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Evaluation of swimming performance for fish passage of longnose dace *Rhinichthys cataractae* using an experimental flume

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The swimming performance of longnose dace *Rhinichthys cataractae*, the most widely distributed minnow (*Cyprinidae*) in North America, was assessed in relation to potential passage barriers. The study estimated passage success, maximum ascent distances and maximum sprint speed in an open-channel flume over a range of water velocities and temperatures (10·7, 15·3 and 19·3° C). *Rhinichthys cataractae* had high passage success (95%) in a 9·2 m flume section at mean test velocities of 39 and 64 cm s^{-1}, but success rate dropped to 66% at 78 cm s^{-1}. Only 20% of fish were able to ascend a 2·7 m section with a mean velocity of 122 cm s^{-1}. *Rhinichthys cataractae* actively selected low-velocity pathways located along the bottom and corners of the flume at all test velocities and adopted position-holding behaviour at higher water velocities. Mean volitional sprint speed was 174 cm s^{-1} when fish volitionally sprinted in areas of high water velocities. Swimming performance generally increased with water temperature and fish length. Based on these results, fishways with mean velocities <64 cm s^{-1} should allow passage of most *R. cataractae*. Water velocities >100 cm s^{-1} within structures should be limited to short distance (<1 m) and structures with velocities ≥158 cm s^{-1} would probably represent movement barriers. Study results highlighted the advantages of evaluating a multitude of swimming performance metrics in an open-channel flume, which can simulate the hydraulic features of fishways and allow for behavioural observations that can facilitate the design of effective passage structures.

Key words: minnow; open-channel flume; sprint; swimming behaviour; temperature; water velocity.

INTRODUCTION

Habitat fragmentation has contributed to freshwater fishes having the highest extinction rates among vertebrates worldwide (Dudgeon *et al.*, 2005; Burkhead, 2012). Culverts, weirs, diversion dams and other potential barriers to fish movement associated with energy, agricultural, urban and infrastructure development in North America's

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Great Plains have resulted in highly fragmented stream systems (Abel *et al.*, 2000; Woodruff, 2014). The variable hydrographs that characterize stream systems in the western Great Plains can exacerbate the negative effects of barriers to fish movement (Dodds *et al.*, 2004). Flash flooding and desiccation repeatedly depopulate suitable habitat patches making recolonization a key factor affecting species and population persistence (Fausch & Bestgen, 1997; Dodd *et al.*, 2003). Thus, frequent and extensive movement is common among prairie fishes for spawning, recolonization, avoiding unfavourable conditions and locating suitable refuges during flooding and desiccation events (Labbe & Fausch, 2000; Scheurer *et al.*, 2003). Barriers that reduce the longitudinal connectivity through a stream inhibit these movements, prevent recolonization events, reduce gene transfer among populations and ultimately increase the risk of local extirpation (Winston *et al.*, 1991; Park *et al.*, 2008). In order to effectively mitigate the negative consequences of potential barriers to fish movement, it is vital to assess the swimming abilities of prairie fishes so barriers can be identified and removed and new fishways can be properly designed to allow natural movements.

Of the 55 fish species native to the Great Plains region of eastern Montana, Wyoming and Colorado, 33 (60%) have been given a conservation designation owing to population declines or rarity (Hubert & Gordan, 2006). Given the paucity of detailed swimming information on these species, it can be advantageous to base fishway design criteria on the weaker swimmers in a fish assemblage. As swimming ability is related to body size, setting design criteria to pass small-bodied fishes will probably ensure that larger, stronger swimmers will also be able to pass (Northcote, 1988). Swimming performance studies and fishway design, however, have traditionally focused on strong swimming species, such as salmonids, while studies on small-bodied fishes are under-represented in the literature (Videler, 1993; Clay, 1995; FAO/DVWK, 2002).

