached; fish were then held at that temperature for a minimum of 24 hours prior to testing.

Passage and Sprint Tests

Passage and sprint tests were conducted in a large (17.10 x 0.91 m) open-channel flume located at the BFTC (Figure 2.1, Figure 2.2). Flume width was set at 0.46 m for all treatments. To obtain the desired hydraulic conditions, the slope was adjusted to 0.50 ± 0.02% for the 51, 80 cm/s, and sprint trials, and 0.80 ± 0.02% for the 93 cm/s velocity trials. Water entered the flume from the headwater tank and flowed through the open-channel into a tailwater tank. A grate was located at the downstream end of the channel to prevent fish escape. The headwater tank provided resting refuge for fish that successfully ascended the flume; a plywood cover was added to create low light conditions and encourage fish to remain there after ascents. A black fabric shroud covered the length of the flume to ensure uniform lighting and prevent outside disturbances from disrupting testing. Water from well water sources was adjusted via pumps to control water temperature and discharge. Reference lines were painted every 61 cm on the bottom of the flume in order to track the position of fish. An array of six digital cameras (Handicam HDR-XR-150, Sony, Tokyo, Japan) were positioned 2 m above the flume every 2.2 m along its length (Figure 2.2). Video recordings of trials allowed observation of swimming behavior, passage success, distance of maximum

ascent (D_{max}), and ground velocities in the passage tests, and V_{max} in the sprint tests. In the passage test, swimming gaits were classified as sustained steady, unsteady, and steady burst using criteria similar to Rome et al. (1990) and Johnson (2007). Steady sustained swimming was characterized by rhythmic, undulatory locomotion that did not involve rapid acceleration or deceleration. Unsteady, burst-glide swimming was characterized by vigorous tail beating, rapid acceleration, followed by passive coasting. Steady burst was characterized by sustained vigorous tail beats.

Water temperature, depth, and velocities in the flume were measured twice daily prior to and after the completion of swimming trials at each treatment combination. Temperature was measured in the headwater and tailwater tanks at 1.0, 6.0, and 12.8 m upstream of the tailwater tank using an Ertco High Precision Thermometer. Ascent distance and passage success were estimated in a 12.8 m test section of the flume. Flow directly below the headwater tank and upstream of the test section created unstable and highly turbulent flow conditions that prevented accurate measurements of water velocity, depth, and fish observations. Thus, this flume section was not included in analysis. Water depth and velocity were measured every 61 cm. Velocities were measured with a Marsh-McBirney Flo-Mate 2000 current meter (Hach Corporation, Loveland, CO, USA) at 0.6 times the water depth to characterize average velocity. Depth was measured to the nearest 0.3 cm using a graduated rod. Varied turbulence intensities encountered by fish among and within treatment combinations warranted the calculation of Reynolds number from water depth and velocity measurements, as turbulence has been shown to influence swimming performance and behavior (Nikora et al. 2003; Lacey et al. 2012).

Discharge was continuously monitored with AquaRod-TruTrack Digital Crest Gages (GEO Scientific LTD, Vancouver, Canada) located in the tailwater and headwater tanks and a flow measurement device (Flexus F601 Flow Recorder, Flexim Aericas Corporation, Edgewood, NY, USA) located on the inflow pipe to the flume. Monitoring confirmed that discharge remained relatively constant for all trials within a treatment combination, which ensured that all fish experienced similar flow and velocity conditions.

In both the passage and sprint tests, individual fish were netted from the holding tank, transported to the flume, and placed at the downstream end. In the passage test, fish were given 30 min to volitionally ascend the flume. A total of ten fish were tested in 88 passage trials. All ten fish were tested in every treatment combination except the 10.0 °C by 51 cm/s treatment combination, in which eight fish were tested. A fungal infection caused the death of two fish prior to this treatment combination. Surviving fish were given a salt treatment (5 ppm) and an eight day recovery period before the next test. All fish had completely recovered before the next test. In eight of the passage trials fish did not attempt ascents and these trials were omitted from analysis.

In the sprint test, fish were confined to the lower 0.90 m of the flume by a removable grate. After a five minute acclimation period, the grate was removed and fish were stimulated to sprint the length of the flume by gently prodding with a net handle. After the initial sprint, fish were coerced back to the downstream end of the flume, the grate was replaced, and fish were allowed thirty seconds of rest before a second stimulation. This sequence was repeated a total of three times in a trial to ensure that at

least one vigorous sprint was observed. Only the fastest sprint velocity for each fish was analyzed. A total of 26 sprint trials were conducted at three test temperatures. Ten fish were tested in the 17.9 °C temperature treatment and eight fish were tested in the 11.5 and 14.4 °C treatments due to the aforementioned mortality. In three trials, fish did not respond to stimulation and these trials were omitted from the analysis. At the end of each passage and sprint trial the fish was removed from the flume, identified by PIT tag, and returned to a separate holding tank.

U_{sprint} Test

U_{sprint} tests were conducted in a swim chamber to measure the maximum velocity a fish could swim for 15 seconds, the approximate maximum duration that sprint swimming can be sustained (Beamish 1978). The swim chamber (185 L, Loligo Systems, Tjele, Denmark) was supplied with air-saturated flow-through water (18.9-30.3 L/min) from the same well sources that supplied the fish-holding tanks and the flume. Fish swam in a test section with a cross section of 25 x 25 cm and a length of 80 cm. Flow straighteners located just upstream of the test section provided rectilinear micro-turbulent flow and a uniform velocity profile. The upstream half of the test section was covered with black plastic and a halogen light was directed on the downstream end. This configuration was designed to deter sauger, which are light sensitive, from resting on the downstream grate and motivate sauger to swim in the low light upper half of the test section. A black plastic shroud was erected around the entire chamber to prevent outside disturbance. A video camera placed in front of the test section allowed continuous monitoring of test fish during trials. Video recordings of the trial allowed for

determination of water velocities associated with gait-transitions and accurate determination of the total time spent swimming.

Water velocity was measured with a Marsh-McBirney Flo-Mate 2000 current meter at 0.6 times the water depth to characterize the average velocity in the swim chamber. A calibration curve relating velocity to the frequency output of the variable speed motor was created (n=30) to allow rapid and precise velocity adjustments. Water temperature was continuously monitored with an Ertco High Precision Thermometer (Barnstead International, Dubuque, Iowa).

At the start of a trial, individual fish were netted from the holding tank, transported to the swim chamber by bucket, and placed in the test section of the swim chamber. U_{sprint} trials began with a ten min acclimation period at a velocity of 46 cm/s. After acclimation, velocity was increased by 7.6 cm/s every 15 seconds until fish became impinged on the downstream grate. If fish remained impinged for 3 seconds the motor was turned off and on rapidly to encourage further attempts. If fish remained impinged, the trial was ended and the time to the impingement was recorded. Ten fish were tested in a total of 33 U_{sprint} trials, with 18 trials conducted with group one fish and 15 trials with group two fish. One fish in group one sustained an eye injury during testing and was not tested in the two subsequent temperature treatments. At the end a trial, fish were identified by PIT tag and returned to a separate holding tank.

Data Analysis

A mixed effect logistic model was used to examine associations between probability of passage success and explanatory variables (water temperature, velocity,

and fish length) and linear mixed effects models were used for all other swimming performance response metrics (D_{max}, ground velocity, V_{max}, and U_{sprint}). Water temperature and velocity were treated as categorical trial-level variables and fork length as a continuous fish-level variable. A random effect was used to account for repeated measures on individual fish. Likelihood ratio tests comparing the final model to the model without the explanatory variable of interest were used to assess the strength of evidence for associations between response and explanatory variables.

The strength of evidence for statistical analysis was defined as strong ($P<0.01$), moderate ($0.01<P<0.05$), suggestive ($0.05<P<0.10$), or lacking ($P>0.10$). Intraclass correlation (ICC) was estimated for all linear mixed models to evaluate how much of the variation in response measures was explained by fish to fish variability. The number of previous tests performed and holding times between tests were not statistically analyzed due to a lack of independence with temperature and velocity treatments. However, possible relationships were examined by graphing holding times and prior number of tests with each response variable.

Plots of residuals versus fitted values and normal quantile-quantile plots of residuals from initial fitted models for response variables in the passage (D_{max} and ground velocity), sprint (V_{max}), and U_{sprint} (U_{sprint}) tests indicated homogeneity of variance and normality assumptions were adequately met. Plots of fish length versus response variables revealed approximately linear relationships. Program R (R Core Team 2014) and the lme4 package (Bates et al. 2014) were used to perform regression analysis.

Passage Test A passage attempt was classified as successful if a fish ascended the test section of the flume. The initial model fit to the passage success data included all two-way interactions among explanatory variables. Interactions were removed if likelihood ratio tests indicated a lack of statistical evidence ($P>0.10$). Interactions were removed sequentially, with interactions with the least statistical support removed first. Distance of maximum ascent was defined as the maximum upstream distance a fish ascended in a trial. The model selection process used for the passage success model was used for D_{max} and other performance response metrics.

Ground velocities were calculated by subtracting the water velocity from the fish swimming velocity. Video analysis was used to calculate the swimming velocity for each 61 cm between reference lines. The average of 14 ground velocities was calculated based on the 8.6 m section of flume with the most uniform flow conditions. The 1.8 m flume section upstream of the downstream grate was excluded from analysis. Ground velocities were calculated for 77 of the 80 trials in which passage attempts were made. In the case of multiple ascents, only ground velocities from the fastest ascent were analyzed. There was suggestive evidence that the relationship between ground velocity and water velocity depended on fish length ($\chi^2=4.83$, df=2, $P=0.09$). However, this interaction was removed from the final model because it was dependent on a single influential observation (83.0 cm/s in the 18.3 °C by 93 cm/s treatment). This observation was not removed from analysis as it did not further affect model selection and had little influence on estimates of coefficients.

Sprint Test Video recordings of sprint trials were analyzed to calculate swimming velocities obtained over each 61 cm length interval within the flume. V_{max} was recorded as the highest swimming velocity observed in each trial.

U_{sprint} Test U_{sprint} values were calculated using the formula provided by Brett (1964):

$$U_{sprint} = U_i + [U (t_i / t)]$$

where U_i is the penultimate velocity (cm/s), t_i is the amount of time (s) the fish swam in the final increment, t is the time increment between velocity increases (15 s) and U is the water velocity increment (7.6 cm/s). Presence of fish in the swim chamber was not expected to alter water velocities as all test fish had cross-sectional areas less than 10% of that of the swim chamber and thus a velocity correction was not warranted (Webb 1975). Data was analyzed separately for group one and group two tests.

U_{sprint} data were used to parameterize the equation from Peake et al. (1997) to predict the maximum distance sauger could ascend upstream at high velocities. The equation is of the form:

$$D = (U_{sprint} - V_f) \times 15 \text{ s}$$

where D is the distance (cm), U_{sprint} is the maximum swimming velocity sustainable for 15 s (cm/s), and V_f is the water velocity (cm/s). To illustrate the use of this relationship for assessing appropriate fishway lengths and water velocities, we graphed the relationship between maximum ascendable distance and water velocity using the highest and lowest U_{sprint} values from the temperature treatments and the mean U_{sprint} from all treatments.

Results

Test Conditions

Flow in the open-channel flume for all trials was non-uniform and turbulent. Non-uniform (varied) flow was caused by the downstream retention grate creating a damming effect near the flume outlet such that water depth decreased and water velocity increased as fish ascended the flume (Figure 2.3). Variation in water velocity within the flume increased with increased test velocity (Table 2.1). In the lowest velocity treatment (51 cm/s), velocity ranged from 8.2 cm/s less than the mean at the downstream end of the flume to 9.3 cm/s greater than the mean at the upstream end, in comparison to 18.1 and 23.8 cm/s, respectively, in the highest (93 cm/s) velocity treatment.

Temperatures varied little among trials within a treatment combination or among velocity treatments within a temperature treatment. In the passage test, temperatures ranged ±0.7 °C from the mean temperature among trials within a treatment combination and ±0.9 °C from the mean temperature among velocity treatments within a temperature treatment. In both the sprint test and U_{sprint} test temperatures ranged ±0.2 °C among trials within a temperature treatment.

Reynolds number, which is the ratio of inertial to viscous forces, was used to characterize flow as turbulent or laminar. Open-channel flow becomes turbulent when the Reynolds number exceeds 2,500 (Chow 1959). The mean Reynolds number exceeded 67,000 in all passage and sprint treatments but varied widely among velocity treatments (range=64,200-201,024) and within treatment combinations (Table 2.1). Reynolds number increased with velocity and temperature, with the 93 cm/s velocity

treatment at 18.3 °C having the largest mean Reynolds number and also having the largest variation within the treatment, with Reynolds number increasing with longitudinal distance upstream.

Passage Test

Sauger showed high motivation to swim upstream in the flume with the majority of fish attempting ascents immediately after being placed in the flume. Passage success across all treatments was high, with 91.3% of sauger (73 of the 80 trials with passage attempts) ascending the entire flume length. Passage rate differed little among treatments (Table 2.1) and mixed effects logistic regression indicated there was no evidence for an association between passage success and temperature (χ^2=2.81, df=2, P=0.25), velocity (χ^2=1.99, df=2, P=0.37), or fish length (χ^2=1.85, df=1, P=0.17).

Mean D_{max} was also high (12.58 m) and varied little among treatments (Table 2.1). Linear mixed effect regression indicated there was no evidence for an association between D_{max} and water temperature (χ^2=1.26, df=2, P=0.53), velocity (χ^2=2.27, df=2, P=0.32), or fish length (χ^2=1.51, df=1, P=0.22). A low ICC value (0.02) indicated that fish to fish variability explained little of the variance in D_{max}. Graphic analysis showed no apparent effects of holding time and number of trials on passage success rate or D_{max}.

Mean ground velocities differed substantially among velocity and temperature treatments. The mean ground velocity of all treatments was 26 cm/s, ranging from 20 cm/s at 10.0 °C, 28 cm/s at 14.3 °C, and 32 cm/s at 18.3 °C (Figure 2.4). There was strong evidence that mean ground velocity was positively associated with water temperature (χ^2=14.3, df=2, P=0.0008; Figure 2.4). There was suggestive evidence for a

positive association between ground velocity and test velocity (χ^2=5.18, df=2, P=0.08). Mean ground velocity was the lowest in the 51 cm/s treatment (23 cm/s), but did not differ between the 80 and 93 cm/s treatments (28 cm/s, respectively). No evidence existed for an association between ground velocity and fish length (χ^2=0.46, df=1, P=0.50). Intraclass correlation value (0.25) indicated that fish to fish variability accounted for a substantial portion of the variance observed among ground velocities, with some fish consistently swimming at low ground velocities and others at high ground velocities (Figure 2.4).

Water velocity influenced the swimming behavior used to ascend the flume. Fish used a steady sustained gait in the 51 and 80 cm/s treatments, but most fish transitioned to unsteady burst swimming (65.4% of test fish) or steady burst swimming (26.9%) in the 93 cm/s treatment. Video analysis revealed that gait transitions occurred at a mean velocity of 97 cm/s, and varied little among temperature treatments (range=93-99 cm/s).

