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Complete List of Authors:	Dockery, David; Montana State University Bozeman, Department of Ecology; US Fish , Bozeman Fish Technology Center McMahon, Thomas; Montana State University Kappenman, Kevin; US Fish , Bozeman Fish Technology Center Blank, Matthew; Montana State University Bozeman, Civil Engineering Department; Montana State University Bozeman, Western Transportation Institute
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Swimming performance of sauger (*Sander canadensis*) in relation to fish passage

DAVID R. DOCKERY

Ecology Department, Fish and Wildlife Program, Montana State University, P. O. Box 173460, Bozeman, MT 59717-3460, USA and United States Fish and Wildlife Service, Bozeman Fish Technology Center, 4050 Bridger Canyon Road, Bozeman, MT 59715-8433, USA.

(email: dockery.david@gmail.com)

THOMAS E. McMAHON

Ecology Department, Fish and Wildlife Ecology and Management Program, Montana State University, P. O. Box 173460, Bozeman, MT 59717-3460, USA.

(email: tmcmahon@montana.edu)

KEVIN M. KAPPENMAN

United States Fish and Wildlife Service, Bozeman Fish Technology Center, 4050 Bridger Canyon Road, Bozeman, MT 59715-8433, USA. (email: kevin_kappenman@fws.gov)

MATTHEW BLANK

Civil Engineering Department, Montana State University, Bozeman, MT 59717-3900, USA and Western Transportation Institute, Montana State University, 2327 University Way, Bozeman, MT 59717-4250, USA. (email: mblank@montana.edu)

*Author to whom correspondence should be addressed. Wild Rivers Consulting, Bozeman, MT 59715-5777, USA. Tel.: +1 406 599 5649, email: dockery.david@gmail.com

ABSTRACT

A lack of information on the swimming abilities may inhibit the design of effective passage structures for sauger (*Sander canadensis*), a highly migratory species particularly sensitive to habitat fragmentation. Passage success, maximum ascent distances, and maximum sprint velocities of sauger were estimated in an open-channel flume over a range of water velocities (51, 78, and 92 cm s⁻¹) and temperatures (10.0, 14.3, and 18.3° C) to assess swimming performance. Passage success was high (91%) over all test velocities, as was the maximum instantaneous burst velocity (219 cm s⁻¹). Water temperature and body size had little effect on swimming performance. Sauger transitioned from steady sustained swimming to unsteady, burst-glide or steady burst swimming at 97 cm s⁻¹. Sauger were capable of sustained sprints of 124 cm s⁻¹ over 15 second duration in a swim chamber. Results suggest passage structures with water velocities less than 97 cm s⁻¹ should provide high probability of successful passage of adult sauger whereas structures with water velocities exceeding 219 cm s⁻¹ may 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 are fragmented as a result (Larinier, 2000; Hughes et al., 2005). Sauger (*Sander canadensis*) are primarily a large-river species and are one of the most widely distributed of North American fishes (Scott and Crossman, 1973; Hesse, 1994). However, their highly migratory nature and preference for large, turbid rivers make them particularly susceptible to habitat fragmentation and disturbance (Penkal, 1992; Hesse, 1994; McMahon and Gardner, 2001). Dams and other instream barriers that block spawning migrations, fragment populations, alter thermal and flow regimes, and reduce suspended sediment have contributed to range-wide declines in their abundance and distribution (Hesse, 1994; Amadio et al., 2005; Jaeger et al., 2005), and resulted in their listing as a species at risk in several parts of their range (Carlson, 2003; Keinath et al., 2003; Latta, 2005). Providing effective fishways to reconnect fragmented habitats and populations is among the most promising management actions for conserving and restoring imperiled sauger populations. However, a lack of information on the swimming behavior and abilities of sauger inhibits the design of effective passage structures for this species.

Traversable distances over a range of velocities, maximum swimming velocities and swimming behavior in relation to hydraulic conditions present in potential passage designs is needed to design effective passage structures and identify barriers. Maximum aerobic capacity is a commonly measured metric because it is assumed that aerobic exercise is sustainable for

indefinitely long durations or distances (Beamish, 1978). However, high velocity zones that require fish to use unsustainable anaerobic exercise are common and sometimes intentional features of passage structures. Thus, measures of anaerobic endurance and maximum swimming velocities are needed to determine passable distances through high velocity zones and identify velocities that will restrict passage. Additionally, biotic and abiotic factors such as fish size and temperature can have significant effects on swimming abilities and should be incorporated into passage design (Beamish, 1978; Rome et al., 1990; Leavy and Bonner, 2009).

Swim chambers are the most commonly used apparatus to measure swimming abilities. In swim chambers, fish swim in a small test section against a current that can be manipulated by the experimenter. Time to fatigue at set velocities is measured and used to estimate traversable distances or velocity is incrementally increased and maximum aerobic or anaerobic capacity is estimated (i.e. U_{crit} and U_{sprint} tests; Brett, 1964; Peake et al., 1997; Starrs et al., 2011). Swim chambers are prevalent due to their small size and affordability and are advantageous due to the ability to precisely control experimental conditions, replicate treatments and conduct numerous trials in a relatively short time span. However, the small size of the test section limits natural swimming behavior and may result in conservative estimates of swimming abilities (Mallen-Cooper, 1992; Peake and Farrell, 2004; Tudorache et al., 2007).

