

Swimming performance of sauger (*Sander canadensis*) in relation to fish passage

David R. Dockery, Thomas E. McMahon, Kevin M. Kappenman, and Matthew Blank

Abstract: A lack of information on the swimming abilities of sauger (*Sander canadensis*), a highly migratory species particularly sensitive to habitat fragmentation, may inhibit the design of effective passage structures for this species. 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 s 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.

Résumé : Le manque d'information sur les habilités natatoires pourrait faire entrave à la conception de passes efficaces pour le doré noir (*Sander canadensis*), une espèce hautement migratrice particulièrement sensible à la fragmentation des habitats. Le succès de passage, les distances d'ascension maximums et les vitesses de sprint maximums de dorés noirs ont été estimés dans un canal jaugeur ouvert pour une fourchette de vitesses (51, 78 et 92 cm·s⁻¹) et de températures (10,0, 14,3 et 18,3 °C) de l'eau afin d'évaluer leur performance natatoire. Le succès de passage était élevé (91 %) pour toutes les vitesses testées, tout comme la vitesse d'impulsion instantanée maximum (219 cm·s⁻¹). La température de l'eau et la taille du corps avaient peu d'effet sur la performance natatoire. Les dorés noirs passaient de la nage stable soutenue à la nage transitoire de type impulsion–glisse ou à la nage par impulsions soutenues à 97 cm·s⁻¹. Les dorés noirs étaient capables de sprints soutenus à 124 cm·s⁻¹ pendant 15 s dans un tunnel de nage. Les résultats donnent à penser que les passes caractérisées par des vitesses de l'eau inférieures à 97 cm·s⁻¹ devraient présenter une forte probabilité de passage réussi des dorés noirs adultes alors que les passes caractérisées par des vitesses de l'eau supérieures 219 cm·s⁻¹ pourraient être infranchissables. [Traduit par la Rédaction]

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 Welcomme 1995; Saunders et al. 2002). In the United States alone there are ~76 000 large dams (>8 m), and 85% of large rivers are fragmented as a result (Larinier 2000; Hughes et al. 2005). Sauger (*Sander canadensis*) is primarily a large-river species and 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 makes 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 sauger abundance and distribution (Hesse 1994; Amadio et al. 2005; Jaeger et al. 2005), resulting 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.

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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 because of their small size and affordability and are advantageous owing 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 that more closely approximates the 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 such that 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 2008).

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, Montana, USA). 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 experiences 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).

Owing 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 a “ 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 1: 20.2, 18.1, 16.3, and 12.0 °C; group 2: 22.3, 14.0, and 10.0 °C). Fish were split into groups to more closely evaluate 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 2012. Tests of fish passage in the flume were conducted first, with a minimum of 2 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 allowed to rest 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 of rest (mean = 7 days, range = 2–33 days) between any trial.

Test fish

Fifteen adult sauger were collected via electrofishing from the Bighorn River near Basin, Wyoming, USA, on 11 May 2012. Fish were transported in an aerated tank to the BFTC and transferred to a 4.2 m × 1.2 m × 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. To identify individuals, a passive integrated transponder (PIT) tag (22 mm × 3 mm) was implanted in the peritoneal cavity through a small incision (no sutures needed) located just anterior to the anal fin. 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 wide × 0.9 m deep × 17.1 m long). 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% ± 0.02% for the 51 and 78 cm·s⁻¹ passage treatments and sprint treatments, and 0.80% ± 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 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}), 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 those of 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 and 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, preventing the 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, Colorado, USA) at 0.6 times the water depth to characterize mean 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 the 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, New York, USA) located on the inflow pipe to the flume. Measurements confirmed that 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 nine different velocity \times temperature treatments; all trials for each treatment were conducted on the same day. The exception was the final 10.0 °C \times 51 cm·s⁻¹ treatment, wherein only eight fish were tested owing to a fungal infection that caused the death of two test fish. Surviving fish were given a salt treatment (5 ppm) and an 8-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 them with a net handle, following similar protocols used in previous sprint tests (Nelson et al. 2002; 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 per 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 owing 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 air-saturated flow-through water (18.9–30.3 L·min⁻¹). The test section had a cross-section of 25 cm \times 25 cm and a length of 80 cm. Flow straighteners located just upstream of the test section provided rectilinear microturbulent flow and an approximately 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 to deter the light-sensitive sauger from resting on the downstream grate and to motivate fish to swim in the low-light upstream half of the test section. A black plastic shroud was erected around the entire chamber to prevent disturbances to test fish. A video camera was used to record the trials, and video analysis allowed the total time fish spent swimming and the water velocities associated with gait transitions to be determined.