Fish passage research has primarily consisted of field studies and laboratory studies conducted in swim chambers. Field studies have shown culverts, weirs and diversion dams can restrict movements, alter distributions and result in local extirpation of small-bodied fishes with water velocity, outlet drop, structure type and barrier length being key factors affecting passage success (Warren & Pardew, 1998; Bouska & Paukert, 2009; Burford *et al.*, 2009; Noonan *et al.*, 2012; Briggs & Galarowicz, 2013; Goerig *et al.*, 2016). Developing passage design criteria based on field studies, however, is difficult owing to an inability to differentiate between passage restrictions, natural longitudinal differences in fish assemblages, or a lack of motivation to move upstream (Schlosser, 1987; Ostrand & Wilde, 2002; Coffman, 2005). Additionally, results from field studies are specific to the hydraulic conditions present during the study, which may not be representative of conditions during other times of the year and can be difficult to apply to other areas due to a lack of control of field conditions and the simultaneous interaction of many variables (Burford *et al.*, 2009; Katopodis & Gervais, 2011).

Laboratory studies allow precise control of experimental conditions and examination of the effects of variables such as fish length and morphology, temperature and water velocity on swimming performance. The majority of laboratory studies have been conducted in small enclosed swim chambers and have examined the time to fatigue at a set velocity (Billman & Pyron, 2005; Bestgen *et al.*, 2010; Ficke *et al.*, 2011) or the maximum aerobic swimming speed using an incremental velocity test (U_{crit} test) in which the velocity is incrementally increased and time to failure at the maximum velocity is measured (Nelson *et al.*, 2003; Holthe *et al.*, 2009; Leavy & Bonner, 2009). Recent studies, however, have suggested that space constraints in swim chambers may restrict volitional behaviour and the ability of fishes to utilize different muscle groups, thereby resulting in an underestimation of swimming abilities (Tudorache *et al.*, 2007, 2010; Castro-Santos *et al.*, 2013; Sanz-Ronda *et al.*, 2015).

Open-channel flumes allow swimming to be examined in a controlled setting that more closely approximates conditions fish experience in passage structures and provide more realistic predictions of passage success in field settings (Haro *et al.*, 2004). The larger scale of flumes allow fishes to move through the flow, employ natural swimming behaviours and use performance enhancing strategies such as gait transitions (burst–glide) and holding behaviour during upstream movements (Haro *et al.*, 2004). Flumes also allow for direct measurement of distance of ascent in contrast to swim chamber studies wherein potential ascent distances are backcalculated from time to fatigue under assumptions of a constant swimming velocity, which does not account for the aforementioned performance enhancing strategies (Peake, 2004). Additionally, the larger scale of flumes allows for unrestricted sprint swimming and measurement of maximum swimming speeds. Because zones of high-velocity flows are common and sometimes intentional features of fishways, data on maximum swimming speeds can be used to identify barriers, set design criteria for maximum water velocity, or to create barriers when it is desirable to limit the upstream distribution of a species (Clay, 1995; Haro *et al.*, 1998). There have been few studies, however, assessing the swimming abilities of small-bodied fishes in flumes (Holthe *et al.*, 2009; Bestgen *et al.*, 2010; Ficke, 2015).

In this study, the swimming performance of longnose dace *Rhinichthys cataractae* (Valenciennes 1842) was assessed using an open-channel flume. *Rhinichthys cataractae* were selected as a study species because of the lack of detailed swimming information on the species and the potential for this information to be applicable over a large area, given *R. cataractae* have the widest distribution of any Cyprinidae in North America (Gilbert & Shute, 1980). Swimming information on *R. cataractae* is limited to swim-chamber studies (Billman & Pyron, 2005; Aedo *et al.*, 2009; Ficke, 2015), passage success data from an experimental rock ramp (Ficke, 2015) and field studies examining passage restriction (Dodd *et al.*, 2003; McLaughlin *et al.*, 2006; Rosenthal, 2007; Ficke, 2015). Detailed information on the volitional swimming abilities and behaviour of *R. cataractae*, however, is limited. Thus, volitional swimming performance tests were conducted with *R. cataractae* over a range of velocities, hydraulic conditions, fish lengths and temperatures that mimicked natural conditions. The objective of the study was to use a variety of swimming performance metrics (passage success, maximum ascent distance and sprint speed) to develop passage criteria for this species.