Open-channel flumes allow fish swimming performance and behavior to be examined in a controlled setting which more closely approximates conditions fish experience in passage structures and may provide more realistic predictions of passage success (Haro et al., 2004). The larger scale of flumes allow fish to move naturally through the flow and traversable distances and maximum swimming velocities can be measured. Additionally, flumes allow the observation

of natural swimming behaviors such as gait transitions, which recent studies have shown are indicative of maximum aerobic capacity (Wilson and Eggington, 1994; Peake and Farrell, 2004; Peake, 2008b).

In this study, swimming capacity of sauger was tested in both a flume and swimming chamber to estimate traversable distances over a range of water velocities, maximum aerobic and anaerobic capacity, and maximum swimming velocity. These metrics combined with observations of swimming behavior can be used to design effective passage structures and identify barriers for sauger. Additionally, the effects of body size and temperature on swimming performance was assessed. The use of both a flume and a swim chamber allowed comparisons between the different testing apparatus.

METHODS AND MATERIALS

STUDY DESIGN

Tests to characterize the swimming abilities and behavior of sauger were conducted in an open-channel flume and swim chamber located at the Bozeman Fish Technology Center (BFTC; Bozeman, MT). Distance of ascent, passage success, and maximum aerobic capacity were measured in a 'passage test' conducted in the flume at the combination of three velocities (51, 78, and 92 cm s⁻¹) and three temperatures (10.0, 14.3, and 18.3° C) for a total of nine treatments. Test velocities and temperatures represent mean values. Test velocities were selected to represent a range of velocities likely encountered within fishways. Test temperatures were selected to approximate the seasonal range of temperatures sauger experience in the wild. The lowest test temperature (10.0° C) represents temperatures encountered during spring spawning migrations, 14.3° C approximates the isotherm defining the northern distribution of sauger (15.6° C), and the

highest test temperature approximates the temperature growth optimum (19.6° C; Hokanson, 1977; Hasnain et al., 2010).

Due to their conservation status only a limited number of sauger could be obtained for testing (Carlson, 2003; Keinath et al., 2003). This necessitated the use of a crossover experimental design (Ramsey and Schafer, 2002) wherein all study fish were subjected to repeated testing. Changes in seasonal availability of groundwater temperatures at the test site and time involved in altering the flume slope to adjust test velocity limited the ability to randomize the order of the nine treatments. As a result, temperature treatments were conducted in the following order: 10.0, 14.3, and 18.3° C, with velocity treatments run in an ascending order (i.e. 51, 78, and 92 cm s⁻¹) 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⁻¹ at 10.0° C) warranted retesting after the completion of all other passage tests.

Maximum burst swimming velocities ($V_{\max}$) were measured in a 'sprint test' conducted in the flume at a single velocity. Water velocity in the flume was set at 46 cm s⁻¹ to provide sufficient velocity to trigger positive rheotaxis yet prevent excessive energy expenditure. $V_{\max}$ 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 was 17.9, 11.5, and 14.4° C.

Time to fatigue of sprint swimming (i.e. maximum anaerobic capacity) and maximum aerobic capacity were measured in an ' U_{sprint} test' conducted in the swim chamber at seven temperatures. 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 temperature changes among treatments. All available fish were randomly assigned to one of two groups; each group was tested in a 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 sprint swimming, increase the number of rest days between consecutive tests, and minimize the number of trials for each fish.

Trials for all tests were completed over a 113 day period between June and September of 2012. Tests of fish passage in the flume were conducted first, with a minimum of two days of rest (mean=4, range=2-7) between trials, except for the retested treatment combination (51 cm s⁻¹ at 10.0° C) which occurred 48 days later when cold water became available again. Fish were rested for 28 days prior to the sprint (flume) and U_{sprint} (swim chamber) trials. Sprint tests were interspersed among U_{sprint} tests with a minimum of 2 days rest (mean=7, range=2-33) between any trial.

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 4.2 × 1.2 × 1.2 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 at the BFTC to alleviate osmotic stress associated with transport. Fish were weighed to the nearest 0.1 g, fork length (L_F) 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 (n=10) were males (mean L_F =39.3 cm; range=34.0-43.9 cm). The five females collected did not adjust to captivity, had high mortality, and were omitted from data analysis. Test fish were fed by

adding 200-300 small (2.5-7.6 cm) rainbow trout to holding tanks, with additional prey added when depleted (~every 3-4 weeks). Prior to testing, holding tank temperatures were adjusted at a maximum rate of 1° C per 8 h until the desired test temperature was reached; fish were then held at that temperature for a minimum of 24 h prior to testing.