A calibration curve relating velocity to frequency output of the motor was created to allow rapid and precise velocity adjustments. Water temperature was continuously monitored with an Ertco high-precision thermometer (Barnstead International, Dubuque, Iowa).

Trials began with a 10 min acclimation period at a velocity of 46 cm·s⁻¹. After acclimation, velocity was increased 7.6 cm·s⁻¹ every 15 s until fish became impinged on the downstream grate. If fish remained impinged for 3 s 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 1 fish and 15 trials with group 2 fish.

Data analysis

Passage success data were analyzed using mixed-effects 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 having 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 with 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 the distance 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 headwater tank 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 did not attempt ascents (passage test; $n = 8$) or did not respond to stimulation (sprint test; $n = 3$) were omitted from analysis.

Linear mixed-effects 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 ($\text{cm}\cdot\text{s}^{-1}$), 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 ($7.6 \text{ cm}\cdot\text{s}^{-1}$). 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 were analyzed separately for group 1 and group 2 tests.

U_{sprint} data were used to parameterize the equation from Peake et al. (1997) to predict the maximum distance that 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 ($\text{cm}\cdot\text{s}^{-1}$), and V_f is the water velocity ($\text{cm}\cdot\text{s}^{-1}$).

All data analysis was conducted with program R version 3.0.2 (R 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 owing 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.