In all trials, fish navigated upstream near the flume bottom, but did not show a preference for swimming along the walls or in the middle of the channel. Holding behavior was observed in all trials, with fish able to hold position during upstream movement at all water velocities (maximum velocity of 116 cm/s). Fish generally held position near flume corners by appressing their body, pelvic and caudal fins against the bottom. Multiple ascent attempts were common, with many fish repeatedly ascending 9.14 to 12.80 m up the flume, passively drifting to the downstream grate, then making another passage attempt. Fish rarely ascended into the headwater tank.

Sprint Test

Sauger responded to stimulation with a burst of rapid tail beats away from the stimulus followed by a glide, with maximum velocity generally observed within a meter of stimulation. Thirteen fish obtained their V_{max} in their first attempt, six in the second, and four in the third attempt. Mean V_{max} was 219 cm/s (range=119 to 350 cm/s) and there was no evidence for a relationship between V_{max} and temperature (χ^2=3.76, df=2, P=0.15; Figure 2.5). Maximum swimming velocity generally increased with fish length, but the strength of the relationship was weak (χ^2=2.38, df=1, P=0.12). An ICC of 0.29 indicated that fish to fish variability accounted for a substantial portion of the variance observed among V_{max} values, with some fish consistently obtaining higher maximum swimming velocities than others (Figure 2.6). Data plots showed a general decrease in V_{max} as number of trials and holding time increased. For example, mean V_{max} ranged from 191 cm/s for fish with the maximum holding time (33 days) and maximum number of prior tests (19) to 246 cm/s for fish with the minimum holding time (2 days) and minimum number of prior tests (12).

U_{sprint} Test

All sauger tested in U_{sprint} trials swam vigorously during the test and clear evidence of fatigue was shown by rapid opercular movements and an inability to maintain positive rheotaxis. Fish preferred the darker front half of the swim chamber and generally held position there during the acclimation period by appressing their body, pelvic fins, caudal fin, and occasionally their pectoral fins against the bottom. However, all test fish began swimming in the water column in the lower lighted area of the swim

chamber as test velocities increased. Fish transitioned from steady sustained swimming to unsteady burst-glide swimming at a mean velocity of 84 cm/s (range= 69 to 99 cm/s). Bursts ended when fish encountered the upstream grate, at which point fish returned to a benthic position and appressed their bodies to the bottom to slow downstream progress. A new burst was initiated when the caudal fin encountered the downstream grate.

Mean maximum velocity sustainable for 15 seconds in the U_{sprint} test was 124 cm/s. U_{sprint} values generally increased with temperature and variation decreased (Table 2.3). In group two there was suggestive evidence that U_{sprint} values were positively associated with temperature (χ^2=6.03, df=2, P=0.05; Table 2.5). Mean U_{sprint} was the lowest in the 10.0 °C treatment (105 cm/s) and highest at 22.3 °C (139 cm/s) for group two (Table 2.3). There was less support for associations between U_{sprint} and temperature in group one (χ^2=5.51, df=3, P=0.14). However, mean U_{sprint} was the lowest in the 12.0 °C (114 cm/s) treatment and highest at 20.2 °C (145 cm/s). There was no evidence for a relationship between U_{sprint} and fish length in group one (χ^2=0.01, df=1, P=0.91) or group two (χ^2=0.12, df=1, P=0.72). Low ICC values for both group one (ICC=0.08) and group two (ICC=0.00) indicated that fish to fish variability explained little of the variance in U_{sprint} values. No consistent patterns were observed between the holding time and the number of previous tests and U_{sprint} values.

The maximum distance sauger were predicted to ascend based on the U_{sprint} data and the equation developed by Peake et al. (1997) differed markedly among temperature treatments. The distance sauger could ascend at a water velocity of 97 cm/s ranged from 1.29 m at 10.0 °C to 7.20 m at 20.2 °C. Using the mean U_{sprint} value (124 cm/s), the

maximum allowable distance was predicted to be 4.05 m. The distance sauger were predicted to ascend decreased rapidly as water velocity increased (Figure 2.6).

Discussion

For fishways to successfully pass fish, several criteria must be met. First, the combination of the length of the structure and its velocities cannot exceed species swimming capacities in terms of endurance and maximum swimming velocities. Second, hydraulic characteristics of the structure must not behaviorally inhibit passage attempts (Castro-Santos 2004; Peake 2008; Ficke et al. 2011). In this study, we provided data on ascent distance and passage success of sauger over a range of water velocities. We also determined maximum swimming velocities and used these values to estimate endurance distances and identify potential barriers to movement. Finally, we used video observation of swimming behavior during passage to identify important gait changes and strategies employed by sauger during upstream migration. Appropriate application of the study results has the potential to evaluate sauger passage throughout its range and reconnect fragmented habitats.

The results of the passage test indicated that passage structures of 12.8 m in length with hydraulic conditions similar to those of an open-channel flume should not inhibit passage of sauger (34.0-43.9 cm) for temperatures between 10.0 to 18.3 °C and average water velocities less than 93 cm/s. The high passage success, multiple successful attempts occurring in all treatments, and similarities in passage success and D_{max} among all treatments indicated that test conditions did not limit upstream sauger movements. In a similar open-channel flume study with the morphologically similar congener, walleye

Sander vitreus, Peake (2008) reported high rates of passage (>80%) in a 25 m and 50 m flume at mean velocities ranging from 39 to 100 cm/s (mean FL=40.0 cm, range=15.0-61.0 cm; mean temperature=15.4 °C, range=5.0-23.0 °C). Whether sauger would be able to traverse a similar distance against this range of velocities awaits investigation in a longer testing apparatus. However, differences in passage success between sauger and walleye of similar size at a vertical slot fishway (40.0% versus 57.1%) suggest that swimming abilities and/or behavior differ between these species (Thiem et al. 2013). Differences in swimming abilities among closely related, morphologically similar species have been previously reported and demonstrate the difficulty of using surrogate species for passage design and evaluation (Haro et al. 2004; Ficke et al. 2011; Underwood et al. 2014).

The ground velocity results suggest that sauger are choosing swimming velocities that maximize ascent distance. Fish can maximize distance of ascent by swimming at a constant ground velocity in relation to changing water velocities (Castro-Santos 2005). Video analysis revealed that sauger generally maintained a constant ground velocity by increasing swimming velocity when encountering higher water velocities. However, when water velocity exceeded a certain threshold (97 cm/s), sauger transitioned to higher ground velocities. For example, in the 10.0 °C treatment fish swam at a mean velocity of 19 cm/s when water velocities were less than 97 cm/s, but increased ground velocity to 28 cm/s when water velocity exceeded 97 cm/s. Similar increases in ground velocity were observed in the 14.3 °C (8 cm/s increase) and 18.3°C treatment (17 cm/s increase). Peake and Farell (2004) and Castro-Santos (2005, 2013) observed similar patterns in

ground velocities for smallmouth bass, American shad, alewife, blueback herring, brook trout and brown trout in flume experiments and Standen et al. (2004) observed a similar pattern in migrating sockeye salmon.

The observation of fish swimming at constant ground velocities up to a threshold velocity has important implications for predicting passage success. Traditionally, passage design and evaluation has been based on models and predictive tools such as FishXing that assume fish will swim at a constant swimming velocity (Beach 1984; Powers et al. 1985; Bell 1991; Clay 1995). Observations of free-swimming sauger did not support this assumption. Holding behavior was common in all treatments and swimming velocity generally increased with water velocity. Our findings suggest that predictive models that assume constant ground velocity, in contrast to constant swimming velocity, may provide more realistic estimates of passage (Castro-Santos 2006). Additionally, models should use estimates of burst swimming endurance to predict passage for fishways with water velocities exceeding the threshold at which gait transitions are observed.

The failure of traditional models to incorporate intraspecific variation in swimming velocities may also limit their predictive power (Castro-Santos 2006). Video analysis and the relatively high ICC value (0.25) for ground velocities and V_{max} (0.29) revealed substantial intraspecific variation in swimming behavior and performance, which has also been reported for other species (Berry and Pimentel 1985; Peake and Farrell 2004; Castro-Santos 2004). Individual variation in swimming behavior was especially apparent at the highest test velocity during gait transitions that incorporated

burst swimming. Differences in energy expenditures among selected swimming gaits and velocities have been shown to affect passage success (Peake and Farrell 2004; Castro-Santos 2006). Although different swimming strategies did not affect passage success or ascent distances in our study, it is likely that they would have an effect in more hydraulically challenging conditions. Further research is needed to determine endurance associated with these different swimming strategies. Stochastic models, such as those presented by Castro-Santos (2006), can account for the variability in swimming strategies and may provide more accurate passage predictions.

The gait transition we observed at 97 cm/s likely reflects the switch from aerobic to anaerobic swimming. Aerobically powered red muscle fibers are believed to support steady sustained swimming (Videler 1993; Rome et al. 1990; Peake and Farrell 2004). However, slow contraction rates of red muscle inhibits rapid tail beats that are needed to attain high swimming velocities (Rome et al. 1990). To ascend high velocity zones, fish must recruit anaerobically powered white muscle fibers that have high contraction rates (Rome et al. 1990). Transitions from sustained steady to unsteady or burst gaits marks the onset of white muscle activity and the velocity at which gait transitions occur has been interpreted as the maximum aerobic swimming capacity (Johnson et al. 1994; Wilson and Eggington 1994; Peake and Farrell 2004). Aerobic exercise is believed to be indefinitely sustainable whereas anaerobic exercise will result in fatigue due to the exhaustion of extracellular energy supplies and/or the accumulation of waste products (Beamish 1978; Johnson et al. 1994; Colavecchia et al. 1998). Our results indicate that sauger use aerobically powered swimming at water velocities less than 97 cm/s and

should be physiologically capable of ascending long distances if water velocities are below this threshold. Conversely, fatigue and passage failure will likely occur when water velocities are greater than this threshold except for short distances.

The U_{sprint} data from the swim chamber and the maximum sprint velocity from the flume both provide measures of anaerobic endurance. Comparison of the results contributes to the growing body of literature that suggests swim chambers may underestimate swimming abilities (Mallen-Cooper 1992; Peake 2004; Peake and Farrell 2006; Holthe et al. 2008). For example, the mean distance a sauger could ascend at a water velocity of 97 cm/s was predicted to be 1.29 m at 10.0 °C using the U_{sprint} data whereas 89% of sauger in the 10.0 °C by 93 cm/s treatment were able to ascend the 3.67 m of open-channel flow that had water velocities greater than 97 cm/s (mean water velocity=99.7 cm/s). These differences are likely a result of the relatively small size of the swim chamber inhibiting natural swimming behaviors and frequent encounters with the downstream and upstream grates inducing stress. For example, when fish used unsteady swimming gaits in the flume bursts were followed by passive glides that presumably allowed some metabolic waste products to be processed and subsequent bursts were always initiated before ground velocity reached zero (Peake and Farrell 2006). In contrast, bursts in the swim chamber ended abruptly when the upstream grate was encountered and fish were forced to oscillate between positive and negative ground velocities in order to swim at an unsteady gait. This behavior is predicted to be comparatively inefficient and may negate energy savings associated with adopting an unsteady gait (Peake and Farrell 2006). The use of swim chambers with longer test

sections relative to body size may allow fish to use more natural swimming behavior and has been shown to provide more realistic estimates of swimming performance (Tudorache et al. 2007). Despite providing conservative estimates, the U_{sprint} test did provide a repeatable and time effective method for measuring sprinting endurance. Additionally, estimates of maximum aerobic swimming velocity from gait transition observations were similar between the U_{sprint} (84 cm/s) and passage test (97 cm/s). Use of conservative estimates of sprinting endurance for passage design and assessment may be prudent as intense anaerobic exercise results in a number of physiological consequences that can result in death (Lee et al. 2003; Burnett et al. 2014). Additionally, designing passage structures using conservative estimates of sprint endurance from a relatively strong swimmer such as sauger may facilitate passage for weaker swimmers in the fish assemblage.

Estimates of maximum swimming velocities from the sprint test can be used to assess whether sauger will be able to ascend areas of high velocity often associated with passage structures. Maximum swimming velocities (V_{max}) in the sprint test were obtained in a low velocity environment, measured over a 61 cm distance, and were generally maintained for less than half a second. Due to the short duration of V_{max}, the results are most applicable to passage structures that consist of short sections of high velocity flows interspersed with areas of low velocities such as vertical slot and pool weir fishways. Using the mean V_{max} (219 cm/s) and the equation provided by Peake et al. (1997), 50% of the tested sauger are predicted to be able to ascend only 5 cm at a water velocity of 200 cm/s and 19 cm at 150 cm/s. Structures with water velocities greater than

219 cm/s would represent a barrier to the majority of tested sauger. The maximum swimming velocity obtained in the passage test was 260 cm/s, indicating maximum velocities of coerced sauger are representative of velocities obtainable by free-swimming sauger. The finding that 43.4% of sauger did not obtain their V_{max} on their first stimulation supports the finding of Nelson and Claireux (2005) that multiple sprint trials are needed to accurately assess the maximum sprint performance of fish.

The lack of evidence for associations between swimming performance metrics and body size is surprising given how widely body size effects have been reported (Beamish 1978; Videler 1993; Haro et al. 2004; Katopodis and Gervias 2011). Previous studies have found that larger fish can swim faster and farther than smaller fish (Beamish 1978; Videler 1993; Bestgen et al. 2010). The lack of evidence for body size associations is likely a result of a relatively small range of body sizes (34.0-43.0 cm) tested. All tested sauger were mature adult males that were likely three years of age or older (Carlander 1950; Preigel 1964; Bozek et al. 2011). Smaller juvenile fish are predicted to have lower endurance and sprinting capabilities, which is consistent with the finding of Jaeger et al. (2005) that diversion dams did not inhibit movements of adult sauger but did restrict upstream movements of juveniles.

There was inconsistent evidence for temperature influencing swimming performance. The lack of evidence for temperature associations with V_{max} is consistent with the findings of Blaxter and Dickson (1959), Brett (1967), and Bennet and Huey (1990) that temperature does not affect anaerobic exercise. However, performance studies in swim chambers indicate that aerobic swimming abilities generally increase

with water temperature up to an optimum temperature then decrease as the upper thermal limit is approached (Beamish 1978; Randall and Brauner 1991; Myrick and Cech 2000; Ojanguren and Brana 2000). In the passage test, there was strong evidence for ground velocities being positively related to temperature, which may be a result of metabolic rate and contraction rates of muscles increasing with temperature (Brett and Glass 1973; Beamish 1990; Rome et al. 1990). However, differences in ground velocities associated with temperature did not affect ascent distance or passage success. We predict that temperature, water velocity, and body size associations would have been observed if higher water velocities that limited upstream movements were tested. In the U_{sprint} test, higher water velocities were tested and a positive association between U_{sprint} values and temperature was observed. It was surprising that the rate of increase of U_{sprint} values with temperature remained similar even when water temperatures exceeded the growth optimum (19.6 °C) of sauger (Hasnain 2010). Testing at water temperature greater than 22.3 °C is needed to determine the thermal optimum for swimming performance. Where performance metrics did differ among temperature treatments, we suggest use of the most conservative estimates associated with low temperature treatments given that sauger spawning migrations occur at low water temperatures (10.3 °C; Hasnain et al. 2010). In all performance tests, our ability to identify associations among swimming performance metrics and explanatory variables was limited by our relatively small sample size.