PASSAGE AND SPRINT TESTS

Passage and sprint tests were conducted in a large open channel flume (0.9 m width × 0.9 m depth × 17.1 m length). The flume was constructed from wood and rested on a metal framework that could be tilted with hydraulic jacks to adjust the slope. Slope was adjusted to $0.50 \pm 0.02\%$ for the 51 and 78 cm s⁻¹ passage treatments and sprint treatments, and $0.80 \pm 0.02\%$ for the 92 cm s⁻¹ passage treatments. A middle wall was placed within the flume to constrict channel width to 0.5 m, which allowed a greater range of water velocities to be tested. Water entered the flume from a headwater tank and flowed through the open-channel into a tailwater tank. A grate located at the downstream end of the channel prevented 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 disturbance to test fish. 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 fish position. An array of six digital cameras (Handicam HDR-XR-150, Sony, Tokyo, Japan) were positioned 2.0 m above the flume every 2.2 m along its length to provide overlapping fields of view and allow fish to be continuously tracked as they ascended the flume. Video recordings of trials allowed observation of swimming behavior, passage success, distance

of maximum ascent ($D_{\max}$), and ground velocities in the passage test and $V_{\max}$ in the sprint test. 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 not involving rapid acceleration or deceleration. Unsteady (i.e. 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 velocity in the flume was measured before and after the completion of each set of daily trials. Water depth and velocity was measured every 61 cm for the 12.8 m ‘test section’ of the flume. Water entering the headwater tank caused unstable flow conditions which prevented accurate measurement of hydraulics and swimming performance upstream of the test section. Velocity was measured with a Marsh-McBirney Flo-Mate 2000 current meter (Hach Corp., Loveland, CO, U.S.A.) at 0.6 times the water depth to characterize average velocity. Depth was measured with a graduated rod to the nearest 0.3 cm. Varied turbulence intensities encountered by fish among treatments warranted the calculation of Reynolds number, as turbulence has been shown to influence swimming performance and behavior (Nikora et al., 2003; Lacey et al., 2012).

Stage height and discharge were 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 Americas Corp., Edgewood, NY, U.S.A.) located on the inflow pipe to the flume. Measurements confirmed

discharge varied little among trials within a treatment, which ensured fish experienced similar hydraulic conditions during testing.

In the passage test, fish placed at the downstream end of the flume were given 30 min to volitionally ascend the flume. Pilot studies indicated that fish reached their maximum ascent distance in less than 30 min. Ten fish were tested in each of the 9 different velocity $\times$ temperature treatments; all trials for each treatment were conducted on the same day. The exception was the final $10.0^{\circ}\text{C} \times 51\text{ cm s}^{-1}$ treatment, wherein only eight fish were tested due to a fungal infection causing the death of two test fish. Surviving fish were given a salt treatment (5 ppm) and an eight day recovery period prior to further testing.

In the sprint test, fish were confined to the lower 0.9 m of the flume by a removable grate. After a 5 min acclimation period, the grate was removed and fish were stimulated to sprint the length of the flume by gently prodding with a net handle, following similar protocols used in previous sprint tests (Nelson et al., 2001; Mesa et al., 2008). After the initial sprint, fish were coerced back to the downstream end of the flume, the grate was replaced, and fish were allowed 30 s of rest before a second stimulation. This sequence was repeated a total of three times in a trial to ensure at least one vigorous burst was observed. A total of 26 sprint trials were conducted. Ten fish were tested at 17.9°C and eight fish were tested in the 11.5 and 14.4°C treatments due to the aforementioned mortality.

U_{SPRINT} TEST

U_{sprint} tests were conducted in a swim chamber to measure the maximum velocity a fish could swim for 15 s, the approximate maximum duration sprint swimming can be sustained (Beamish 1978). The swim chamber (185 L, Loligo Systems, Tjele, Denmark) was supplied with

220 air-saturated flow-through water ($18.9\text{--}30.3\text{ L min}^{-1}$). The test section had a cross section of $25 \times$
221 25 cm and a length of 80 cm . Flow straighteners located just upstream of the test section
222 provided rectilinear micro-turbulent flow and an approximately uniform velocity profile. The
223 upstream half of the test section was covered with black plastic and a halogen light was directed
224 on the downstream end in order to deter the light sensitive sauger from resting on the
225 downstream grate and motivate fish to swim in the low-light upstream half of the test section. A
226 black plastic shroud was erected around the entire chamber to prevent disturbances to test fish. A
227 video camera recorded trials and video analysis allowed the total time spent swimming and water
228 velocities associated with gait transitions to be determined.

229 Water velocity was measured with a Marsh-McBirney Flo-Mate 2000 current meter at
230 0.6 times the water depth to characterize the average velocity in the swim chamber. A calibration
231 curve relating velocity to frequency output of the motor was created to allow rapid and precise
232 velocity adjustments. Water temperature was continuously monitored with an Ertco High
233 Precision Thermometer (Barnstead International, Dubuque, Iowa).