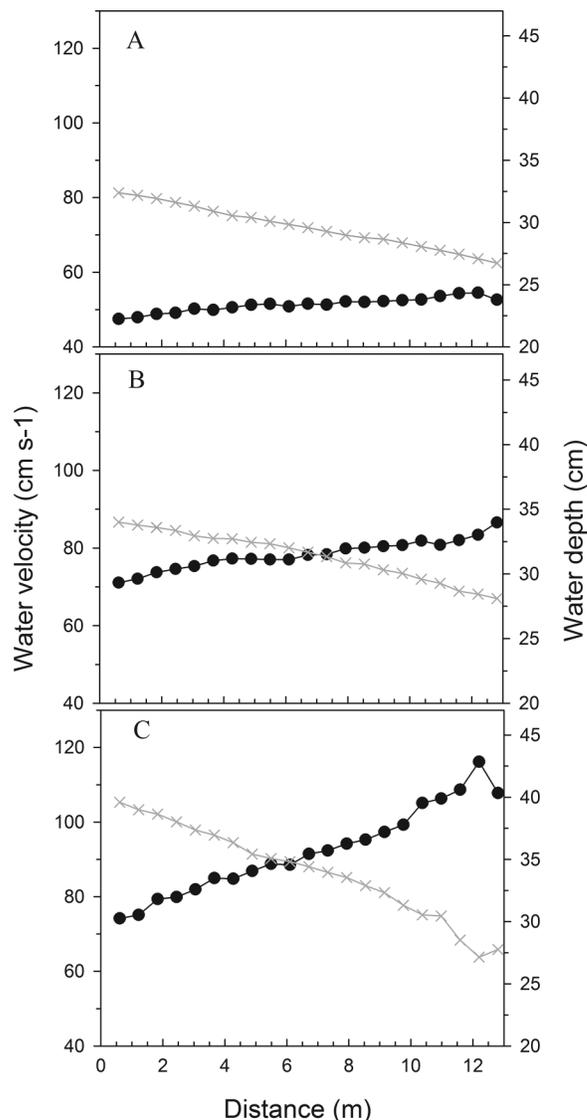
Results

Test conditions

Flow in the open-channel flume for all trials was nonuniform and turbulent. Nonuniform (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 $51 \text{ cm}\cdot\text{s}^{-1}$ treatments, 9% less to 10% greater in the $78 \text{ cm}\cdot\text{s}^{-1}$ treatments, and 20% less to 26% greater in the $92 \text{ cm}\cdot\text{s}^{-1}$ treatments.

Flow in all passage and sprint tests was characterized as turbulent. The Reynolds number, which is the ratio of inertial to viscous forces, was used to characterize flow as turbulent ($Re > 2500$) or laminar ($Re < 2500$; 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; Tables 1, 2). Turbulence was positively related to water velocity and generally

Fig. 1. Mean water velocity ($\text{cm}\cdot\text{s}^{-1}$; circles and black line) and depth (cm; \times symbols and grey line) measurements along the length of the flume test section for the $51 \text{ cm}\cdot\text{s}^{-1}$ (A), $78 \text{ cm}\cdot\text{s}^{-1}$ (B), and $92 \text{ cm}\cdot\text{s}^{-1}$ (C) velocity treatments in the passage test.



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 their position during upstream movement at all water velocities (maximum test velocity of $116 \text{ cm}\cdot\text{s}^{-1}$). Fish generally held their position near flume corners by pressing their body, pelvic fins, and caudal fins against the bottom. Multiple ascent attempts were common, with many fish repeatedly ascending 9.1–12.8 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

Table 1. Summary of test conditions and results for the nine velocity and temperature (*T*) treatments during sauger passage testing in the experimental flume.

Test velocity (cm·s ⁻¹)	<i>T</i> (°C)	Mean velocity (cm·s ⁻¹)	Re	Participation rate	Passage rate	<i>D</i> _{max} (m)	Ground velocity (cm·s ⁻¹)
51	10.7	48±2	67 800±1 600	0.75	0.83	12.3±1.3	18±8
	14.3	52±2	78 800±1 400	0.90	1.00	12.8±0.0	24±9
	17.6	52±1	94 400±1 700	1.00	1.00	12.8±0.0	26±13
78	10.1	73±4	105 000±2 000	0.90	0.78	12.2±1.3	20±9
	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
92	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

Note: The Reynolds number (Re) is dimensionless. Mean velocity, Re, *D*_{max}, and ground velocity are presented as mean ± 1 standard deviation (SD).

Table 2. Effect of three test temperatures (*T*) on the participation rate and maximum swimming velocity (*V*_{max}) of sauger in the experimental flume.

<i>T</i> (°C)	No. of trials	Re (SD)	Participation rate	<i>V</i> _{max} (cm·s ⁻¹)		
				Mean	Range	SD
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

Note: The mean Reynolds number (Re; dimensionless) is also shown.

entire flume length. Passage success rate differed little among treatments (Table 1), and mixed-effects logistic regression indicated there was no evidence of 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-effects regression indicated there was no evidence of 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 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}.

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 that ground velocity was positively associated with water temperature ($\chi^2 = 14.3$, *df* = 2, *P* = 0.0008); ground velocity was 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 of 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 for both). There was no evidence of an association between ground velocity and fish length ($\chi^2 = 0.46$, *df* = 1, *P* = 0.50). The ICC value (0.25) indicated that 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 metre of stimulation. Thirteen fish obtained their *V*_{max} in their first attempt, six in the second attempt, and four in the third attempt. Mean *V*_{max} was 219 cm·s⁻¹ (range = 119–350 cm·s⁻¹; Table 2), and there was no evidence of 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 that 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 their 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 = 69–99 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 2 there was evidence suggesting that *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 2 (Table 3). There was less support for associations between *U*_{sprint} and temperature in group 1 ($\chi^2 = 5.51$, *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 of a relationship between *U*_{sprint} and fish length in group 1 ($\chi^2 = 0.01$, *df* = 1, *P* = 0.91) or group 2 ($\chi^2 = 0.12$, *df* = 1, *P* = 0.72). Low ICC values for both group 1 (ICC = 0.08) and group 2 (ICC = 0.00) indicated that fish-to-fish variability explained little of the variance in *U*_{sprint} values. No