A limitation of the use of a flume to assess passage is that results are specific to the hydraulic conditions fish experienced within the flume. The longitudinal velocity and depth profiles present in our test flume were most similar to backwater flow, which

occurs when flooded downstream conditions cause water to back up in the structure (Harvey 2009). Sauger may encounter these conditions in fishways during springtime spawning migrations. The smooth walls and floor of the open-channel flume resulted in a lack of structured turbulence and results are most applicable to similarly designed passage structures such as box culverts or breached dams with minimal structure in the flow (Haro et al. 2004). The lack of structure combined with the observed high Reynolds numbers likely resulted in highly chaotic non-periodic turbulence that can negatively affect fish stability, increase energetic costs of swimming, and deter upstream fish movements (Pavlov et al. 2000; Enders et al. 2003; Lupandin 2005). The observation of many fish terminating their ascent at the end of the test section may have resulted from the highly turbulent conditions further upstream in the flume deterring further upstream movements. Alternatively, studies have shown fish are generally attracted to structured turbulence created by some roughness elements, weirs, and other objects in the flow and can utilize the structure to reduce energy expenditures, assist upstream movements, and enhance station holding abilities (Webb 1998; Hinch and Rand 1998; Pavlov et al. 2000; Liao et al. 2003). Given that sauger swam along the bottom of the flume and frequently held position, it is likely that they could use structured turbulence to ascend passage structures with average velocities exceeding their swimming abilities. However, the effects of turbulence on swimming behavior and performance remain poorly understood and require further research.

Repeated measures of swimming performance on a limited number of test fish was a recognized limitation of our study. However, given that passage success and

maximum ascent distances were similar across all passage treatments, it appears that repeated testing did not strongly influence passage results. The sprint and U_{sprint} tests both involved anaerobic exercise that requires a recovery period to process waste products and restore energy reserves (Milligan 1996). However, Farrell et al. (1998), Jain et al. (1998), and Handelsman et al. (2010) demonstrated that swimming performances that resulted in fatigue were repeatable in the same day and Nelson et al. (2002) and Reidy et al. (2000) found sprint performance to be repeatable over the course of three months. Thus, it is not expected that the minimum (2 days) or maximum holding time (33 days) affected the results. Alternatively, Farrell et al. (1990) reported that a period of exercise training can result in improvements in swimming performance. In both the sprint and U_{sprint} tests, the number of previous trials was negatively associated with performance, indicating that no training effects were occurring. Moreover, repeated testing allowed detection of intraspecific variation in sprint performance.

Based on the results of the passage test, we suggest that passage structures with average water velocities less than 97 cm/s should provide passage for most sauger. Passage structures with water velocities exceeding 219 cm/s will likely represent barriers to sauger and structures with water velocities greater than 124 cm/s should provide frequent resting refuges. It is important to note that recommendations are based on average water velocities, which differ substantially from the water velocities experienced by sauger swimming along the bottom. Measurements revealed bottom water velocities in the flume were 26% lower than average water velocity. Greater use of actual water

velocities experienced by fish in their migration paths for passage design and assessment may limit inconsistencies between laboratory predictions and field observations.

Future studies on sauger should focus on accessing endurance at water velocities exceeding 97 cm/s. Additionally, information on the swimming abilities of juvenile and female sauger is needed. Given that sauger are relatively strong swimmers, we also suggest further research examining behavioral aspects of swimming that may affect passage success. Using field studies and monitoring to identify structures that are inhibiting fish passage and replicating these field conditions in the laboratory to identify hydraulic characteristics that are preventing passage may be an effective method for increasing our understanding of how fish swimming abilities and behavior affect fish passage.

Tables

Table 2.1. Summary of test conditions and results for the nine velocity and temperature (T) treatment combinations during sauger passage testing in the experimental flume. Reynolds number (Re) is dimensionless. Mean velocity, Reynolds number, D_{max}, and ground velocity are presented as mean ±1 SE (standard error).

Nominal Velocity (cm/s)	T (°C)	Mean Velocity (cm/s)	Re	Participation Rate	Passage Rate	D_{max} (m)	Ground Velocity (cm/s)
51	10.7	48.0 ± 0.5 (44.1, 52.6)	67,760 ± 351	0.75	0.83	12.30 ± 0.56	18.2 ± 3.7
	14.3	51.8 ± 0.5 (47.3, 56.4)	78,806 ± 311	0.9	1	12.81 ± 0.00	23.5 ± 2.7
	17.6	52.3 ± 0.3 (50.9, 55.8)	94,420 ± 372	1	1	12.81 ± 0.00	25.9 ± 4.0
80	10.1	72.9 ± 0.7 (68.4, 81.7)	105,036 ± 436	0.9	0.78	12.23 ± 0.48	19.8 ± 1.6
	14.3	80.2 ± 1.1 (69.4, 91.2)	125,199 ± 736	1	0.9	12.75 ± 0.06	30.4 ± 4.1
	18.4	84.9 ± 0.9 (74.0, 91.0)	154,235 ± 914.1	1	1	12.26 ± 0.58	34.4 ± 5.9
93	9.1	90.4 ± 1.7 (77.8, 104.0)	179,509 ± 1,439	0.9	0.89	12.74 ± 0.07	20.5 ± 2.0
	14.1	93.7 ± 3.2 (72.7, 125.3)	152,458 ± 2,573	0.7	0.86	12.55 ± 0.28	29.3 ± 4.5
	18.8	92.9 ± 3.0 (72.0, 126.9)	177,010 ± 3,109	1	1	12.81 ± 0.00	35.4 ± 5.9

Note: Standard error (SE) calculated as the sample standard deviation divided by the square-root of the number of observations in the sample.

Table 2.2. Summary of hydraulic conditions and test results for the three temperature (T) treatments during sauger sprint testing in the experimental flume. Reynolds number (Re) is dimensionless. Trials represent the total number of trials performed within a given treatment.

				V_{max} (cm/s)		
T (°C)	Trials	Re (SE)	Participation Rate	Mean	Range	SE
11.5	8	96,462 (335)	0.88	212.9	(121.1, 309.9)	27.8
14.4	8	107,755 (377)	0.88	190.9	(119.3, 258.3)	17.1
17.9	10	78,001 (305)	0.90	245.6	(196.1, 350.4)	16.3

Note: Standard error (SE) calculated as the sample standard deviation divided by the square-root of the number of observations in the sample.

Table 2.3. Summary of test results from the seven sauger U_{sprint} temperature treatments. Results are split for the two groups. Temperature (T) recorded in °C and U_{sprint} in cm/s. Trials represent the total number of trials performed within a given treatment.

			U_{sprint}		
Group	Temperature	Trials	Mean	Range	SE
1	12.0	4	113.8	(90.9,155.0)	14.2
	16.3	4	129.8	(106.0, 155.7)	12.3
	18.1	5	128.1	(109.3, 150.8)	6.8
	20.2	5	144.8	(123.9, 185.6)	11.2
2	10.0	5	105.4	(80.6, 138.9)	11.7
	14.0	5	111.7	(87.8, 144.9)	10.5
	22.3	5	139.1	(107.2, 155.0)	9.0

Table 2.4. Coefficient estimates from the final linear mixed effect model describing the relationship between the maximum swimming velocity of sauger, as estimated in sprint tests, and temperature (°C), and fish length (cm).

Variable	Coefficient Estimate	Standard Error	P-value
Intercept	22.9	182.7	0.9
ind.14	-21.7	22.2	0.34
ind.18	25.17	22.6	0.28
Fish Length	0.5	0.47	0.12

Note: The 12.0 °C treatment was designated as the reference level and coefficient values represent the effect size relative to this treatment. P-values come from likelihood ratio tests comparing the final model to the model without the coefficient of interest.

Table 2.5. Coefficient estimates from the final linear mixed effect models describing relationships between U_{sprint}, as estimated in sauger swim chamber U_{sprint} tests, and temperature (°C), and fish length (cm). Data presented separately for group one (top) and group two (bottom).

Group	Variable	Coefficient Estimate	Standard Error	P-value
1	Intercept	124.9	177.3	0.37
	ind.16	16	14.4	0.22
	ind.18	15.83	13.9	0.22
	ind.20	32.57	13.9	0.02
	Fish Length	-0.03	0.44	0.91
2	Intercept	83.5	62.3	0.21
	ind.14	6.33	13.1	0.63
	ind.22	33.7	13.1	0.02
	Fish Length	0.06	0.16	0.73

Note: Indicator variables were used to model the categorical variable temperature, with ind.16 equal to 1 for the 16.3 °C treatment and 0 otherwise. The ind.18, ind.20, ind.14 and ind.22 variables similarly define the 18.1, 20.2, 14.0, and 22.3 °C treatments, respectively. The 11.5 °C treatment was designated as the reference level for group one and the 10.0 °C treatment for group two. P-values come from likelihood ratio tests comparing the final model to the model without the coefficient of interest.

Figures

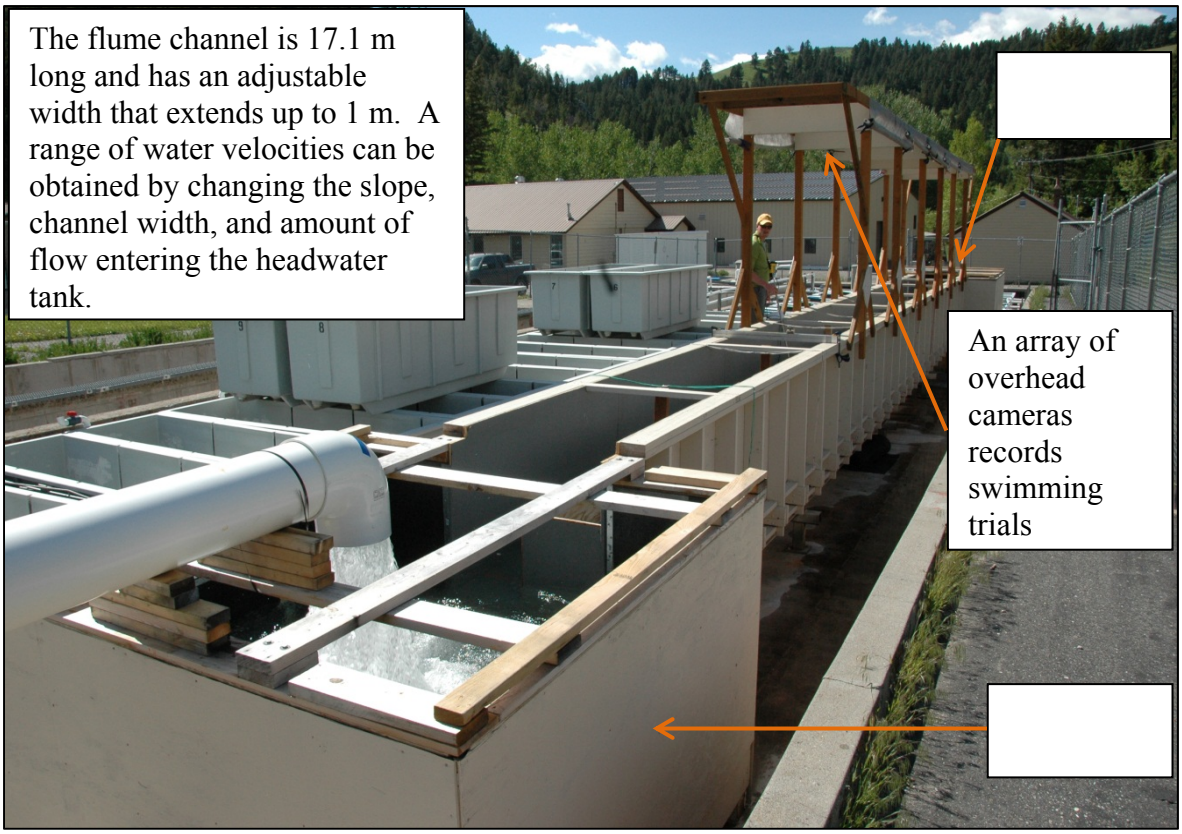

Figure 2.1. Picture of the open-channel flume located at the Bozeman Fish Technology Center.

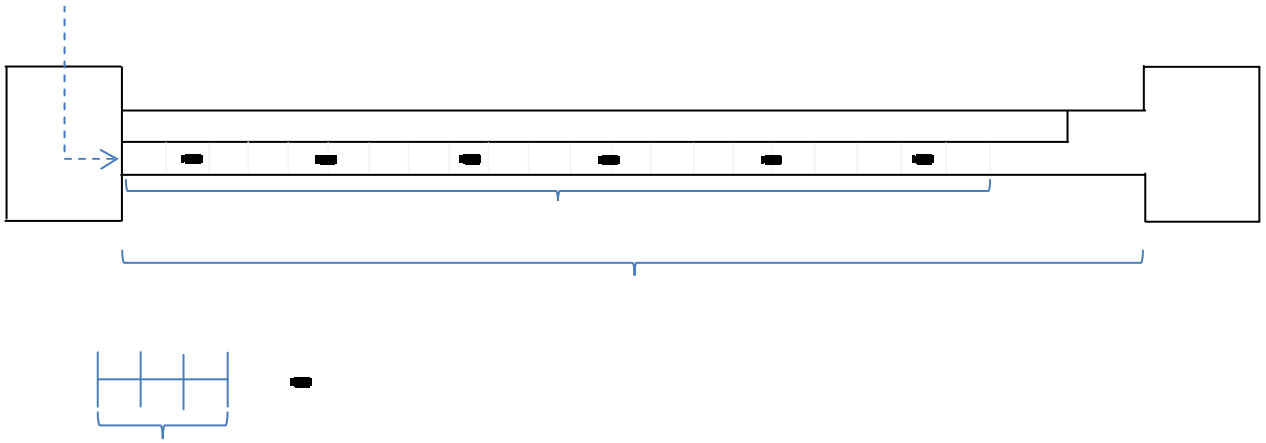

Figure 2.2. Plan view diagram to scale of the open-channel flume located at the Bozeman Fish Technology Center.