234 Trials began with a 10 min acclimation period at a velocity of 46 cm s^{-1} . After
235 acclimation, velocity was increased 7.6 cm s^{-1} every 15 s until fish became impinged on the
236 downstream grate. If fish remained impinged for 3 s the motor was turned off and on rapidly to
237 encourage further attempts. If fish remained impinged, the trial was ended and the time to the
238 impingement was recorded. Ten fish were tested in a total of $33\text{ }U_{\text{sprint}}$ trials, with 18 trials
239 conducted with group one fish and 15 trials with group two fish.

240 DATA ANALYSIS

Passage success data was analyzed using mixed effect logistic regression. Passage attempts were classified as successful if a fish ascended the 12.8 m test section, and unsuccessful otherwise. Model covariates were water temperature, velocity, and fish length. A random effect was included to account for repeated measures on individual fish. All two-way interactions were included in an initial regression model and evaluated with likelihood ratio tests (Ramsey and Schafer, 2002). Interactions with low statistical support ($P > 0.10$; Curran-Everett and Benos, 2004) were removed in a stepwise fashion, with interactions with the least statistical support removed first. Statistical evidence for associations between the odds of passage success and explanatory variables were assessed using likelihood ratio tests comparing the final model to the model without the explanatory variable or interaction of interest.

Maximum ascent distance ($D_{\max}$; passage test), ground velocity (swimming velocity minus water velocity; passage test), and maximum burst velocity ($V_{\max}$; sprint test) in relation to temperature, velocity, and fish length were analyzed using linear mixed effects regressions. Ground velocity for each 61 cm long flume section was calculated as the time required for a fish to traverse between the reference lines delineating each section divided by the distance traversed (accounting for the selected path). Ground velocities for the three sections closest to the downstream retention grate were omitted to eliminate possible startle-response effects. Similarly, ground velocities from the four sections nearest the headtank were also excluded because some fish did not fully ascend into this area. Ground velocities from the fastest ascent in the remaining 14 flume sections spanning 8.6 m were averaged for each trial for analysis. Ground velocities were calculated for 77 of the 80 trials in which passage attempts were made. Burst velocities were calculated for each 61 cm flume section between reference lines and $V_{\max}$ was defined as

the highest swimming velocity observed among all test sections. Trials in which fish that did not attempt ascents (passage test; $n=8$) or did not respond to stimulation (sprint test; $n=3$) were omitted from analysis.

Linear mixed effect regression was used to assess relationships among temperature, body length, and U_{sprint} values (i.e. time to fatigue of sprint swimming). U_{sprint} values were calculated using the formula provided by Brett (1964):

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

where U_i is the penultimate velocity (cm s^{-1}), 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^{-1}). 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 was 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:

$$(2) \quad D = (U_{\text{sprint}} - V_f) \times 15 \text{ s}$$

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

All data analysis was conducted with program R version 3.0.2 (R Development Core Team 2014) and the lme4 package (Bates et al., 2014). All linear mixed models were fit using maximum likelihood estimators when comparing models with different fixed effects structures

but the final model was fit using restricted maximum likelihood estimators (Zuur et al., 2009). Assumptions of homogeneity of variance, normality, and linearity for regression analyses were assessed using plots of residuals versus fitted values, normal quantile-quantile plots, and plots of response variables versus continuous explanatory variables, respectively. All assumptions were adequately met. 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 was not statistically analyzed due to collinearity with temperature and velocity. However, possible relationships were examined by graphical comparison of holding time and prior number of tests with each response variable.

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 (Fig. 1). Velocity ranged from 7% less than the mean longitudinal velocity at the downstream end to 6% greater at the upstream end in the 51 cm s⁻¹ treatments, 9% less to 10% greater in the 78 cm s⁻¹ treatments, and 20% less to 26% greater in the 92 cm s⁻¹ treatments.

Flow in all passage and sprint tests was characterized as turbulent. Reynolds number, which is the ratio of inertial to viscous forces, was used to characterize flow as turbulent (Re >2,500) or laminar (Re <2,500; Chow 1959). The mean Reynolds number exceeded 67,000 in all passage and sprint treatments but varied widely among test velocities (range=64,200-201,000;

Table 1, 2). Turbulence was positively related to water velocity and generally increased with longitudinal distance upstream. Higher Reynolds numbers correlate to larger variance in three-dimensional velocity vectors.

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. 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 test velocity of 116 cm s⁻¹). Fish generally held position near flume corners by pressing their body, pelvic and caudal fins against the bottom. Multiple ascent attempts were common, with many fish repeatedly ascending 9.1 to 12.8 m up the flume, passively drifting to the downstream grate, then making another passage attempt. Fish rarely ascended into the headwater tank.

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 success rate differed little among treatments (Table 1) and mixed effects logistic regression indicated there was no evidence for an association between passage success and temperature ($\chi^2=2.81$, df=2, P=0.25), velocity ($\chi^2=1.99$, df=2, P=0.37), or fish length ($\chi^2=1.85$, df=1, P=0.17).