MATERIALS AND METHODS

TEST APPARATUS

Swimming tests were conducted in a large open-channel flume (0·9 m width × 0·9 m depth × 17·1 m length) at the Bozeman Fish Technology Center (BFTC; Bozeman, MT). The flume was constructed from wood and rested on a metal framework that could be tilted with hydraulic jacks to adjust the slope, which was set at 0·69%. A middle wall was placed within the flume to constrict channel width to 0·5 m, which allowed a larger range of water velocities to be tested. Sections of the middle wall were removed to create holding areas at the downstream end of the flume (0·5 m width × 1·0 m length) and 10·0 m upstream (0·5 m width × 2·0 m length). Near zero water velocities in the holding areas provided refuges from which fish could volitionally enter or exit the main current. Grates located at the upstream and downstream ends of the flume prevented fish escape. The flume floor and walls were covered with smooth plastic sheeting and reference lines were painted on the bottom every 0·3 m in order to track fish position. The smooth lining, consistent slope and straight walls and floor of the flume reduced structured turbulence, boundary layer effects and flow friction. An array of seven digital video cameras (Handicam HDR-XR-150, Sony; www.sony.com) were positioned 2 m above the flume to record swimming trials. A black fabric shroud covered the flume to ensure uniform lighting and prevent disturbances to test fish.

On-site warm and cold water wells supplied water to the flume and allowed a range of temperatures to be tested (10–20° C). Three temperatures within this range (10·7, 15·3 and 19·3° C) were selected for testing. These temperatures are representative of stream temperatures in the Great Plains during the spring and autumn when fish move frequently for spawning or in response to stream desiccation (Gillette *et al.*, 2006; Falke *et al.*, 2010; Hargrave & Taylor, 2010). Water was pumped from a holding reservoir through a 0·2 m diameter pipe to a headwater tank (2·4 m width × 1·2 m depth × 2·4 m length), flowed through the flume into a tailwater tank (3·0 m width × 1·8 m depth × 3·0 m length) and was recirculated to the reservoir. Valves on the supply pipe controlled discharge and were adjusted to obtain four test velocities with mean longitudinal velocities of 39, 64, 78 and 90 cm s^{-1}. Velocities were selected to provide a wide range of ascent distances and induce sprint swimming and were based on previous knowledge of *R. cataractae* swimming abilities (Billman & Pyron, 2005; Rosenthal, 2007; Aedo *et al.*, 2009).

Hydraulics and swimming performance were measured in a 9·2 m test section between holding areas. Water entering the headwater tank and backing up against the downstream grate created unstable flow conditions that prevented the accurate measurement of swimming performance upstream and downstream of the test section. Longitudinal velocity and depth profiles were measured at the beginning and end of each set of daily trials using a Marsh-McBirney Flo-Mate 2000 (Hach Corp.; www.hach.com) and a graduated wading rod, respectively. Water velocity and depth were measured every 0·6 m longitudinally. At each measurement location, water velocity was measured at 0·6 times the water depth to characterize average velocity and at 3 cm off the bottom (bottom velocities) to characterize velocities where fish were observed swimming. Reported velocities refer to the mean velocity of the longitudinal measurements at 0·6 times the depth unless denoted otherwise. A cross-sectional water velocity profile (Fig. 1) was measured 3 m upstream of the downstream grate using a Sontek Acoustic Doppler Velocimeter (YSI Inc.; www.ysi.com) at each test velocity. Measurements were taken every 1·5 cm in a grid spanning the width and depth of the flume cross-section to characterize the spatial variation in water velocity at a scale relevant to the size of test fish. Stage height and discharge were continuously monitored with AquaRod-TruTrack Digital Crest Gages (GEO Scientific Ltd; www.geoscientific.com) located in the tailwater and headwater tanks and a flow measurement device (Flexus F601 Flow Recorder, Flexim Americas Corp.; www.flexim.com) located on the supply pipe to the flume. Monitoring confirmed discharge remained relatively constant among trials within a treatment, which ensured fish experienced similar hydraulic conditions.