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

Group	T ($^{\circ}\text{C}$)	No. of trials	U_{sprint} ($\text{cm}\cdot\text{s}^{-1}$)		
			Mean	Range	SD
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

Note: SD, standard deviation.

consistent patterns were observed between the holding time and the number of previous tests and U_{sprint} values.

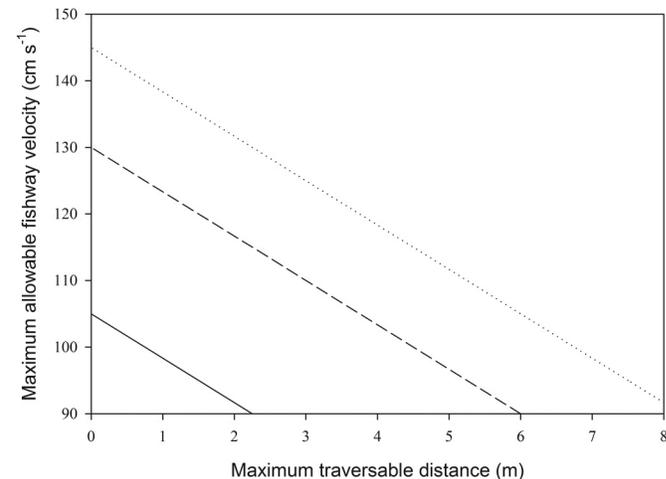
The eight mean U_{sprint} values were used to parameterize eq. 2 and predict maximum passable distances and water velocities that sauger could ascend in areas of high velocity. Predictions of maximum passable distances differed markedly among temperature treatments. The distance sauger could ascend at a water velocity of $97 \text{ cm}\cdot\text{s}^{-1}$ (the water velocity that induced 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 ($124 \text{ cm}\cdot\text{s}^{-1}$), 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 velocity combinations suitable for passing sauger at low (10.0°C), high (22.3°C), and intermediate (16.3°C) temperatures 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 2008; 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 were provided. Additionally, maximum swimming velocities and passable distances of high velocity flow were estimated in both a flume and swim chamber 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 that passage structures 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 and 18.3°C and mean water velocities $<92 \text{ cm}\cdot\text{s}^{-1}$. The high passage success, multiple successful attempts occurring in all treatments, and similarities in passage success and D_{max} among all treatments indicated that test conditions did not limit upstream sauger movements. In a comparable open-channel flume study with walleye (*Sander vitreus*), a morphologically similar congener, Peake (2008) reported high rates of passage ($>80\%$) in a 25 and 50 m flume at mean velocities ranging from 39 to $100 \text{ cm}\cdot\text{s}^{-1}$. 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 that 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).



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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 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 ($97 \text{ cm}\cdot\text{s}^{-1}$), sauger transitioned to higher ground velocities. For example, in the 10.0°C treatment, fish swam at a mean ground velocity of $19 \text{ cm}\cdot\text{s}^{-1}$ when water velocities were $<97 \text{ cm}\cdot\text{s}^{-1}$, but increased ground velocity to $28 \text{ cm}\cdot\text{s}^{-1}$ when water velocity was $>97 \text{ cm}\cdot\text{s}^{-1}$. Similar increases in ground velocity were observed in the 14.3°C ($8 \text{ cm}\cdot\text{s}^{-1}$ increase) and 18.3°C ($17 \text{ cm}\cdot\text{s}^{-1}$ increase) treatments. 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 that assume 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 wa-