Mean $D_{\max}$ was also high (12.6 m) and varied little among treatments (Table 1). Linear mixed effect regression indicated there was no evidence for an association between $D_{\max}$ and water temperature ($\chi^2=1.26$, df=2, P=0.53), velocity ($\chi^2=2.27$, df=2, P=0.32), or fish length ($\chi^2=1.51$, df=1, P=0.22). A low ICC value (0.02) indicated 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 $D_{\max}$.

The mean ground velocity for all treatments was 26 cm s^{-1} but ranged from 18 to 35 cm s^{-1} among treatments. There was strong evidence ground velocity was positively associated with water temperature ($\chi^2=14.3$, $df=2$, $P=0.0008$), ranging from 20 cm s^{-1} at 10.0° C , 28 cm s^{-1} at 14.3° C , and 32 cm s^{-1} at 18.3° C . There was suggestive evidence for a positive association between ground velocity and test velocity ($\chi^2=5.18$, $df=2$, $P=0.08$). Mean ground velocity was the lowest in the 51 cm s^{-1} treatment (23 cm s^{-1}), but did not differ between the 78 and 92 cm s^{-1} treatments (28 cm s^{-1} , respectively). No evidence existed for an association between ground velocity and fish length ($\chi^2=0.46$, $df=1$, $P=0.50$). The intraclass correlation value (0.25) indicated fish to fish variability accounted for a substantial portion of the variance among ground velocities, with some fish consistently swimming at low ground velocities and others at high ground velocities.

Water velocity influenced the swimming behavior used to ascend the flume. Fish used a steady sustained gait in the 51 and 78 cm s^{-1} treatments, but most fish transitioned to unsteady burst swimming (65.4% of test fish) or steady burst swimming (26.9%) in the 92 cm s^{-1} treatment. Video analysis revealed gait transitions occurred at a mean velocity of 97 cm s^{-1} (range= 93 - 99 cm s^{-1}), and varied little among temperature treatments.

SPRINT TEST

Sauger responded to stimulation with a burst of rapid tail beats away from the stimulus followed by a glide, with the maximum burst 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^{-1} (range=119 to 350 cm s^{-1} ; Table 2) and there was no evidence for a relationship between $V_{\max}$ and temperature ($\chi^2=3.76$, $df=2$, $P=0.15$). Maximum swimming velocity generally increased with fish length, but the relationship was not significant ($\chi^2=2.38$, $df=1$, $P=0.12$). An ICC of 0.29 indicated fish to fish variability accounted for a substantial portion of the variance among $V_{\max}$ values, with some fish consistently obtaining higher maximum swimming velocities than others. 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^{-1} for fish with the maximum holding time (33 days) and maximum number of prior tests (19) to 246 cm s^{-1} 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 pressing their body, pelvic fins, caudal fin, and occasionally their pectoral fins against the bottom. However, all test fish began swimming in the water column as test velocities increased. Fish transitioned from steady sustained swimming to unsteady burst-glide swimming at a mean velocity of 84 cm s^{-1} (range= 69 to 99 cm s^{-1}). Bursts ended when fish encountered the upstream grate, at which point fish returned to a benthic position and pressed 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 s in the U_{sprint} test was 124 cm s^{-1} and U_{sprint} values generally increased with temperature (Table 3). In group two there was suggestive evidence U_{sprint} values were positively associated with temperature ($\chi^2=6.03$, $df=2$, $P=0.05$; Table 3). Mean U_{sprint} was the lowest at 10.0° C (105 cm s^{-1}) and highest at 22.3° C (139 cm s^{-1}) for group two (Table 3). There was less support for associations between U_{sprint} and temperature in group one ($\chi^2=5.51$, $df=3$, $P=0.14$). However, mean U_{sprint} was the lowest at 12.0° C (114 cm s^{-1}) and highest at 20.2° C (145 cm s^{-1}). There was no evidence for a relationship between U_{sprint} and fish length in group one ($\chi^2=0.01$, $df=1$, $P=0.91$) or group two ($\chi^2=0.12$, $df=1$, $P=0.72$). Low ICC values for both group one ($ICC=0.08$) and group two ($ICC=0.00$) indicated 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 eight mean U_{sprint} values were used to parameterize equation (2) and predict maximum passable distances and water velocities sauger could ascend for areas of high velocity. Predictions of maximum passable distances differed markedly among temperature treatments. The distance sauger could ascend at a water velocity of 97 cm s^{-1} , the water velocity inducing burst swimming in the passage test, ranged from 1.3 m at 10.0° C to 7.2 m at 20.2° C . Using the mean U_{sprint} value (124 cm s^{-1}), the maximum allowable distance was predicted to be 4.1 m. The distance sauger were predicted to ascend decreased rapidly as water velocity increased (Fig. 2). Maximum lengths of high velocity areas and maximum water velocities combinations suitable for passing sauger at a low (10.0° C), high (22.3° C) and intermediate temperatures (16.3° C) are presented in Fig. 2.