Water velocity, depth and channel dimensions were used to calculate flow regime and state. Reynolds number (R_e), the ratio of inertial to viscous forces, was used to classify flow into laminar ($R_e \leq 2500$) or turbulent ($R_e > 2500$) regimes (Chow, 1959). The Froude number (F), which is the ratio of inertial and gravitational forces, was used to characterize open-channel flow state as subcritical ($F < 1$), critical ($F = 1$) or supercritical ($F > 1$). For both subcritical and supercritical states water velocity increased and depth decreased with the distance upstream due to the sloped floor and the fine mesh on the downstream retention grate creating backwater conditions. Subcritical flow was maintained throughout the length of the flume in the 39, 64 and 78 cm s^{-1} treatments. In the 90 cm s^{-1} treatment, however, critical flow occurred at a transition zone from supercritical to subcritical. Critical flow is characterized by a standing wave and is undesirable in fish swimming studies as it can create turbulence and unsteady flow profiles downstream of the wave (Chow, 1959; Castro-Santos *et al.*, 2013). Thus, swimming data from the 90 cm s^{-1} treatment was analysed separately and volitional sprint swimming speeds and ascent distances were examined in a 2·7 m section of high velocity supercritical flow. In the 39, 64

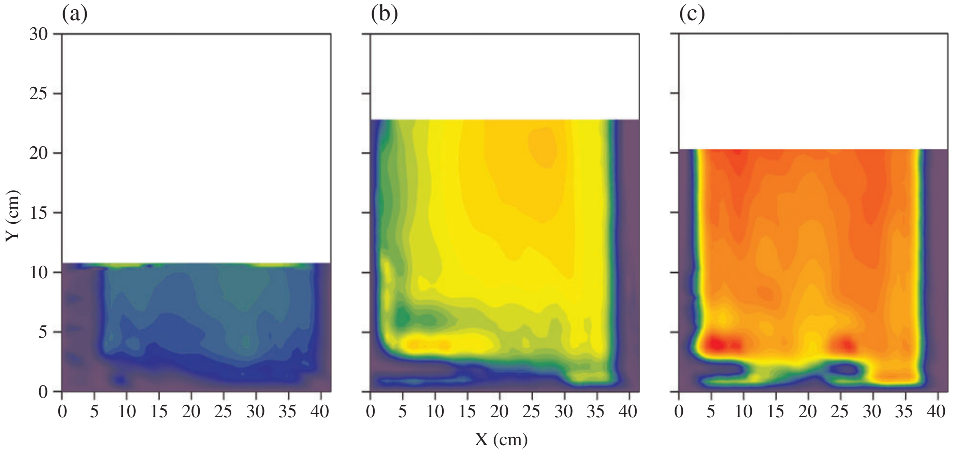

FIG. 1. Cross-sectional velocity profile (cm s^{-1}) of the experimental flume for the (a) 39, (b) 64 and (c) 78 cm s^{-1} treatments measured 3 m upstream of the downstream end of the flume. In cm s^{-1}: 🟪, 0; 🟪, 10; 🟦, 20; 🟦, 30; 🟩, 40; 🟩, 50; 🟨, 60; 🟧, 70; 🟥, 80.

and 78 cm s^{-1} treatments, the ability of fish to ascend the 9·2 m test section (passage success) and ascent distances were examined.