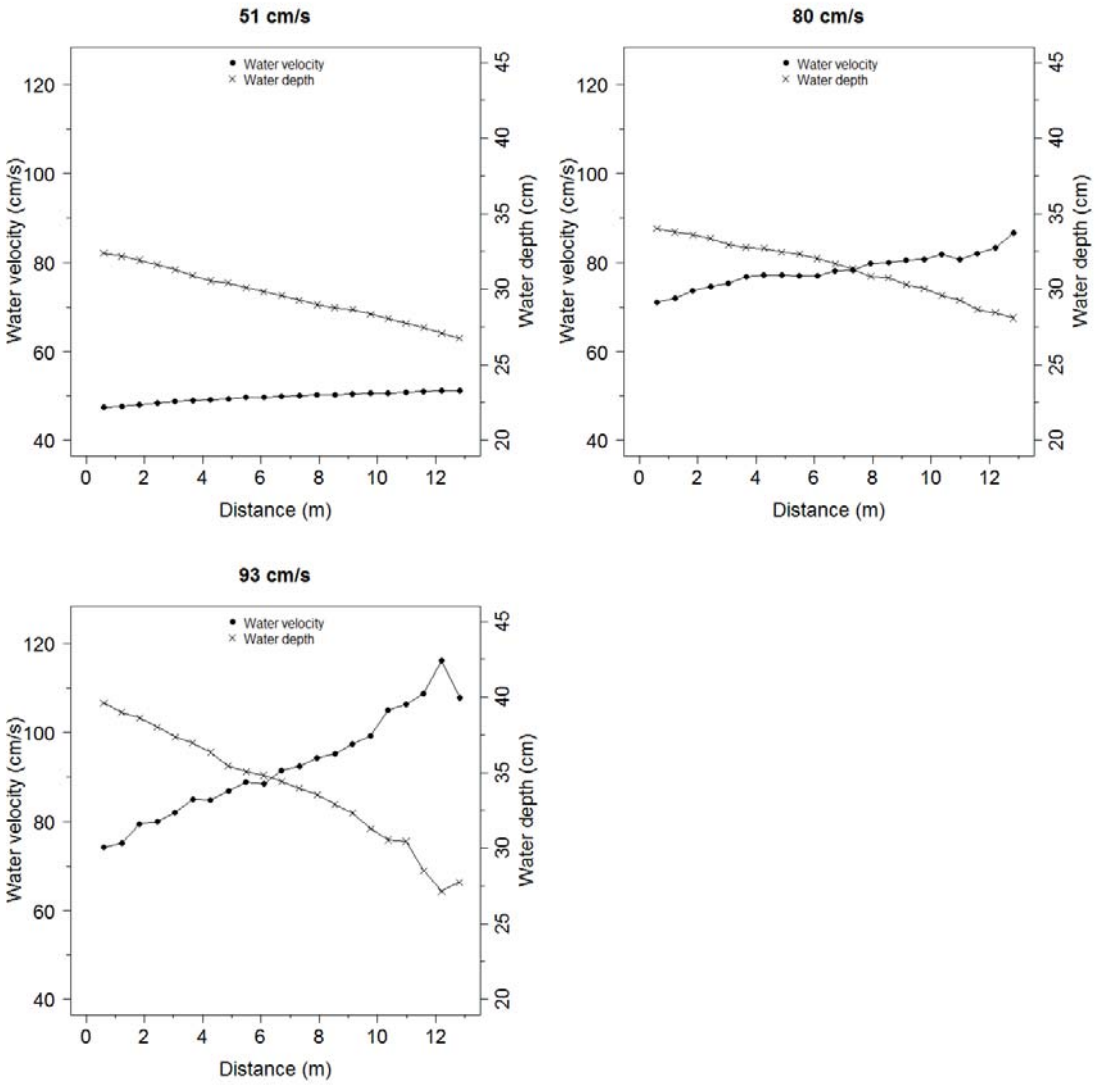

Figure 2.3. Mean water velocity and depth measurements along the length of the flume test section for each of the three velocity treatments in the sauger passage test.

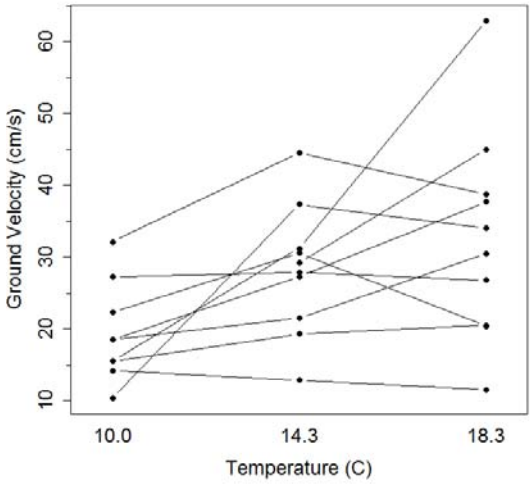

Figure 2.4. Average ground velocities of individual sauger for the three temperature treatments in the passage test. Each point represents an individual's average ground velocity for the three velocity treatments within each temperature treatment. Lines connect an individual's average ground velocities

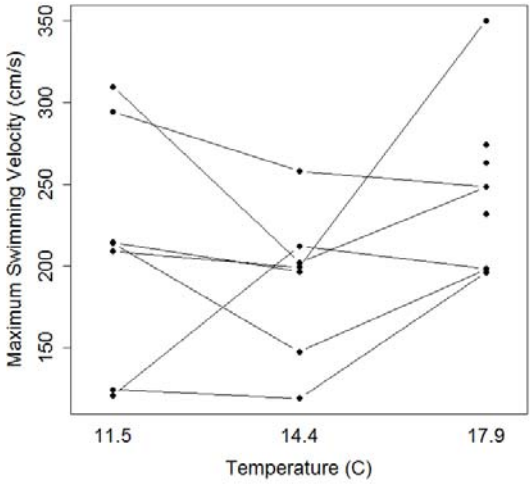

Figure 2.5. Maximum swimming velocity (V_{max}) of individual sauger for the three temperature treatments in the sprint test. Lines connect an individual's V_{max} for the temperature treatments in which it was tested.

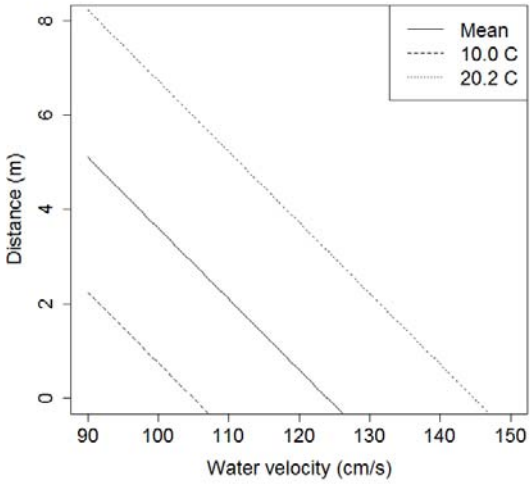

Figure 2.6. Combinations of distances between resting refuges and water velocities that are predicted to allow passage of sauger. The equation of Peake et al. (1997) and the mean U_{sprint} of all temperature treatments (124 cm/s), the highest mean U_{sprint} (145 cm/s; 20.2 °C), and the lowest mean U_{sprint} (105 cm/s; 10.0 °C) were used to develop the depicted curves. Any combination of distance and water velocity in the region above the line for a given temperature are predicted to result in passage failure of sauger.

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CHAPTER 3

RELATIONSHIPS AMONG SWIMMING PERFORMANCE, BEHAVIOR, WATER VELOCITY, TEMPERATURE, AND BODY SIZE FOR LONGNOSE DACE *RHINICHTHYS CATARACTAE*

Abstract

Longnose dace are one of the most widely distributed prairie fishes. Like other prairie fishes, seasonal movement among habitats is an important aspect of their life history in the small, intermittent streams they inhabit. To assess their swimming performance in relation to potential passage barriers, we estimated passage success, maximum ascent distances, and maximum sprint velocities in an open-channel flume over a range of water velocities (39, 64, 78, and 90 cm/s) and temperatures (10.7, 15.3, and 19.3 °C). Longnose dace had high passage success in the test flume (95%) at test velocities of 39 and 64 cm/s, but success rate dropped markedly at higher velocities (66% at 78 cm/s and 19.7% at 90 cm/s). Dace swam along the bottom of the flume at all test velocities, but increased position-holding as velocity increased. Their maximum sprint velocity was 139 cm/s. Swimming performance generally increased with water temperature and body size. Based on these results, fishways with mean velocities less than 64 cm/s should allow passage of most longnose dace, water velocities greater than 139 cm/s would be impassable, and water velocities greater than 100 cm/s within structures should be limited, as these velocities induced continuous burst swimming, which is sustainable for only brief periods. Study results highlighted the advantages of

evaluating a multitude of metrics for assessing swimming performance and the use of open-channel flumes, which more closely simulate the hydraulic features of fishways and allowed for unique observations of behavioral changes that species employ during upstream navigation.

Introduction

Habitat fragmentation has contributed to freshwater fish having the highest extinction rates among vertebrates worldwide (Dudgeon et al. 2005; Nilsson et al. 2005; Bunn et al. 2010; Burkhead 2012). Culverts, weirs, diversion dams, and other potential barriers to fish movement associated with energy, agricultural, urban, and infrastructure development in North America's western Great Plains have resulted in highly fragmented stream systems (Abel et al. 2000). The variable hydrographs that characterize stream systems in the western Great Plains can exacerbate the negative effects of barriers to fish movement. Flash flooding and desiccation repeatedly depopulate suitable habitat patches making recolonization a key factor affecting species and population persistence (Fausch and Bestgen 1997; Dodd et al. 2003). Thus, frequent and extensive movement is common among Great Plains fishes for spawning, recolonization of upstream habitats, avoiding unfavorable conditions, and locating suitable refuges during flooding and desiccation events (Schlosser and Angermeier 1995; Platania and Altenbach 1993; Labbe and Fausch 2000; Scheurer et al. 2003). Barriers that reduce the longitudinal connectivity through a stream can inhibit these movements, prevent recolonization events, reduce gene transfer among populations, and ultimately increase the risk of local extirpation (Winston et al. 1991; Toepfer et al. 1999; Park et al. 2008). In order to

effectively mitigate the negative impacts of potential barriers to fish movement, it is vital to assess the swimming abilities of plains fishes so that barriers can be identified and removed and new fishways can be properly designed to allow natural fish movements.

Of the 55 fish species native to the Great Plains region of eastern Montana, Wyoming and Colorado, 33 (60%) have been given a conservation designation due to population declines or rarity (Hubert and Gordan 2006). Given the paucity of detailed swimming information on these fish species, it can be advantageous to base fishway design criteria on the weaker swimmers in a fish assemblage. As swimming ability is strongly associated with body size, setting design criteria to pass small-bodied fish will likely ensure that larger, stronger swimmers will also be able to pass (Northcote 1988). However, the majority of fish passage studies have focused on larger, stronger swimming fish such as salmonids (Katopodis and Gervias 2011).

Swimming studies on small-bodied fish have primarily consisted of field studies and laboratory studies conducted in swim chambers. Field studies have assessed passage of small-bodied fish through examination of differences in fish assemblages above and below potential barriers (Winston et. al 1991; Dodd et al. 2003; Rajput 2003; McLaughlin et al. 2006), mark-recapture studies on sections of streams and rivers containing potential barriers (Warren and Pardew 1998; Rajput 2003; Coffman 2005; Benton et al. 2008; Bouska and Paukert 2010; Briggs and Galarowicz 2013), and active displacement studies at potential barriers (Burford 2005; Rosenthal 2007). These studies and similar studies on larger fish have found that culverts, weirs, and diversion dams can restrict fish movements and alter the distribution of fish to varying degrees with barrier

length and water velocity being important factors affecting passage success (Belford and Gould 1989; Warren and Pardew 1998; Burford 2005; Bouska and Paukert 2010; Briggs and Galarowicz 2013). However, it can be difficult to determine whether differences in fish assemblages above and below potential barriers are due to passage restrictions, natural longitudinal differences in fish assemblages, or lack of motivation to move upstream (Schlosser 1987; Ostrand and Wilde 2002; Coffman 2005). Additionally, results from field studies are specific to the hydraulic conditions present during the study, which may not be representative of conditions during other times of the year, and can be difficult to apply to other areas due to a lack of control of field conditions and the simultaneous interaction of many variables (Buford 2005; Katopodis and Gervias 2011).

Laboratory studies allow for precise control of experimental conditions and for examination of the effects of variables such as fish length and morphology, temperature, and water velocity on swimming performance. The majority of laboratory studies on small-bodied fish have been conducted in enclosed swim chambers and have examined the time to fatigue at a set velocity (Toepfer et al. 1999; Adams et al. 2000; Billman and Pyron 2005; Bestgen et al. 2010; Ficke et al. 2011) or the maximum aerobic swimming velocity using an incremental velocity test ('U_{crit} test') in which the velocity is incrementally increased and time to failure at the maximum velocity obtained is measured (Brett 1967; Nelson et al. 2003; Holthe et al. 2008; Leavy and Bonner 2009). However, recent studies have suggested that the artificial settings created in swim chambers may add stress, reduce swimming motivation, inhibit natural behaviors associated with energy conserving strategies and can substantially underestimate a

species ability to navigate potential barriers (Mallen-Cooper 1992; Peake 2004a; Peake 2004b; Castro-Santos 2005; Peake and Farrell 2006; Holthe et al. 2008).

Open-channel flumes allow fish swimming to be examined in a controlled setting that more closely approximates conditions fish experience in passage structures and may provide more realistic correlates of passage success in natural conditions (Haro et al. 2004). The larger scale of flumes allow fish to move through the flow, employ natural swimming behaviors, and use energy conserving strategies such as gait transitions ('burst-glide') and holding behavior during upstream movements (Haro et al. 2004). Flumes also allow for direct measurement of distance of ascent in contrast to swim chamber studies wherein potential ascent distances are back-calculated from time to fatigue under assumptions of a constant swimming velocity, which does not account for the aforementioned energy-conserving strategies (Peake 2004a). By allowing the distance of ascent over a range of hydraulic conditions to be measured, flumes provide a powerful tool to predict passage probabilities in field settings. Additionally, the larger scale of flumes allow for unrestricted sprint swimming and measurement of maximum swimming velocities. Because zones of high-velocity flows are common and sometimes intentional features of fishways, data on maximum swimming velocities can be used to identify barriers, set design criteria for maximum allowable water velocities, or to create barriers when it is desirable to limit the upstream distribution of a species (Clay 1995; Haro et al. 1998). However, due to a limited number of experimental flumes and difficulty in tracking and tagging small-bodied fish, there have been few studies assessing

the swimming abilities of small-bodied fish in flumes (Holthe et al. 2008; Bestgen et al. 2010).

To accurately assess swimming abilities, the effects of water velocity, temperature, and body size should be considered. Water velocity dictates swimming velocities and energy expenditures necessary to make upstream progress. At low water velocities, low swimming speeds powered by aerobic processes that can be maintained indefinitely without fatigue can be used to progress upstream (Beamish 1978). High water velocities require use of fast glycolytic white muscle powered by anaerobic processes, which are sustainable for only short periods of time (Beamish 1978). Given the variety of water velocities associated with passage structures, assessment of swimming abilities over a range of water velocities is necessary to inform passage design. As thermal conformers, temperature has a profound effect on all physiological functions of fish, including swimming abilities (Coutant 2006). Given the wide range of temperatures experienced by stream fish in the Great Plains, the temperatures associated with fish movements are an important consideration when designing passage structures (Gillette et al. 2006; Falke et al. 2010; Hargrave and Taylor 2010). Body size has also been shown influence swimming performance and is another important component of passage assessment (Fry and Cox 1970; Brett 1965).

We evaluated the swimming abilities of longnose dace *Rhinichthys cataractae* using an open-channel flume and examined associations among swimming performance and water velocity, temperature and body size. Longnose dace were selected as a study species because of the lack of detailed swimming information on the species, evidence

that they may be among the weaker swimmers within the Great Plains fish assemblage, and the potential for this information to be applicable over a large area, given that longnose dace have the widest distribution of any Cyprinidae in North America (Gilbert and Shute 1980; Dodd et al. 2003; McLaughlin et al. 2006; Rosenthal 2007). Swimming information on longnose dace is limited to two laboratory studies that evaluated time to fatigue at 67 cm/s (Billman and Pyron 2005) and maximum sprint velocities and U_{crit} values (Aedo et al. 2009), field studies examining abundance above and below potential barriers (Dodd et al. 2003; McLaughlin et al. 2006), and an active displacement study that measured passage success rates of tagged fish (Rosenthal 2007). Dodd et al. (2003) and McLaughlin et al. (2006) found the abundance of longnose dace to be lower above passage structures than below, indicating that passage structures may be limiting upstream movements. Rosenthal (2007) examined fish passage through culverts in eastern Montana streams and found longnose dace to be the only species among the four most abundant species studied wherein passage restrictions were observed.