DISCUSSION

For fishways to successfully pass fish, several criteria must be met. The combination of the length of the structure and its velocities cannot exceed a species' swimming capacities in terms of endurance and maximum swimming velocities. Additionally, hydraulic characteristics of the structure must not behaviorally inhibit passage attempts (Castro-Santos, 2004; Peake, 2008c; Ficke et al., 2011). In this study, data on ascent distance and passage success of sauger swimming in a flume over a range of water velocities and temperatures was provided. Additionally, maximum swimming velocities and passable distances of high velocity flow were estimated in both a flume and swim chamber in order to identify potential barriers to movement. Finally, video observation of swimming behavior in the flume was used to identify gait transitions and strategies employed by sauger during upstream movements. 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 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 92 cm s⁻¹. The high passage success, multiple successful attempts occurring in all treatments, and similarities in passage success and $D_{\max}$ among all treatments indicated test conditions did not limit upstream sauger movements. In a comparable open-channel flume study with the morphologically similar congener, walleye (*Sander vitreus*), Peake (2008a) reported high rates of passage (>80%) in a 25 m and 50 m flume at mean velocities ranging from 39 to 100 cm s⁻¹. Whether sauger would be able to traverse a similar distance against this range of velocities awaits investigation in a longer testing apparatus. Differences in passage success

between sauger and walleye of similar size at a vertical slot fishway (40.0% versus 57.1%) suggest swimming abilities and/or behavior differ between these species (Thiem et al., 2013). Differences in swimming ability 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 similarities in ground velocities maintained by sauger in the flume over a wide range of test velocities suggest they are altering swimming velocities to maximize ascent distance. Fish can maximize distance of ascent and optimize energy expenditure by swimming at a constant ground velocity in relation to changing water velocities (Castro-Santos, 2005). Video analysis revealed 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^{-1}), sauger transitioned to higher ground velocities. For example, in the 10.0° C treatment fish swam at a mean ground velocity of 19 cm s^{-1} when water velocities was less than 97 cm s^{-1} , but increased ground velocity to 28 cm s^{-1} when water velocity exceeded 97 cm s^{-1} . Similar increases in ground velocity were observed in the 14.3° C (8 cm s^{-1} increase) and 18.3° C treatment (17 cm s^{-1} increase). Peake and Farrell (2004) and Castro-Santos (2005; et al., 2013) observed similar patterns in ground velocities for smallmouth bass (*Micropterus dolomieu*), American shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in flume experiments and Standen et al. (2004) observed a similar pattern in migrating sockeye salmon (*Oncorhynchus nerka*).

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 have been based on models and predictive tools such as FishXing that assume fish will swim at a constant velocity (e.g. 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 predictive models assuming constant ground velocity, in contrast to constant swimming velocity, may provide more realistic estimates of passage (Castro-Santos, 2006). Additionally, models should incorporate estimates of burst swimming endurance to predict passage success 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 during gait transitions, with some fish transitioning to an unsteady gait at a water velocity of 97 cm s^{-1} and others transitioning to steady 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 the study, it is likely 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 observed in the flume at 97 cm s^{-1} likely reflects a 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 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 higher 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 (Wilson and Eggington, 1994; Peake and Farrell, 2004; Peake, 2008b). 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 sauger use aerobically powered swimming at water velocities less than 97 cm s^{-1} and should be physiologically capable of ascending long distances if water velocities are below this threshold and fish are not behaviorally inhibited from entering or ascending the structure. Two swimming gaits involving anaerobic exercise were observed above this threshold: unsteady burst-glide and steady sustained burst swimming. Burst-glide swimming may represent an intermediate gait in which both aerobic and anaerobic respiration are used and may be analogous to the prolonged swimming mode described by Brett (1964) and Beamish (1978), which can be sustained for

480 durations of 20 s to 200 min before fatigue (Castro-Santos et al., 2013). Steady sustained burst
481 swimming is powered solely by anaerobic exercise and can be sustained for durations of less
482 than 20 s (Beamish, 1978; Jayne and Lauder 1994, 1996). We observed some fish transitioning
483 to steady-sustained burst swimming at water velocities greater than 97 cm s^{-1} and conservatively
484 recommend areas above this threshold be limited to short distances ($<1 \text{ m}$) to avoid fish fatigue
485 and passage failure.