TEST FISH

Rhinichthys cataractae were collected from the Madison and Gallatin Rivers in south-west Montana during the summer of 2013 using a backpack electrofishing unit. Fish were transported in an aerated tank to the BFTC and transferred to 1·5 m diameter by 1·5 m deep circular tanks that mimicked river temperature at the time of collection (±0·5° C). Water velocities were maintained at 5–10 cm s^{-1} to exercise fish. Tank temperatures were adjusted at a maximum rate of 2° C day^{-1} until the test temperature was obtained and fish were allowed to acclimate at the test temperature for a minimum of 4 days before testing. The short acclimation period was not predicted to affect swimming performance as the collected fish are adapted to daily temperature fluctuations that can exceed the maximum temperature change (6° C; USGS, 2016) experienced at the testing facility. Fish were individually netted from the circular tanks and randomly assigned to one of four 75 l rectangular flow-through tanks (120 cm × 35 cm × 25 cm). Each tank was then randomly assigned to a velocity treatment. Fish were fed daily to satiation with a commercial trout feed and feeding ceased 12 h prior to testing. A fungal infection in the 19·3° C holding tank resulted in mortality of the majority of fish in that tank despite the application of salt treatments (5 mg l^{-1}). No signs of infection were observed in any of the other tanks and fish from the 19·3° C tank were not used for testing. Subsequently, another group of *R. cataractae* collected earlier in the summer were acclimated to 19·3° C. These fish were smaller than other test fish, however, resulting in unequal fish sizes among treatments.

SWIMMING TESTS

Tests to characterize the swimming abilities of *R. cataractae* were conducted in June and July of 2013. Fish were tested in 12 treatments consisting of the combination of four test velocities (39, 64, 78 and 90 cm s^{-1}) and three test temperatures (10·7, 15·3 and 19·3° C). Fish were tested in groups of three, with fish of varying size selected to allow individual identification during video analysis. Seven trials occurred in each treatment, yielding a total of 252 fish. All trials within a treatment occurred within the same day and fish were tested only once. At the start of a trial, fish were placed in the downstream holding area and given 40 min to volitionally ascend the flume. Pilot studies revealed this was adequate time for the majority of *R. cataractae* to reach their maximum ascent distance. At the end of a trial, fish were weighed to the nearest 0·1 g (mean = 3·3, range = 1·0–23·1) and fork length was (L_F) measured to the nearest 0·1 cm (mean = 6·4, range = 4·6–12·4).

VIDEO ANALYSIS

Cameras recorded trials at 30 frames s^{-1} and video files (mpeg) were analysed in PlayMemories Home 5.1 (Sony) to record fish behaviour, maximum ascent distance, passage success and sprinting speeds. Cameras recorded 2·4 m lengths of the flume and were spaced 1–1·8 m apart to provide overlapping fields of view and allow fish to be continuously tracked as they ascended the flume. Reference lines allowed the maximum ascent distance (D_{max}) to be recorded. D_{max} was measured as distance traversed of the 9·2 m test section in the 39, 64 and 78 cm s^{-1} treatments and of the 2·7 m test section in the 90 cm s^{-1} treatment. If the entire test section was traversed, observations were recorded as censored. Passage attempts were classified as successful if a fish ascended the entire test section and unsuccessful otherwise. Video analysis was used to calculate sprint velocities in the 90 cm s^{-1} treatment for each 0·3 m section between reference lines in the 2·7 m test section. The time required for a fish to traverse between reference lines divided by the distance traversed (accounting for the selected path) provided measures of ground speed. Sprint speeds were calculated as the sum of the ground speed and the average water velocity between reference lines.

DATA ANALYSIS

Logistic regression was used to examine associations among passage success, velocity, temperature and L_F for the 39, 64, 78 cm s^{-1} treatments. Each fish was treated as an independent observation as fish tended to ascend the flume independently. The minimum Akaike information criterion with a correction for a finite sample size (AICc) was used to select the inferential model from a model set including all possible combinations of the covariates (velocity, temperature, L_F). All two-way interactions among covariates were represented in the model set. Models with ΔAIC values <4 were considered viable candidates for the inferential model (Burnham & Anderson, 2002). Statistical evidence for associations among passage success and the covariates were assessed using drop-in deviance tests (DiD) comparing the inferential model to the model without the covariate of interest (Ramsey & Schafer, 2002).

Kaplan-Meier survival analysis (Klein & Moeschberger, 2012) was used to examine the relationship between water velocity and maximum ascent distance (D_{max}) in the 39, 64 and 78 cm s^{-1} treatments. Length and water velocity limitations of the flume prevented determination of the true D_{max} for many fish and therefore resulted in censored data. For example, fish that ascended the 9·2 m test section were included in the analyses as censored observations because it was impossible to know how far they would have ascended in a longer flume. Kaplan-Meier estimators were used to estimate the probability of passing distances up to 9·2 m for each treatment.