In this study, we assessed swimming performance of longnose dace over a range of velocities and temperatures to provide better estimates of passage success and restriction at current and future fishways. Using an open-channel flume, we estimated passage success, maximum ascent distance, and maximum sprint velocity and examined relationships among swimming performance, velocity, temperature, and body size.

Methods

Study Design

Tests to characterize the swimming abilities of longnose dace were conducted in an open-channel flume located at the Bozeman Fish Technology Center (BFTC; Bozeman, MT) from June to September of 2013. In the passage test, fish were tested at a combination of four velocity (nominally 39, 64, 78, and 90 cm/s) and three temperature treatments (nominally 10.7, 15.3, and 19.3 °C) for a total of twelve unique treatment combinations. Nominal velocities and temperature represent mean velocities and temperatures, respectively. Seven trials occurred at each of the twelve treatment combinations. Three fish were tested per trial, and all trials in each treatment combination were conducted in the same day. Fish were only tested once in the passage test. The range of temperatures is representative of spring and fall conditions in Great Plains streams when fish may be moving upstream to spawn or in response to stream desiccation (Gillette et al. 2006; Falke et al. 2010; Hargrave and Taylor 2010). The velocity treatments were selected to represent a range of velocities likely encountered within fishways. Upper temperature and velocity limits were the maximum that could be tested at the BFTC.

Due to the changing seasonal availability of different temperatures of well water and the time involved adjusting water temperature, a sequential rather than a random test design was used. Temperature treatments were ordered from 15.3, to 10.7, to 19.3 °C, and the full set of velocity treatments were run sequentially from lowest to highest test velocity at each test temperature.

Sprint tests were conducted with individual test fish at a single water velocity. Water velocity was set at 18 cm/s to provide sufficient velocity to trigger positive rheotaxis yet prevent excessive energy expenditure. Maximum sprint velocity was evaluated at three test temperatures similar to those used in the passage trials (12.3, 14.5 and 19.2 °C). The order of the treatments was 14.5, 12.3, and 19.2 °C.

Test Fish

Longnose dace were collected from the Madison and Gallatin rivers in southwestern Montana during summer 2013 using a backpack electrofishing unit. Fish were transported in an aerated tank to the BFTC and transferred to 1.5 m diameter by 1.5 m deep circular tanks that mimicked river temperature at time of collection (± 0.5 °C). A salt treatment (5 ppm) was applied to alleviate osmotic stress associated with transport. Fish were fed daily to satiation with a commercial trout feed and feeding ceased 12 hours prior to testing. Prior to testing, temperatures in holding tanks were adjusted at a maximum rate of 1°C every 8 h until the test temperature was obtained. Once the test temperature was reached, fish were individually netted and randomly assigned to one of four 75 L rectangular flow-through tanks (120 x 35 x 25 cm) for each velocity treatment. The tank to which fish were assigned was not expected to affect swimming performance as all tanks had identical fish densities and dimensions. Fish were held in holding tanks for a minimum of two days prior to testing. A fungal infection in the 19.3 °C holding tank resulted in mortality of the majority of fish in that tank. No signs of infection were observed in any of the other tanks and fish from this tank were not used for testing.

Subsequently, another group of dace were acclimated to 19.3 °C. However, these fish were smaller than other test fish resulting in unequal sizes of test fish among treatments.

Passage and Sprint Tests

Passage and sprint tests were conducted in a large (17.10 x 0.91 m) open-channel flume located at the BFTC (Figure 3.1). Flume width and slope were set at 0.46 m and 0.69%, respectively, in order to obtain the desired range of hydraulic conditions. Water entered the flume from a headwater tank and flowed through the open-channel into a tailwater tank. Grates located at the upstream and downstream ends of the open-channel prevented fish escape. A downstream holding area (1.00 x 0.46 m) located just upstream of the downstream grate and an upstream holding area (2.00 m x 0.46 m) located 10 m upstream were created by removing small sections of the flume wall to create small backwater areas with near zero water velocity. Holding areas provided refuge from the current and allowed fish to volitionally enter and exit the open-channel during passage trials (Figure 3.1). A 5 cm (ID) pipe provided attraction flow within the upstream holding area that encouraged fish to remain in the holding area and thereby limit the number of multiple ascents, which complicated video analysis. Water from well water sources was adjusted via pumps to control water temperature and discharge. The bottom of the flume was covered with white polyvinyl chloride sheeting and reference lines were painted on the bottom every 30 cm in order to track fish position. An array of seven digital video cameras (Handicam HDR-XR-150, Sony, Tokyo, Japan) were positioned 2 m above the flume and spaced 1-1.8 m apart to allow fish to be tracked as they ascended the flume (Figure 3.1). Video recordings of trials allowed observation of swimming

behavior, passage success, and distance of maximum ascent (D_{max}) in the passage tests and maximum swimming velocity (V_{max}) in the sprint tests. A black fabric shroud covered the flume to ensure uniform lighting and prevent outside disturbances from disrupting tests.

Water temperature, depth, and velocity in the flume were measured before and after the completion of each set of daily trials. Temperature was measured in the headwater and tailwater tanks and 1.0, 6.0, and 12.8 m upstream of the downstream grate using an Ertco High Precision Thermometer (Barnstead International, Dubuque, Iowa). Water depth and velocity was measured every 61 cm in the passage test and every 30 cm in the sprint test for the 9.15 m long 'test section' between the downstream and upstream holding areas. Water entering the head tank caused unstable and highly turbulent flow conditions that prevented accurate measurements of velocity and depth, ascent distances, and swimming velocities upstream of this test section. The lowermost one meter of the flume also did not exhibit stable flow conditions due to water damming up against the downstream grate and circulating in the downstream holding area. Thus, measurements in the flume upstream and downstream of the test section were not included in analysis. Velocities were measured with a Marsh-McBirney Flo-Mate 2000 current meter (Hach Corporation, Loveland, CO, USA) at 0.6 times the water depth to characterize average velocity and at 3 cm off the bottom to characterize bottom velocities. Depth was measured to the nearest 0.3 cm using graduated rod. Varied flow states and turbulence intensities encountered by fish within and among treatment combinations warranted calculation of Froude and Reynolds numbers, respectively, as these hydraulic

characteristics have been found to influence swimming behavior and performance (Nikora et al. 2003; Lacey et al. 2012).

Discharge during testing was continuously monitored with AquaRod-TruTrack Digital Crest Gages (GEO Scientific LTD, Vancouver, Canada) located in the tailwater and headwater tanks and a flow measurement device (Flexus F601 Flow Recorder, Flexim Aericas Corporation, Edgewood, NY, USA) located on the inflow pipe to the flume. Monitoring confirmed that discharge remained relatively constant for all trials within a treatment combination, which ensured that fish experienced similar flow and velocity conditions.

A three-dimensional cross-sectional water velocity profile (Figure 3.2) was measured 3 m upstream of the downstream grate using a Sontek Acoustic Doppler Velocimeter (YSI Incorporated, Yellow Springs, OH, USA) at each test velocity in the passage test. Measurements were taken every 1.5 cm in a grid spanning the width and depth of the flume cross-section to characterize the variation in water velocity at a scale relevant to the size of the tested fish.

In the passage test, three fish of varying sizes (mean= 6.4 cm; range=4.6 – 12.4 cm) were selected from a holding tank, transported to the flume by bucket, and placed in the downstream holding area. Fish of varying sizes were selected in order to allow individual identification of fish during video analysis and ensure that a similar range of fish sizes were represented in each trial. Fish were given 40 min to volitionally ascend the flume. Pilot studies revealed this was adequate time for the majority of dace to reach their maximum ascent distance. A total of 252 dace were tested in 84 passage trials.

Seven fish failed to move out of the downstream holding area to attempt upstream passage and were classified as nonparticipants. Nonparticipants were not included in data set used for logistic and Kaplan-Meier analyses. At the end of passage and sprint trials, fish were removed from the flume, weighed to the nearest 0.1 gram, and fork length (FL) was measured to the nearest mm before return to a separate holding tank. Fish tested in the 39 and 64 cm/s treatments were held at the test temperature for a minimum of six days (range=6-48 days) before performing in the sprint test. These fish were selected because it was assumed that time to recovery after the passage test would be the shortest in the lower velocity treatments.

In the sprint test, fish (mean FL=7.0 cm; range=5.0-11.4 cm) were individually transported to the flume and placed in the downstream end of the flume. A retention grate was used to keep fish in the first 0.90 m of the flume. After a 5 minute acclimation period, the retention grate was removed and fish were stimulated to sprint the length of the flume by gently prodding with a net handle. Maximum sprint velocity tests were performed with a total of 126 fish. Twenty-five fish did not respond to stimulation and were classified as nonparticipants and excluded from analysis.

Data Analysis

Regression analysis was used to examine associations between explanatory variables (water temperature, velocity, and fish length) and passage probability and V_{max}. Holding times of fish prior to passage and sprint tests varied, but this effect could not be statistically examined due to holding times varying directly with temperature and velocity treatments. However, plots of holding times versus response variables did not reveal any

consistent patterns and thus holding time did not appear to influence results. Given that body size effects on swimming metrics have been widely reported (Webb 1975; Beamish 1978; Peake 2008), differences in mean lengths among treatments may have affected interpretation of results. Thus, one-way analysis of variance (ANOVA) was used to assess if mean lengths differed among treatments in both the passage and sprint test. The strength of evidence for statistical analysis was defined as strong ($P<0.01$), moderate ($0.01<P<0.05$), suggestive ($0.05<P<0.10$), or lacking ($P>0.10$). All data analysis was conducted with program R version 3.0.2 on Windows 7 (R Core Team 2014).

Passage Test Measured responses in the passage test included participation rate, passage success, and D_{max}. Water temperature was treated as a categorical variable with three levels and fish length and water velocity were treated as continuous variables, with the mean velocity for each treatment combination used for analysis. Because fish were tested in groups of three, there was a possibility that measured responses within a trial were related. To assess the lack of independence among observations within a trial, response variables were plotted by trial number. No relationships between trial number and response variables were apparent. Therefore, observations from individual fish were treated as independent observations.

Participation rate was calculated by dividing the number of participants by the total number of individuals tested. Passage attempts were classified as successful if a fish ascended the 9.15 m test section between the downstream and upstream holding areas. Percent success was calculated by dividing the number of successful passages by the number of participants. Potential relationships between explanatory variables and the

odds of successful passage were assessed with binary logistic regression. Plots of empirical logits versus continuous variables were used to assess linear or higher order relationships. The empirical logit plots revealed an approximately linear relationship between the empirical logits and fish length and an approximately quadratic relationship with water velocity. The quadratic relationship was believed to be biologically meaningful, possibly representing a transition from aerobic to anaerobic exercise at higher water velocities, and thus was included in the final model. All two-way interactions between explanatory variables were included in the initial regression model. Interactions were removed if drop-in-deviance (DiD) tests (Ramsey and Schafer 2002) indicated a lack of statistical evidence ($P>0.10$). Interactions were removed in a stepwise fashion, with interactions with the least statistical support removed first.

Maximum ascent distance (D_{max}) was measured as the maximum distance a fish travelled upstream from the downstream holding area. Length and water velocity limitations of the flume prevented determination of true maximum ascent distance for many fish and therefore resulted in censored data. For example, fish that ascended the 9.15 m test section were included in the analyses as censored observations because it was impossible to know how far they would have swam in a longer flume. Kaplan-Meier survival estimators were used to estimate the mean D_{max} (Klein and Moeschberger 2012). Log-rank survival analysis was used to test for differences in D_{max} among velocity treatments, which was predicted to have the strongest influence on D_{max}. The inability of Kaplan-Meier survival analysis to examine multiple explanatory variables prevented the examination of potential influences of temperature and fish length.

Sprint Test Video recordings of sprint trials were first analyzed to calculate swimming velocities obtained over each 30 cm length interval along the flume. Maximum swimming velocity (V_{max}) was then estimated as the highest swimming velocity exhibited among all length intervals. Multiple linear regression was used to examine associations among V_{max}, water temperature and fish length. The same model selection process used for the logistic passage model was used to select the final model, with extra-sum of squares F-tests (Ramsey and Schafer 2002) used to assess the strength of statistical evidence. Plots of residuals versus fitted values and normal quantile-quantile plots of residuals from the initial model fit (including two-way interactions) indicated homogeneity of variance and normality assumptions were adequately met. Plots of fish length versus V_{max} revealed an approximately linear relationship.

Results

Test Conditions

Flow in the open-channel flume for all treatments was characterized as non-uniform turbulent flow. Non-uniform flow was caused by retention grates creating a damming effect near the flume outlet such that water depth decreased and water velocity increased as fish ascended the flume (Figure 3.3). Variation in water velocity within the flume increased with test velocity (Table 3.1, Table 3.3). In the lowest passage velocity treatment (39 cm/s), mean velocity ranged from 11.5 cm/s less than the mean at the downstream end of the flume to 15.3 cm/s greater than the mean at the upstream end in comparison to 33.9 and 38.0 cm/s, respectively, in the highest (90 cm/s) velocity treatment (Table 3.1).

The ratio of bottom velocity to average water velocity differed little among treatments and the mean of the ratios was 74:100 (bottom 26% lower than average velocity). Variation in water velocities within a cross-section generally increased with test velocity, with the lowest variation in the 39 cm/s treatment (SE=1.03) and highest in the 78 cm/s treatment (SE=1.71). In all treatments, flume corners had the largest areas of low velocity (Figure 3.2).

Temperatures varied little within treatments. Temperatures were ±0.7 °C from the mean test temperature in passage tests and ±0.9 °C from the mean in sprint tests.

Flow in the open-channel flume for all treatments was characterized as turbulent. Reynolds number, which is the ratio of inertial to viscous forces, was used to characterize flow as turbulent or laminar. Open-channel flow becomes turbulent when the Reynolds number exceeds 2,500 (Chow 1959). The mean Reynolds numbers exceeded 27,000 in all passage and sprint treatments but varied widely among velocity treatments (Table 3.1). Turbulence was positively related to discharge and generally increased with longitudinal distance upstream (Table 3.1). Higher Reynolds numbers correlate to larger variance in three-dimensional velocity vectors.

Flow state varied among and within treatment combinations. Only subcritical flow (see Chow 1959) was present in the 39, 64, and 79 cm/s treatment trials and the sprint trials. Velocity increased and depth decreased with distance upstream in an approximately linear fashion in these trials (Figure 3.3). In the 90 cm/s treatment, the flow transitioned from subcritical to supercritical flow, which is characterized by high velocities and shallow depths (mean velocity=121.5 cm/s, mean depth=13.2 cm), at 6.41

m upstream (Chow 1959). At the transition point, flow was critical, which is characterized by a turbulent standing wave in which energy is dissipated and velocity decreases substantially (Chow 1959). These flow conditions resulted in a 29.4 cm/s velocity increase occurring over the 1.2 m section centered on the standing wave (Figure 3.3).