486 Direct observation of swimming behavior in relation to hydraulic conditions in the flume
487 was an important aspect of the study. Video recordings of passage trials revealed sauger used
488 low-velocity pathways located along the bottom of the flume, frequently used holding behavior
489 during their ascent, and were able to hold position on a smooth-bottomed surface at average
490 velocities in excess of 100 cm s^{-1} . Given these observations, it seems likely roughness elements
491 and other design features that increase boundary layer thickness and provide structured
492 turbulence would allow sauger to pass structures with mean velocities higher than the
493 recommendations, which has been demonstrated in other species (Pavlov et al. 2000; Liao et al.,
494 2003; Bestgen et al. 2010). Conversely, observations of sauger terminating ascents before
495 reaching the resting refuge provided by the headtank indicate the chaotic turbulence and aerated
496 water created by water plunging into the headtank or the low light conditions created by the
497 plywood cover may deter upstream movements. Thus, structures such as pool-weir or denil
498 fishways with similar turbulent conditions or long covered structures may inhibit sauger
499 movements. Combining field and laboratory studies to identify structures inhibiting passage in
500 the field, then testing key swimming attributes and observing behavior in an experimental flume
501 with similar hydraulic features is needed to further determine factors affecting passage.

Comparison of anaerobic endurance estimates from the highest passage test velocity and the U_{sprint} chamber test contributes to the growing body of literature suggesting swim chambers underestimate anaerobic swimming abilities (e.g. Peake, 2004; Peake and Farrell, 2006; Holthe et al., 2009). For example, the mean distance a sauger could ascend at a water velocity of 97 cm s^{-1} was predicted to be 1.3 m at 10.0° C using the U_{sprint} data from the swim chamber whereas 89% of sauger in the 10.0° C by 92 cm s^{-1} treatment were able to ascend the 3.7 m of open-channel flow with water velocities exceeding 97 cm s^{-1} . 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 venous oxygen stores to be replenished and subsequent bursts were always initiated before ground velocity reached zero (Farrell and Clutterham, 2003; 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 inefficient behavior likely negates 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 have 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 efficient method for measuring sprinting endurance. Additionally, estimates of maximum aerobic capacity from gait transition observations were similar between the U_{sprint} (84 cm s^{-1}) and passage test (97 cm s^{-1}).

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). These consequences can be mitigated by providing resting areas between areas of high velocity to allow fish to recover. 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.

Maximum sprint velocity is a useful parameter for defining upper thresholds that will inhibit upstream movement. Because maximum swimming velocities ($V_{\max}$) in the sprint test were obtained in a low velocity environment (46 cm s^{-1}), measured over a 61 cm distance, and were generally maintained for less than half a second, they are representative of instantaneous maximum burst velocity. Thus, the sprint results indicate most sauger would be unable to move upstream when water velocity exceeded 219 cm s^{-1} . The maximum swimming velocity observed in the passage test was 260 cm s^{-1} for a fish swimming against a current of 107 cm s^{-1} , indicating maximum velocities of coerced sauger are representative of velocities obtainable by free-swimming sauger. However, it is possible volitional burst velocities would have been higher if higher water velocities were tested. The finding that 43.4% of sauger did not obtain their $V_{\max}$ on their first stimulation supports the finding of Nelson and Claireaux (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 (e.g. Videler, 1993; Haro et al., 2004; Katopodis and Gervais, 2011). Previous studies have found larger fish can

swim faster and farther than smaller fish (e.g. Beamish, 1978; Videler, 1993; Bestgen et al., 2010). The lack of evidence for body size associations is likely a result of the relatively small range of body sizes (34.0-43.0 cm) tested. All tested sauger were likely mature adult males 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. Females are also expected to have lower swimming abilities due to a smaller proportion of their mass devoted to swimming muscle and a larger proportion devoted to reproductive organs (Glebe and Leggett, 1981; Reidy et al., 2000). However, the larger size of mature females in comparison to males may offset these differences in swimming abilities and results from a single female ($L_F=52.6$ cm; omitted from analysis) in the flume trials suggest the distances and velocities tested would not inhibit large mature females (Carufel, 1960).

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 aerobic swimming abilities generally follows a bell-shaped curve in response to temperature: reduced at low temperatures, increasing to a maximum near the optimum metabolic temperature, then decreasing as the upper thermal limit is approached (Beamish, 1978; Myrick and Cech, 2000; Ojanguren and Brana, 2000). Although ground velocities in the passage test differed among test temperatures, there was no evidence for differences in ascent distance or passage success among

test temperatures. We predict temperature, water velocity, and body size associations would have been observed if higher water velocities limiting 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. A surprising result was the similar rate of increase of U_{sprint} across all temperatures even when temperatures exceeded the growth optimum (19.6°C) of sauger (Hasnain et al., 2010), suggesting 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, use of the most conservative estimates associated with low temperature treatments is suggested because sauger spawning migrations occur at low water temperatures (10.3°C ; Hasnain et al., 2010). In all performance tests, the ability to identify associations among swimming performance metrics and explanatory variables was limited by a relatively small sample size.