ter 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 inhibit 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 2008). Aerobic exercise is believed to be indefinitely sustainable, whereas anaerobic exercise will result in fatigue owing 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 <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), a mode which can be sustained for durations of 20 s to 200 min before fatigue (Castro-Santos et al. 2013). Steady, sustained burst swimming is powered solely by anaerobic exercise and can be sustained for <20 s (Beamish 1978; Jayne and Lauder 1994, 1996). We observed some fish transitioning to steady, sustained burst swimming at water velocities >97 cm·s⁻¹ and conservatively recommend that areas above this threshold be limited to short distances (<1 m) to prevent fish fatigue and passage failure.

Direct observation of swimming behavior in relation to hydraulic conditions in the flume was an important aspect of the study. Video recordings of passage trials revealed that sauger used low-velocity pathways located along the bottom of the flume, frequently used holding behavior during their ascent, and were able to hold position on a smooth-bottomed surface at mean velocities >100 cm·s⁻¹. Given these observations, roughness elements and other design features that increase boundary layer thickness and provide structured turbulence would likely allow sauger to pass structures with mean velocities higher than those recom-

mended, which has been demonstrated in other species (Pavlov et al. 2000; Liao et al. 2003; Bestgen et al. 2010). Conversely, observations of sauger terminating ascents before reaching the resting refuge provided by the headwater tank indicate that the chaotic turbulence and aerated water created by water plunging into the headwater tank or the low light conditions created by the plywood cover may deter upstream movements. Thus, structures such as pool-weir or denil fishways with similar turbulent conditions or long, covered structures may inhibit sauger movements. Combining field and laboratory studies to identify structures that inhibit passage in the field, then testing key swimming attributes and observing behavior in an experimental flume with similar hydraulic features is needed to further determine the factors affecting passage.

Comparison of anaerobic endurance estimates from the passage test with the highest velocity and the U_{sprint} chamber test contributes to the growing body of literature suggesting that 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 >97 cm·s⁻¹. These differences are likely a result of the sauger's natural swimming behaviors being inhibited by the relatively small size of the swim chamber as well as the stress induced by frequent encounters with downstream and upstream grates. 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 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 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 efficient method for measuring sprinting endurance. Additionally, estimates of maximum aerobic capacity from gait transition observations were similar between the U_{sprint} test (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 generally maintained for less than half a second, they are representative of instantaneous maximum burst velocity. Thus, the sprint results indicate that most sauger would be unable to move upstream when water velocity was >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 that maximum velocities of coerced sauger are representative of velocities obtainable by free-swimming sauger. How-

ever, 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 3 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 owing to a smaller proportion of their mass being devoted to swimming muscle and a larger proportion 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 that temperature influences swimming performance. The lack of evidence for temperature associations with V_{\max} is consistent with the findings of Blaxter and Dickson (1959), Brett (1964), and Bennet and Huey (1990) that temperature does not affect anaerobic exercise. However, performance studies in swim chambers indicate that aerobic swimming abilities generally follow a bell-shaped curve in response to temperature: aerobic swimming is 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 in U_{sprint} across all temperatures, even when temperatures exceeded the growth optimum (19.6 °C) of sauger (Hasnain et al. 2010), suggesting that testing at water temperature >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 that passage success and maximum ascent distance were similar across all passage treatments, repeated testing does not appear to have influenced 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 1 h even if metabolic recovery was not complete and Nelson et al. (2002) and Reidy et al. (2000) found sprint performance to be repeatable over the course of 3 months. Thus, it is not expected the minimum (2 days) or maximum (33 days) holding time 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 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 with 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 mean water velocities <97 cm·s⁻¹ should be passable, velocities >100 cm·s⁻¹ should be limited to short distances (1 m), and structures with water velocities >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 that 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 >97 cm·s⁻¹.

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