Passage Test

Fish were highly motivated to enter and ascend the open-channel of the flume, with 97.2% (245 of 252) of fish making passage attempts. The majority of fish quickly exited the downstream holding area, with 56.4% beginning their ascent in less than 30 s and 78.9% in less than 300 s after release. Entry times decreased with increasing water velocity, with 72.9% of fish entering the open-channel in under 300 s in the 39 cm/s treatment (27.1 cm/s at entry point) compared to 82.3% of fish entering the flume in under 300 s in the 78 cm/s treatment, which had the fastest velocity at the point of entry (64.9 cm/s). Entry times also varied with temperature, with the longest mean entry time occurring in the 10.7 °C treatment (273 s), followed by the 19.3 °C treatment (207 s) then the 15.3 °C treatment (165 s).

In all treatment combinations, fish typically swam along the bottom of the flume and the majority of fish made use of the large zones of low velocities associated with the flume corners (Figure 3.2). Although fish commonly entered the open-channel in groups of two or three, it was rare for fish to remain in groups for their entire ascent. Fish commonly held position in flume corners by appressing their snout, pelvic fins, and caudal fin against the bottom. The frequency and length of holding behavior was

positively related to water velocity. Fish were able to maintain station holding at all velocities except for those experienced upstream of the standing wave in the 90 cm/s trials (minimum water velocity of 91.7 cm/s). In the 90 cm/s treatment, fish used the area of energy dissipation and low velocity associated with the standing wave to stage multiple upstream attempts. Video analysis revealed that fish used continuous burst swimming when ascending supercritical flow conditions and burst-glide swimming when ascending subcritical flow conditions.

Passage success, the probability of ascending the 9.15 m test section of the flume, was 68.2%. The final logistic regression model included water velocity, temperature, and fish length as explanatory variables, where:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\text{ind.15}) + \beta_2(\text{ind.19}) + \beta_3(\text{Velocity}) + \beta_4(\text{Velocity}^2) + \beta_5(\text{Fish length}) + \beta_6(\text{ind.15})(\text{Velocity}) + \beta_7(\text{ind.19})(\text{Velocity}) + \beta_8(\text{ind.15})(\text{Velocity}^2) + \beta_9(\text{ind.19})(\text{Velocity}^2)$$

Indicator variables were used to model the 15.3 (ind.15) and 19.3 °C (ind.19) treatments with the 10.7 °C treatment as the reference level. The equation can be used to estimate the log odds of passage by inserting the estimated coefficients (Table 3.4) along with specific values for water velocity, temperature, and fish length into the logistic model.

Passage success decreased markedly with increased velocity, ranging from a mean of 94.7 % (SE=0.05) success in the low velocity 39 cm/s treatment to 19.7% (SE=0.05) success in the high velocity 90 cm/s treatment (Table 3.2). Passage success generally increased with temperature, ranging from 62% at 10.7 °C, 75% at 15.3 °C, and 69% at 19.3 °C. There was strong evidence for an interaction of water velocity and

temperature on passage success (DiD test=20.81, df=4, P=0.0003; Figure 3.5). Probability of successful passage was predicted to be high (≥80% for 6.4 cm fish) up to water velocities of 74 cm/s regardless of water temperature, but decreased rapidly at higher velocities, especially at lower temperatures (Figure 3.5).

Fish length also appeared to strongly influence passage success (Wald's test z=4.69, P<0.0001). A one centimeter increase in fish length was associated with an estimated 4.84 times increase in the odds of passage after accounting for water velocity and temperature (95% CI: 2.63, 9.97). Given the strong influence of fish size, differences in fish size among treatments may have affected estimation of coefficients. There was strong evidence for mean fish length differring among temperature treatments (one-way ANOVA: $F_{2,242}$=34.48, P<0.0001). The mean fish length was 11 mm shorter (95% CI: 7,14) and 13 mm shorter (95% CI: 9,16) in the 19.3 °C temperature trials than the 10.7 °C and 15.3 °C temperature trials, respectively.

Distance of maximum ascent (D_{max}) was negatively associated with water velocity (log-rank survival analysis: χ^2=123, df=3, P<0.001). D_{max} ranged from 9.02 m (SE=0.13) in the 39 cm/s treatment and decreased by 18.5% to 7.61 m (SE=0.31) at 90 cm/s (Table 3.2). D_{max} differed little between the 39 and 64 cm/s velocity treatments (9.02 and 9.00 m respectively), but declined to 8.49 m at 78 cm/s and 7.61 m at 90 cm/s. The percentage of fish ascending a minimum flume length of 4.5 m was greater than 95% regardless of velocity treatment. However, when the maximum velocity exceeded 100 cm/s in the upper flume section at the highest test velocity, percent passing dropped dramatically. Eighty-six percent of fish successfully ascended the first 6.41 m in the 90 cm/s treatment

when the maximum velocity encountered was less than 100 cm/s, but only 19.7% of fish were able to successfully ascend the remaining 2.75 m of supercritical flow, which had a maximum velocity of 128.8 cm/s and a mean velocity of 121.5 cm/s. Fish rarely swam upstream of the test section in the 90 cm/s treatment and attempts to move upstream of the standing wave generally lasted less than 10 s before fish returned to a holding position below the standing wave.

Sprint Test

Fish responded to stimulation by moving off the bottom and employing burst-glide swim behavior away from the stimulus. Video observation showed that the frequency of tail beats during bursts decreased and lengths of glides increased with distance upstream. Bursts rarely exceeded 60 cm and swimming behavior did not differ among temperature treatments.

The mean (V_{max}) was 139 cm/s and V_{max} ranged from 72 to 242 cm/s. Multiple linear regression indicated evidence for relationships between V_{max}, water temperature, and fish length. The final regression model was:

$$\text{Mean } V_{max} = \beta_0 + \beta_1(\text{ind.15}) + \beta_2(\text{ind.19}) + \beta_3(\text{Fish length})$$

The model can be used to estimate V_{max} by inserting the estimated coefficients (Table 3.5) along with specific values for water temperature and fish length into the regression model.

Mean V_{max} generally increased with water temperature (Table 3.3). There was moderate evidence (t_{97}=2.29, P=0.02) for mean V_{max} differing between the 12.3 and 14.5 °C treatments, with mean V_{max} estimated to be 16 cm/s (95% CI: 2, 29) faster in the 14.5

°C treatment. There was less evidence for mean V_{max} differing between the 12.3 and 19.2 °C temperature treatments (t_{97}=1.70, P=0.09) and mean V_{max} was estimated to be 12 cm/s faster (95% CI: -2, 26) in the 19.2 °C treatment. There was no evidence for a difference between the 19.2 and 14.5 °C temperature treatments (t_{97}=0.53, P=0.60).

There was strong evidence for a positive linear relationship between V_{max} and fish length (t_{97}=0.11, P<0.0001). A one cm increase in fish length was associated with a 11 cm/s increase in mean maximum swimming velocity after accounting for temperature (95% CI: 6, 15). There was no evidence for fish lengths differing among treatments (one-way ANOVA: $F_{2,242}$=0.71, P=0.49).

Discussion

Results from swimming performance tests indicate that longnose dace are surprisingly strong swimmers relative to body size. The majority (95%) of tested dace could ascend 9.15 m of open-channel flow at mean water velocities up to 64 cm/s (relative velocity of 10.8 BL/s). Ten body lengths per second is generally accepted as the velocity that defines burst swimming, which can only be sustained for short periods (Bainbridge 1960; Ryland 1963; Hammer 1995). However, longnose dace were able to swim at these velocities for the majority of the 40 minute passage trials, indicating that classifications of swimming modes based on relative velocities should not be universally applied. The mean burst velocity we observed (139 cm/s; 21.7 BL/s) is similar to those reported by Bestgen et al. (2010) for Rio Grande silvery minnow (118 cm/s; 20.9 BL/s) and Aedo et al. (2009) for longnose dace (120 cm/s; 18.5 BL/s) but exceeds relative burst velocities reported for many large-bodied fish such as rainbow trout (7.6-10.2 BL/s),

largemouth bass (7.3 BL/s), and northern pike (10 BL/s; Gray 1953; Bainbridge 1960; Leavy and Bonner 2009). These comparisons are consistent with the findings of Bainbridge (1960), Blaxter and Dickson (1959), and Brett and Glass (1973) that smaller fish are better swimmers than large fish relative to body size.

However, given that absolute swimming performance decreases with body size, the small relative size of longnose dace and other minnows places important limitations on fishway design (Brett 1965; Adams et al. 2000; Bestgen et al. 2010). The results of both the passage and sprint tests contributed to the general finding that larger fish can swim faster and farther than smaller fish. Design criteria are often based on maximum sustainable velocities of large bodied fish (Beach 1984; Powers et al. 1985; Bell 1991; Clay 1995). However, these velocities may require small-bodied fish to employ unsustainable burst swimming. For example, design criteria for culverts in Washington recommend maximum water velocities of 122 cm/s for passage structures between 3.0 and 30.5 m in length (Barnard et al. 2013). While large-bodied fish may be able to swim at sustained velocities to pass these structures, our results indicate that velocities over 100 cm/s would require longnose dace to employ continuous burst swimming. Realistically, velocities greater than 100 cm/s may be necessary in many passage structures located in high gradient or high flow environments. Thus, these passage structures should provide frequent velocity refuges to allow sprinting individuals to recover. Data from the passage tests showed that 50% of tested dace could ascend 1.5 m at average velocities of 120.7 cm/s, indicating that velocity refuges should be closely spaced to allow passage of small-bodied species.

It is important to note that the velocities that induced burst swimming reported here are much larger than those reported for other minnow species. Water velocities of 60 cm/s required burst swimming for Topeka shiner (Adams et al. 2000), 32-67 cm/s for brassy minnows, Arkansas darters, and common shiners (Ficke et al. 2011), and Billman and Pyron (2005) reported burst swimming occurring at 67 cm/s for 15 species of North American minnows. Interspecific differences in swimming abilities, which have been widely reported even for fish of similar size and morphologies (Haro et al. 2004; Ficke et al. 2011; Underwood et al. 2014), may explain these differences. Alternatively, measurement of swimming abilities of the aforementioned species based on data from swim chambers may have resulted in an underestimation of abilities, which has been suggested for other species (Mallen-Cooper 1992; Peake 2004a; Peake 2004b; Castro-Santos 2005; Peake and Farrell 2006; Holthe et al. 2008). Comparisons of passage predictions from the swim chamber data of Billman and Pyron (2005) on longnose dace to those from our logistic model support this hypothesis. Using the equation provided by Peake et al. (1997) to convert endurance data (50.9 s at 67 cm/s; Billman and Pyron 2005) to a traversable distance results in a prediction of 50% passage at water velocities of 49 cm/s and a distance of 9.15 m. In comparison, the logistic model from our study predicts almost twice the passage rate (99.8%) at similar fork lengths and temperatures (3.94 cm FL vs 3.94 cm standard length and 19.3 vs 20.4°C). This is similar to the finding of Peake (2004a) that velocity criteria based on swim chamber studies can underestimate maximum passable water velocities by at least 50%. Underestimation of swimming abilities can lead to misidentification of barriers and more expensive design

criteria. Given that there are an estimated 1.4 million instream structures associated with road-crossings in the United States (Hudy, USFS, unpublished data), the value of low-cost mitigation efforts is not trivial. Increased use of testing apparatus, such as flumes, that do not inhibit swimming behaviors and allow accurate estimation of swimming performance is needed so that restoration funds can be efficiently appropriated.

The results of our study represent a departure from traditional swimming tests in which time to fatigue is examined. The logistic model and Kaplan-Meier estimators allow for direct estimation of passage success and ascent distance over a range of velocities, temperatures, and fish sizes. In contrast, transformation of time to fatigue data to estimate passage rests on the assumption that fish will swim at a constant velocity (Peake 2004a). Observation of free-swimming fish in the passage test did not support this assumption. Variable ground velocity, station holding, and burst-glide swimming was observed in all velocity and temperature treatments. Additionally, time to fatigue data in swim chambers may be confounded by the refusal of fish to swim within the confines of a swim chamber. This was observed in swim chamber pilot studies, in which longnose dace station held on the bottom of the chamber until velocity exceeded holding capabilities. Such tests provide little swimming performance information and may not be appropriate for benthic-oriented fish.

Logistic regression indicated that water velocity was a key factor limiting passage success. Passage success remained high (≥95%) up to a water velocity of 64 cm/s, but decreased rapidly at water velocities exceeding this threshold. This observation may reflect a shift from sustainable aerobic swimming to unsustainable anaerobically fueled

swimming (Beamish 1978; Jones 1982; Peake and Farrell 2004). This would suggest that longnose dace could ascend long distances at velocities less than 64 cm/s, but this hypothesis needs to be validated in longer testing apparatus. Contrary to expectations, we observed a decrease in passage success and D_{max} in the lowest velocity and temperature treatment. This decrease may be explained by fish having lower motivation to swim at low water velocities and temperatures, which has been suggested in other studies (Ficke 2006; Piper et al. 2012). Our observation of increased time to entry at the lowest velocity and temperature treatment also support this hypothesis. Thus, providing relatively high entry velocities (i.e. 60-70 cm/s) may help stimulate passage attempts of longnose dace, especially for movements associated with low water temperatures.

The results of the passage test indicated temperature has a strong influence on swimming performance and should be considered when designing passage structures. For most species, swimming performance is reduced at low temperatures, increases to a maximum at an optimum temperature, and then decreases as the upper thermal limit is approached (Randall and Brauner 1991; Myrick and Cech 2000; Ojanguren and Brana 2000; Lee et al. 2003). The general increase in passage success and D_{max} with temperature and the lack of decreased performance at the highest temperature tested (19.3 °C) indicates that temperatures greater than the thermal optimum were not tested. Although response metrics were similar between the 15.3 and 19.3 °C treatments, it is expected that response metrics would have been highest in the 19.3 °C treatment if fish had not been substantially smaller (13 mm) in this treatment. To avoid creating seasonal barriers, it is suggested that conservative estimates of swimming performance at the

lowest temperatures associated with fish movements be used for passage design and barrier identification.

Interactions among covariates may also influence swimming ability. For example, logistic regression on the passage data indicated that the relationship between passage success and water velocity depended on temperature, with water velocity having the largest negative effect on passage at low temperatures. Interaction between water velocity and water temperature on swimming performance have not been reported in the literature. The interaction may be a result of physiological or behavioral aspects of swimming performance varying with both water temperature and velocity, which awaits further exploration. Alternatively, interactions may be a result of the shape of each logistic curve being estimated from passage data at only four velocities and these four velocities varying among temperature treatments. For example, the velocity in the nominal 39 cm/s treatment at 10.7 °C was 8 cm/s higher than the 15.3 and 19.3 °C treatments at 39 cm/s (44 versus 36 cm/s). This difference results in an unrealistically low estimate of passage success (14.0%) at a velocity of 39 cm/s for a 6.4 cm longnose dace at 10.7 °C. This highlights the importance of interpreting the logistic regression results only within the range of conditions for which the logistic curves were defined.

Estimates of maximum swimming velocities from the sprint test can be used to identify barriers to longnose dace movements. Maximum swimming velocities (V_{max}) in the sprint test were obtained in a low velocity environment, measured over a 30 cm distance, and were generally maintained for less than a quarter second. Due to the short duration of V_{max}, use of the data to determine lengths of high velocity flows may be of

limited use. For example, using the mean V_{max} (139 cm/s) and the equation provided by Peake et al. (1997), 50% of the tested longnose are predicted to be able ascend only 6 cm at a water velocity of 110 cm/s, 4 cm at 120 cm/s, and 0 cm at 139 cm/s. Thus, structures with water velocities greater than 139 cm/s would represent a barrier to the majority of tested longnose dace.