Repeated measures of swimming performance on a limited number of test fish was a recognized limitation of the study. However, given passage success and maximum ascent distance were similar across all passage treatments, it appears repeated testing did not influence passage results. The sprint and U_{sprint} tests both involved anaerobic exercise requiring a recovery period to process waste products, restore energy reserves, and replenish venous oxygen stores (Milligan, 1996; Farrell and Clutterham, 2003). However, Farrell et al. (1998), Jain et al. (1998), Farrell (2007), and Handelsman et al. (2010) demonstrated swimming performances resulting in fatigue were repeatable in less than an hour even if metabolic recovery is not complete 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 the minimum (2 days) or maximum holding time

(33 days) affected the results. Alternatively, Farrell et al. (1990) reported 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 no training effects were occurring. Moreover, repeated testing allowed detection of intraspecific variation in sprint performance and selected ground velocities.

The results of this study provide managers and engineers the first estimates of swimming performance for sauger and if appropriately applied, they should allow for better design of fishways, identification of barriers, and ultimately reduced habitat and population fragmentation throughout the range of sauger. Based on the study results, passage structures with average water velocities less than 97 cm s^{-1} should be passable, velocities greater than 100 cm s^{-1} should be limited to short distances (1 m), and structures with water velocities exceeding 219 cm s^{-1} may represent barriers to sauger. This study also highlighted the importance of swimming behavior when evaluating and designing passage structures. Specifically, results indicated sauger use lower velocity pathways along the bottom of structures to move upstream, highly chaotic turbulence created by plunging water may deter passage attempts, low light conditions may inhibit passage, and flume studies that allow natural swimming behavior provide more realistic estimates of swimming performance than swim chamber studies. Future studies on sauger should focus on how hydraulic associated with common fishway designs affect swimming behavior and passage success, the swimming performance of juveniles and females, and swimming endurance at water velocities exceeding 97 cm s^{-1} .

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Figure Captions

Fig. 1. Mean water velocity (cm s^{-1}) and depth (cm) measurements along the length of the flume test section for the 51 (A), 78 (B), and 92 (C) cm s^{-1} velocity treatments in the passage test.

Fig. 2. Lines representing maximum velocities (cm s^{-1}) predicted to allow sauger to pass areas of high velocity in fishways at 10.0° C (solid line), 16.3° C (dashed line), and 22.3° C (dotted line) based on the U_{sprint} data collected in a swim chamber. Any combination of distance and water velocity in the region above the line for a given temperature are predicted to result in passage failure.

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TABLES

Table 1. Summary of test conditions and results for the nine velocity (cm s^{-1}) and temperature (T ; $^{\circ}\text{C}$) treatments 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 S.D.

Test							Ground
Velocity		Mean Velocity		Participation	Passage		Velocity
(cm s^{-1})	T ($^{\circ}\text{C}$)	(cm s^{-1})	Re	Rate	Rate	D_{max} (m)	(cm s^{-1})
51	10.7	48 ± 2	$67,800 \pm 1,600$	0.75	0.83	12.3 ± 1.3	18 ± 8
	14.3	52 ± 2	$78,800 \pm 1,400$	0.90	1.00	12.8 ± 0.0	24 ± 9
	17.6	52 ± 1	$94,400 \pm 1,700$	1.00	1.00	12.8 ± 0.0	26 ± 13
78	10.1	73 ± 4	$105,000 \pm 2,000$	0.90	0.78	12.2 ± 1.3	20 ± 9

92	14.3	80 ± 5	125,200 ± 3,300	1.00	0.90	12.8 ± 0.2	30 ± 14
	18.4	85 ± 4	154,200 ± 4,200	1.00	1.00	12.3 ± 1.7	34 ± 18
	9.1	90 ± 8	179,500 ± 6,600	0.90	0.89	12.7 ± 0.2	21 ± 6
	14.1	94 ± 15	152,500 ± 11,800	0.70	0.86	12.6 ± 0.7	29 ± 12
	18.8	93 ± 14	177,000 ± 14,200	1.00	1.00	12.8 ± 0.00	35 ± 19

Table 2. Effect of three test temperatures (T ; ° C) on the participation rate and maximum swimming velocity ($V_{\max}$; cm s^{-1}) of sauger in the experimental flume. The average Reynolds number (Re ; dimensionless) is also shown.

T (° C)	Trials (#)	Re (S.D.)	Participation Rate	$V_{\max}$ (cm s^{-1})		
				Mean	Range	S.D.
11.5	8	96,500 (1,500)	0.88	213	(121, 310)	73
14.4	8	107,800 (1,700)	0.88	191	(119, 258)	45
17.9	10	78,000 (1,400)	0.90	246	(196, 350)	49

Table 3. Effect of temperature (T; ° C) on the maximum sprint velocity sustainable for 15 s (U_{sprint}) of sauger in a swim chamber.

Group	T (° C)	Trials (#)	U_{sprint} (cm s ⁻¹)		
			Mean	Range	S.D.
1	12.0	4	114	(91, 155)	28
	16.3	4	130	(106, 156)	25
	18.1	5	128	(109, 151)	15
	20.2	5	145	(124, 186)	25
2	10.0	5	105	(81, 139)	26
	14.0	5	112	(88, 145)	24
	22.3	5	139	(107, 155)	20

279x361mm (300 x 300 DPI)

279x482mm (300 x 300 DPI)