Some disagreement exists in the literature on whether temperature affects anaerobic exercise and maximum swimming velocities. A number of earlier studies have suggested that anaerobic exercise is not affected by temperature (Blaxter and Dickson 1959; Beamish 1966; Brett 1967), but more recent studies have indicated that anaerobic exercise is temperature dependent (Rulifson 1977; Webb 1978, Batty and Blaxter 1992; Johnson and Bennett 1995). The results of the sprint test contribute to the latter finding, with maximum swimming velocity negatively associated with low temperature (12.3 °C). The lower maximum velocities observed in the 12.3 °C trials may be a result of white muscle contraction times decreasing at lower temperatures, which has been observed in other cyprinid species (Wardle 1975; Johnson and Bennett 1995).

To prevent the creation of size selective barriers, body size should be considered when evaluating existing passage structures and designing new structures. There was strong evidence for body size effecting both passage success and maximum swimming velocity. Because we tested a wide range of body sizes (4.6-12.6 cm) in our sample, our regression models should be applicable to most age-classes (age 1+). However, given the time of collection and body sizes, it is unlikely any age 0 fish were in our sample (Brazo et al. 1978; Mullen and Burton 1995). Due to the variable hydrographs that characterize

many prairie streams, movements of age 0 fish may be necessary to avoid deleterious environmental conditions and recolonize suitable habitat. Future work on longnose dace should investigate the swimming abilities of age 0 fish. Passage structures on dynamic prairie streams should use swimming information on the smallest 'migrating' fish to ensure the passage success of all age-classes.

A limitation of our study is that results are specific to the hydraulic conditions of the flume. The smooth walls and floor of the flume and high Reynolds numbers likely resulted in highly chaotic non-periodic turbulence, which can negatively affect fish stability and is expected to increase energetic costs of swimming (Pavlov et al. 2000; Enders et al. 2003; Lupandin 2005). These conditions are most similar to box culverts or breached dams with minimal structure in the flow (Haro et al. 2004). Caution is suggested when applying results from the study to complex and highly turbulent conditions associated with many passage structures as the effects of different turbulence characteristics on swimming performance and behavior are poorly understood and are an important subject for future study. However, recent studies have indicated that structured turbulence associated with roughness elements, weirs, and other objects in the flow can reduce energy expenditures, assist forward movements, and enhance station holding abilities (Webb 1998; Hinch and Rand 1998; Pavlov et al. 2000; Liao et al. 2003). Given that longnose dace are a benthic oriented species adapted to live in the high velocity and turbulent conditions associated with riffles, it is expected that they would be able to ascend passage structures with average water velocities exceeding their swimming capabilities if structured turbulence and thick boundary layers were present (McPhail and

Lindsey 1970). This prediction is consistent with the finding of longnose dace inhabiting areas with surface velocities (182 cm/s) greater than their swimming capabilities (McPhail and Lindsey 1970).

Based on the results of our study, we suggest that passage structures with average velocities less than 64 cm/s should allow passage of most longnose dace. This suggestion is similar to those made by Ficke et al. (2006) for three small-bodied Great Plains minnows (75 cm/s), Bestgen et al. (2010) for Rio Grande silvery minnow (45-60 cm/s), and Peake (2008b) for longnose dace (68 cm/s). Despite similarities in velocity criteria recommendations, differences in swimming abilities were observed among these species, which demonstrates the difficulty of using surrogate species. In systems with multiple species of concern, criteria should be based on the weakest swimming species, which can be identified with field studies. Water velocities greater than 100 cm/s should be limited, as these velocities induced continuous burst swimming, which was sustainable for only short periods. Results from the sprint test indicate that instantaneous water velocities greater than 139 cm/s would be impassable for the majority of dace. It is important to note that recommendations are based on average water velocities which are substantially greater than the water velocities experienced by fish swimming along the bottom. Multiplying recommendations by 0.76, the ratio of bottom to average water velocity, results in bottom water velocity recommendations. The behavioral observations of longnose dace swimming exclusively along the bottom in the passage tests suggests that weirs, baffles, and other passage structures that do not allow passage to occur along the bottom or require jumping may inhibit passage. Application of our results is limited by

the relatively short length of the flume. Longer testing apparatus with increased flow capacities may be necessary to fully evaluate the multitude of conditions fish may encounter at passage structures. Combining field and laboratory studies to identify structures that are inhibiting passage in the field, then testing key swimming attributes in relation to field conditions in an experimental flume should allow more precise estimates of factors that restrict passage.

Tables

Table 3.1. Summary of hydraulic conditions for the 12 velocity and temperature (T) treatment combinations during longnose dace passage testing in the experimental flume. Reynolds (Re) and Froude (Fr) numbers are dimensionless. Bottom velocity, mean velocity (measured at 0.6 x water depth), and Reynolds number are given as mean ±1 SE; water velocity and Froude number ranges are in parentheses.

Nominal velocity (cm/s)	T (°C)	Bottom Velocity (cm/s)	Mean Velocity (cm/s)	Q (m^3/s)	Re	Fr
39	10.6	34 ± 2 (23, 51)	44 ± 2 (30, 62)	0.03	30,753 ± 1,099	0.35 (0.22, 0.60)
	15.1	26 ± 2 (17,41)	36 ± 2 (25,52)	0.02	27,151 ± 980	0.31 (0.18, 0.50)
	19.4	30 ± 2 (22, 43)	36 ± 2 (26, 48)	0.02	32,193 ± 844	0.30 (0.20, 0.45)
64	10.6	48 ± 2 (36, 59)	64 ± 1 (52, 72)	0.06	59,439 ± 851	0.41 (0.30, 0.49)
	15.4	46 ± 2 (37, 60)	63 ± 1 (54, 73)	0.06	65,625 ± 906	0.39 (0.31, 0.49)
	19.4	49 ± 2 (36, 68)	66 ± 2 (53, 80)	0.06	79,660 ± 1,753	0.41 (0.32, 0.54)
78	10.9	62 ± 2 (50, 75)	84 ± 3 (67, 107)	0.08	75,334 ± 1,727	0.55 (0.40, 0.75)
	15.4	55 ± 2 (42, 72)	75 ± 2 (63, 98)	0.08	77,805 ± 1,763	0.48 (0.38,0.68)
	19.5	57 ± 2 (46, 72)	75 ± 5 (65, 89)	0.08	90,098 ± 1,530	0.48 (0.38, 0.60)
90	10.8	65 ± 5 (40, 103)	88 ± 5 (57, 122)	0.05	62,882 ± 1,785	0.71 (0.40,1.17)
	15.4	67 ± 6 (40, 106)	90 ± 7 (56, 128)	0.06	74,752 ± 3,286	0.71 (0.38,0.1.14)
	18.9	68 ± 6 (30, 109)	92 ± 7 (55, 138)	0.06	86,705 ± 3,393	0.74 (0.38,1.27)

Note: Standard error (SE) calculated as the sample standard deviation divide by the square-root of the number of observations in the sample.

Table 3.2. Participation and passage success proportions and maximum ascent distances of longnose dace during passage tests conducted in an experimental flume in relation to temperature, velocity, and fish length. Fish lengths and D_{max} presented as mean ±1 SE. Sample size (N) is number of fish that attempted upstream passage.

Velocity (cm/s)	T (°C)	N	Fish length (cm)	Participation	Success	D_{max} (m)
39	10.6	19	6.8 ± 0.2	0.90	0.84	8.77 ± 0.23
	15.1	20	7.0 ± 0.4	0.95	1.00	9.15 ± 0.00
	19.4	20	5.7 ± 0.2	0.95	1.00	9.15 ± 0.00
64	10.6	20	6.8 ± 0.2	0.95	1.00	9.15 ± 0.00
	15.4	21	6.8 ± 0.3	1.00	0.95	8.91 ± 0.26
	19.4	21	5.5 ± 0.1	1.00	0.90	8.91 ± 0.19
78	10.9	20	6.7 ± 0.2	0.95	0.55	8.07 ± 0.41
	15.4	21	6.9 ± 0.4	1.00	0.80	8.76 ± 0.21
	19.5	21	5.7 ± 0.1	1.00	0.62	8.64 ± 0.20
90	10.8	21	6.6 ± 0.2	1.00	0.10	7.16 ± 0.20
	15.4	20	7.1 ± 0.3	0.95	0.25	7.45 ± 0.31
	18.9	20	5.8 ±0.2	0.95	0.24	8.21 ± 0.24

Note: Standard error (SE) calculated as the sample standard deviation divide by the square-root of the number of observations in the sample.

Table 3.3. Summary of hydraulic conditions and test results for the three temperature (T) treatments during longnose dace sprint testing in the experimental flume. Mean velocity, fish length (FL), and V_{max} presented as mean ±1 SE.

T	Mean Velocity (cm/s)	N	FL (cm)	Participation	V_{max} (cm/s)
12.3	20 ± 0.4	32	6.8 ± 0.14	0.76	127 ± 4.7
14.5	17 ± 0.4	37	7.0 ± 0.25	0.88	142 ± 5.6
19.2	16 ± 0.3	32	7.2 ± 0.25	0.76	145 ± 5.8

Note: Standard error (SE) calculated as the sample standard deviation divide by the square-root of the number of observations in the sample.

Table 3.4. Coefficient estimates from the final logistic model describing relationships between the log-odds of passage success of longnose dace and water velocity (cm/s), temperature (ind.15, ind.19; °C), and fish length (cm).

Variable	Coefficient Estimate	Standard Error	P-value
Intercept	-68.02	22.77	0.0028
ind.15	63.71	26.51	0.0206
ind.19	99.91	37.41	0.0076
Velocity	2.09	0.76	0.0062
$Velocity^2$	-0.017	0.59	0.0048
Fish length	1.58	0.34	<0.0001
ind.15 x Velocity	-1.98	0.87	0.0225
ind.19 x Velocity	-2.95	1.07	0.006
ind.15 x $Velocity^2$	0.014	0.0064	0.0255
ind.19 x $Velocity^2$	0.021	0.0075	0.0053

Note: Indicator variables were used to model the categorical variable temperature, with ind.15 equal to 1 for the 15.3 °C treatment and 0 otherwise, ind.19 similarly defined for the 19.3 °C treatment, and the 10.7 °C as the reference level.

Table 3.5. Coefficient estimates from the final multiple linear regression model describing relationships between maximum swimming velocity of longnose dace, as estimated in sprint tests, and water temperature (°C) and fish length (cm).

Variable	Coefficient estimate	Standard error	P-value
Intercept	52.0	15.7	<0.0001
ind.15	15.6	6.8	0.02
ind.19	12.0	7.1	0.6
FL	11	2.2	<0.0001

Note: Indicator variables were used to model the categorical variable temperature, with ind.15 equal to 1 for the 14.5 °C treatment and 0 otherwise, ind.19 similarly defined for the 19.2 °C treatment, and the 12.3 °C as the reference level.

Figures

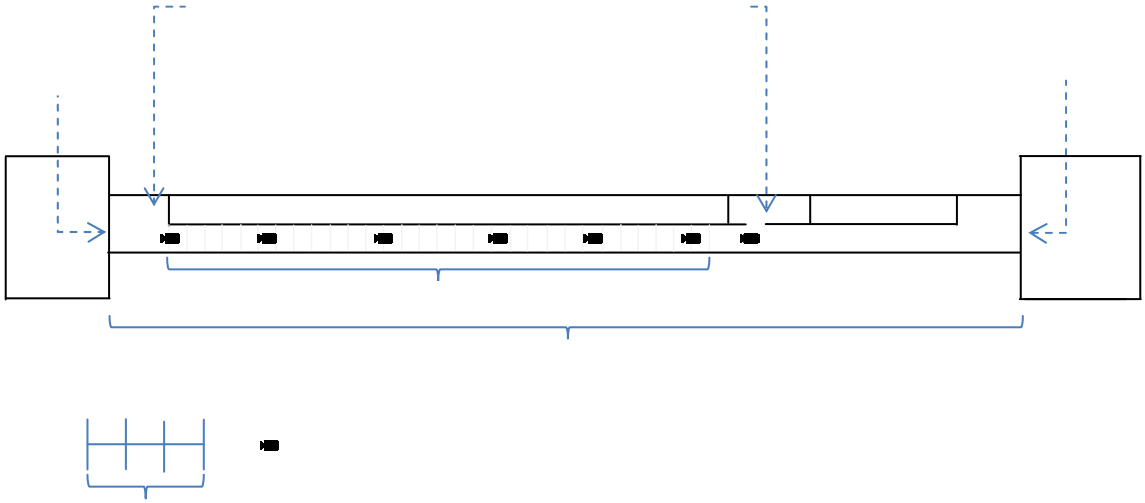

Figure 3.1. Plan view diagram to scale of the open-channel flume located at the Bozeman Fish Technology Center.

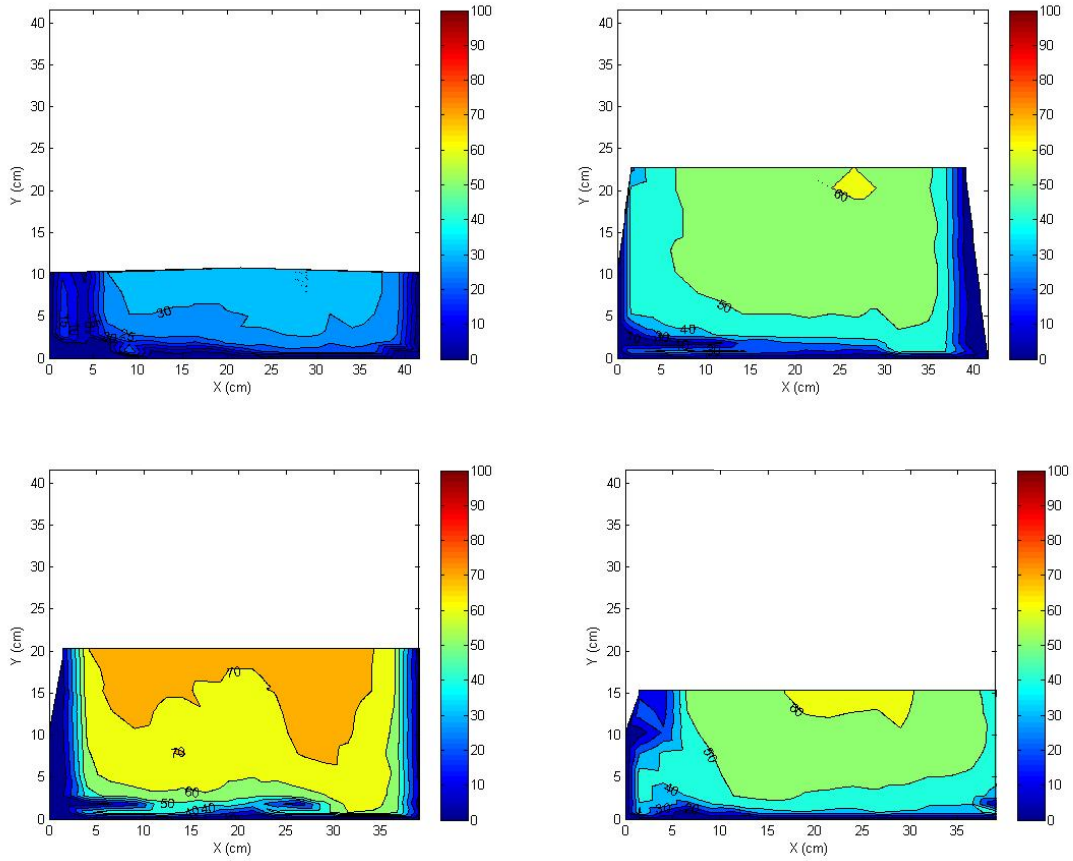

Figure 3.2. Cross-sectional velocity profile (m/s) of the experimental flume for the 39, 64, 78, and 90 cm/s longnose dace passage velocity treatments measured 3 m upstream of the flume end. Blank areas indicate flume sections near walls that could not be accurately measured.

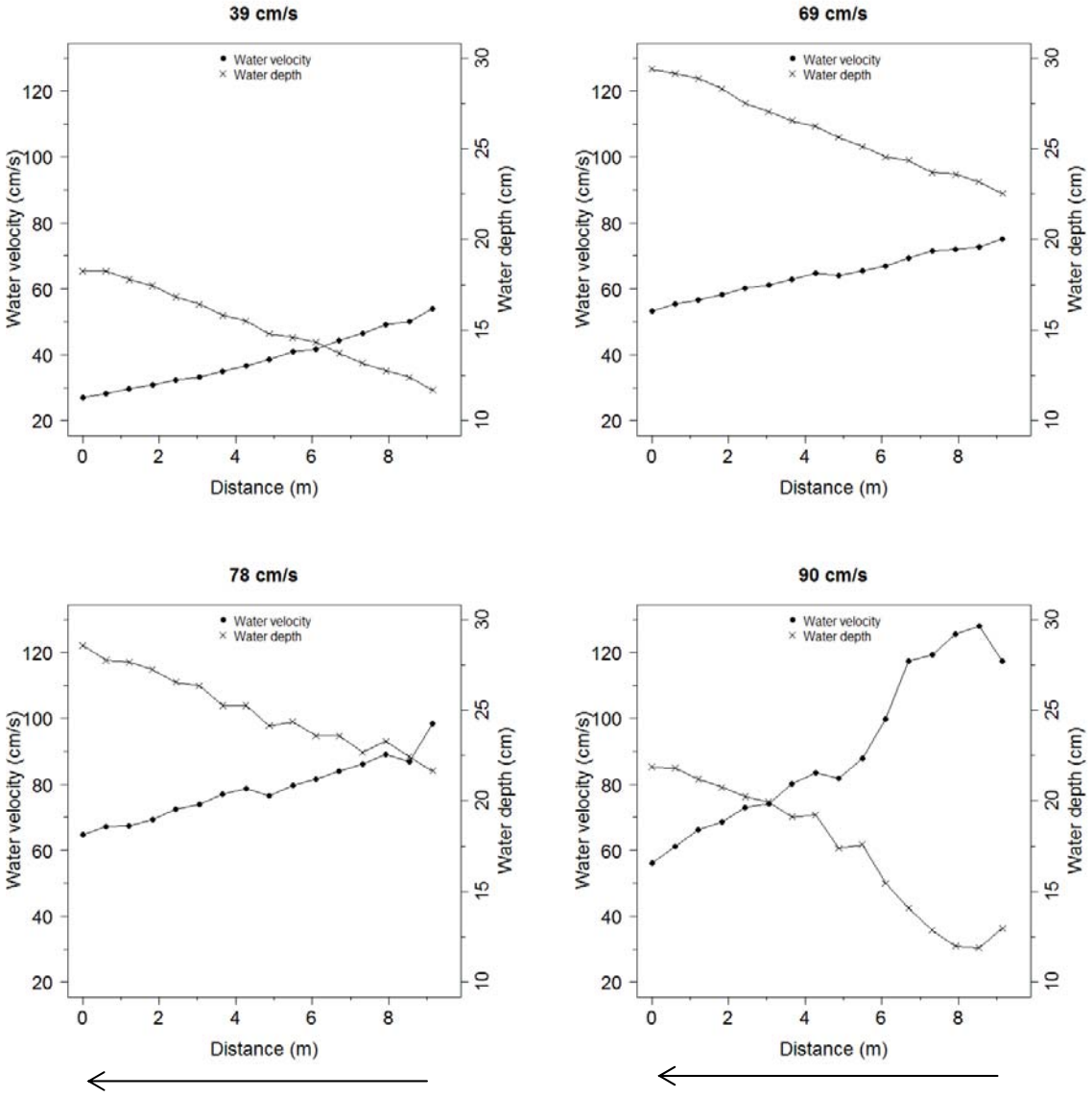

Figure 3.3. Mean water velocity and depth measurements along the length of the flume test section for each of the four velocity treatments in the longnose dace passage test.

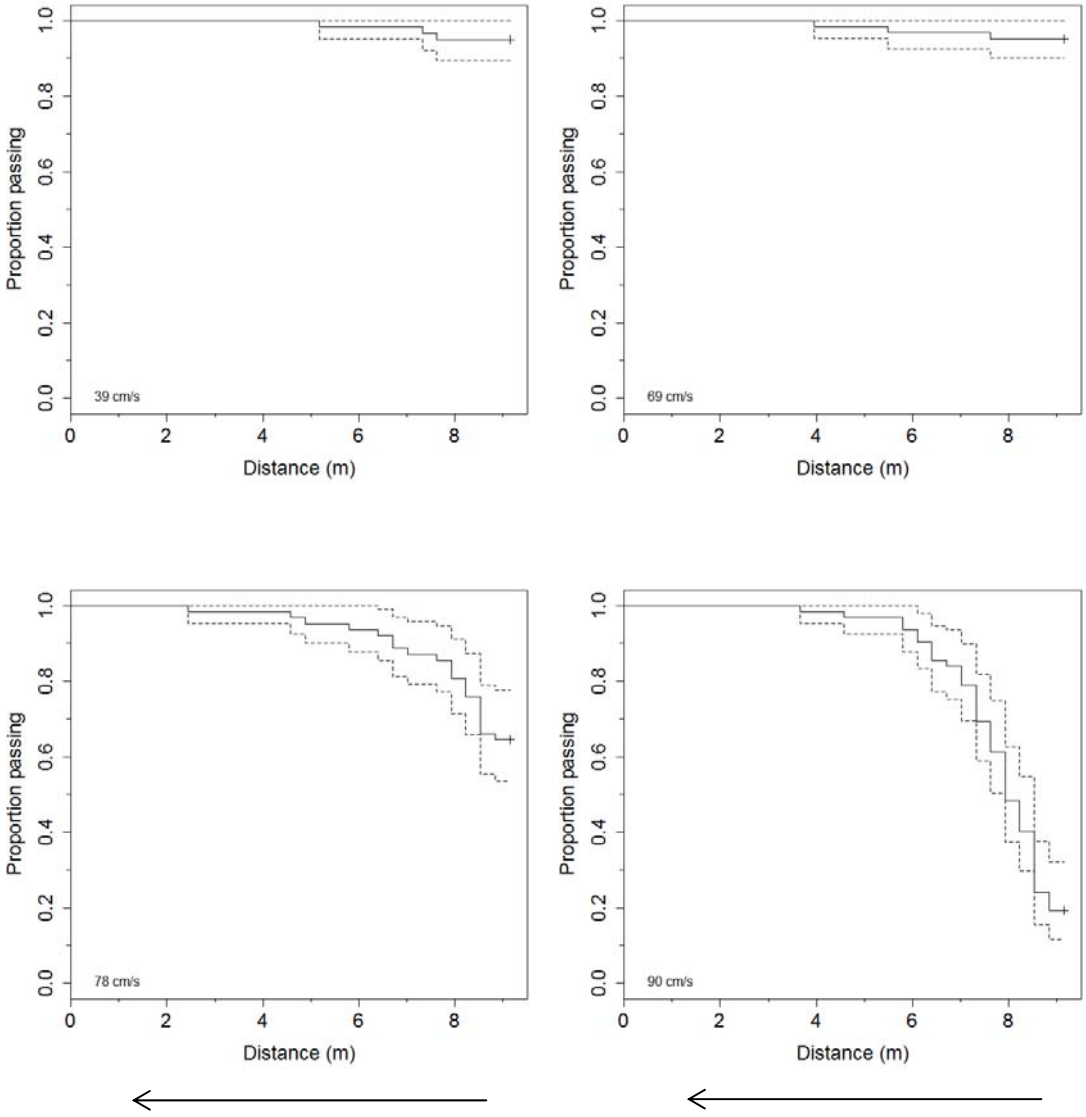

Figure 3.4. Estimated probability curves for the maximum ascent distance of longnose dace at the four velocity treatments in the passage test. Proportion passing (shown as solid line in graphs) and 95% confidence intervals (shown as dashed lines in graphs) were estimated using Kaplan-Meier survival analysis. Censoring is indicated by a vertical hash mark at 9.15 m.

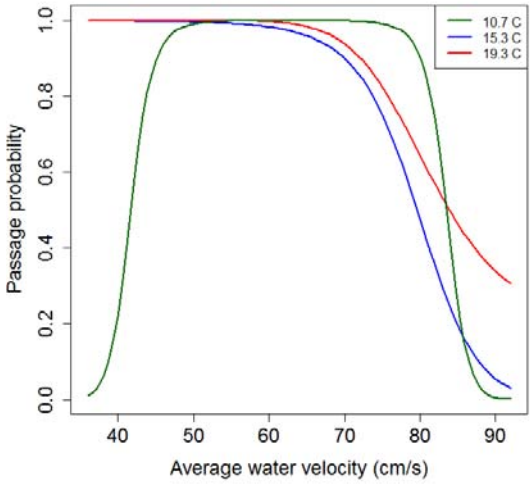

Figure 3.5. Estimated logistic regression relationships between passage success and water velocity at the three temperature treatments in the passage test for a 6.4 cm longnose dace.

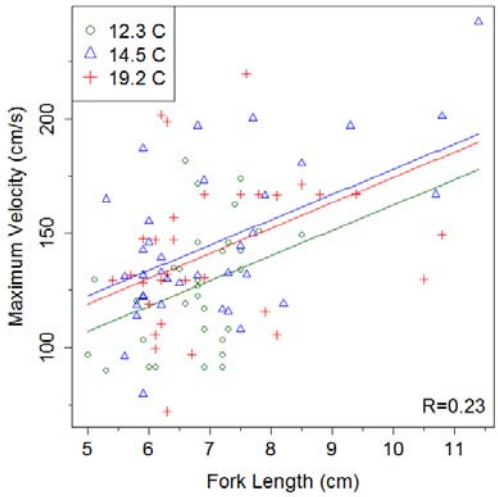

Figure 3.6. Estimated linear relationships between maximum swimming velocity and fish length of longnose dace for the three temperature treatments in the sprint test.

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CONCLUSION

Barriers to fish movement represent a significant threat to freshwater and anadromous fish populations worldwide (Winston et al. 1991; Frankham 1995; Gehrke et al. 2002; Quinn and Kwak 2003; Lundqvist et al. 2008; Morita et al. 2009). Removing barriers and providing effective passage structures have been identified as being among of the most effective restoration techniques available to managers (Scully et al. 1990; Roni et al. 2002). We provided detailed swimming information on sauger and longnose dace that can be used by managers and engineers to identify barriers and design effective passage structures for these species.

Based on the results of our study, mean water velocities less than 64 cm/s and maximum water velocities less than 100 cm/s in passage structures are recommended to provide passage for longnose dace. Mean water velocities less than 97 cm/s and limiting water velocities greater than 124 cm/s to short sections of passage structures is recommended to provide passage for sauger. The longnose dace study revealed that water temperature has a strong positive influence on swimming performance and conservative estimates of swimming performance at the lowest temperatures associated with fish movements should be used for passage design and barrier identification to prevent the creation of seasonal barriers. Similarly, fish size was positively associated with longnose dace swimming performance. Thus, passage design and barrier identification should be based on the abilities of the smallest fish undergoing movements to prevent the creation of size selective barriers. I suspect the same associations hold for sauger and the general lack of evidence for these associations resulted from hydraulic

conditions in the flume not challenging sauger and a relatively small sample size resulting in low statistical power for identifying effects.

Comparison of the results of the sauger and longnose dace studies revealed differences in swimming performance and behavior that have important implications for fish passage. Hydraulic conditions in the 93 cm/s treatment in the sauger passage test did not inhibit passage (passage success=92%) whereas similar conditions in the 90 cm/s treatment in the longnose dace passage test prevented passage of over 80% of longnose dace. This comparison indicates that passage structures based on swimming information on large-bodied fish may represent barriers to small-bodied fish. Ideally, design of passage structures and barrier identification should be based on the abilities of the weakest swimmers within the fish assemblage. Further studies on small-bodied fish are needed in order to identify these species.

Differences in swimming behavior between sauger and longnose dace illustrated the importance of using behavioral observations to direct fish swimming studies and guide the application of the results. In the sauger passage test, almost all individuals displayed gait-transitions at a consistent water velocity. Peake and Farrell (2004) observed similar behavior in smallmouth bass and used physiological data to show that gait-transitions represent the maximum aerobic capacity. This is an important finding, as maximum aerobic capacity is a commonly used metric for passage design criteria and traditional methods for estimating maximum aerobic capacity (i.e. U_{crit} tests) have been shown to greatly underestimate swimming abilities (Powers et al. 1985; Mallen-Cooper 1992; Peake 2004, Peake and Farrell 2006; Holthe et al. 2008). However, universal use

of the gait-transition criteria is not recommended, as gait-transitions may not represent maximum aerobic capacity for many species. For example, gait-transitions were observed at all velocities tested in the longnose dace passage test and likely did not represent a transition from aerobic to anaerobic exercise. Similarly, many pelagic species have only a single swimming mode and experiments to identify gait-transitions for these species will likely be uninformative (Plaut 2001).

I recommend species-specific testing protocols that comply with swimming behaviors and address the passage concerns of the species. The majority of swimming studies have been based on the U_{crit} test developed by Brett (1964) to assess the ability of salmonids to ascend lotic systems during spawning migrations, and endurance tests that use time to fatigue thresholds to classify swimming modes (Beamish 1978). Recent studies have indicated that swimming modes of many species fail to adhere to the time to fatigue thresholds developed by Beamish (1978) and that these testing protocols often inhibit natural swimming behavior (Bernatchez and Dodson 1985; Peake et al. 1997; Haro et al. 2004; Bestgen et al. 2010; Castro-Santos et al. 2013). Strict adherence to these protocols may lead to false conclusions about the swimming abilities of species and a failure to provide useful information on the ability of fish to pass structures they encounter. I recommend increased use of flumes and other larger testing structures that do not inhibit natural swimming behaviors and allow direct examination of the abilities of fish to ascend hydraulic conditions similar to existing passage structures or prospective structures. Using field studies and monitoring to identify structures that are inhibiting passage in the field then replicating field conditions in the laboratory to determine what

hydraulic characteristics are preventing passage may be an effective method for increasing our understanding of how fish swimming abilities and behavior affect fish passage.

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