Parametric survival analysis methods were used in the 90 cm s^{-1} treatment to estimate maximum ascent distance (D_{max}) in the 2·7 m test section of supercritical flow and examine relationships among D_{max}, temperature and L_F (Haro *et al.*, 2004; Therneau, 2015). Fish that ascended the 2·7 m test section were included in analysis as censored observations and only fish that attempted ascents in this section were included in analysis. Regression models to describe associations among the ln-transformed D_{max} values and the covariates were estimated with the survreg function (Therneau, 2015) in program R (www.r-project.org):

$$\ln\ D_{max} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ \dots\ + \beta_k x_k \tag{1}$$

where D_{max} is the observed maximum distance a fish traversed, βs are estimated coefficients and x_i values are the k-covariates. The multiplicative effect of a covariate on D_{max} can be calculated as exp(β_k). The distribution of the data was determined by fitting a model with covariates for temperature, L_F and their interaction to exponential, Weibull, Gaussian, logistic, log-normal and log-logistic distribution. AIC model selection was used to determine the distribution that best described the data (Burnham & Anderson, 2002). Using the selected distribution, a model set including all combinations of L_F, temperature and two-way interactions was created and AIC model selection was used to select the inferential model. Statistical evidence for associations among D_{max} and the covariates was assessed using log-likelihood tests comparing the inferential model to the model without the covariate of interest (Ramsey & Schafer, 2002).

Multiple linear regression was used to examine relationships among the maximum sprinting speed (V_{max}), temperature and L_F in the 90 cm s^{-1} treatment. V_{max} was defined as the maximum sprint speed observed among all 0·3 m sections in the 2·7 m test section. AIC model selection was used to select the inferential model. Extra-sum of squares (ESS) *F*-tests were used to assess statistical evidence of coefficients by comparing the inferential model to the model without the covariate of interest (Ramsey & Schafer, 2002).

All data analysis was conducted in R 3.0.2 (www.r-project.org). Assumptions of homogeneity of variance, normality and linearity for regression analyses were assessed using plots of residuals *v.* fitted values, normal quantile–quantile plots and plots of response variables *v.* continuous explanatory variables, respectively. All assumptions were adequately met. The strength of evidence was classified as significant at the $P < 0{\cdot}05$ level.

RESULTS

TEST CONDITIONS

Hydraulic conditions for the 39, 64 and 78 cm s^{-1} treatments are presented in Table I. Mean longitudinal velocity varied <2 cm s^{-1} among tests conducted at the target velocities of 64 and 90 cm s^{-1} and <5 cm s^{-1} among the 39 and 78 cm s^{-1} tests. Because hydraulic conditions were similar among the three temperature treatments performed at each test velocity, these test conditions were averaged. Velocity increased and depth decreased with distance upstream in an approximately linear fashion in the subcritical flow of the 39, 64 and 78 cm s^{-1} treatments (Fig. 2). In the 90 cm s^{-1} treatment, flow was subcritical for the first 6·4 m of the flume but changed to supercritical for the remaining 2·7 m of the test section, resulting in a 29 cm s^{-1} increase in water velocity at the transition point. The supercritical section was characterized by high velocities (mean velocity = 122 cm s^{-1}) and shallow depths (mean depth = 13 cm) that varied <±4·5 and ±1·3% from mean values, respectively. All treatments were well within the turbulent flow regime ($R_e > 2500$). The mean R_e exceeded 27 000 in all passage and sprint treatments but varied widely among velocity treatments (Table I). Higher R_e correlate to larger variance in three-dimensional velocity vectors.

The ratio of bottom velocity to mean water column velocity differed little among treatments with bottom velocity averaging 26% less than average velocity (S.D. = 3%). Variation in water velocities within a cross-section generally increased with test velocity, with the lowest variation in the 39 cm s^{-1} treatment (S.D. = 12) and highest in the 78 cm s^{-1} treatment (S.D. = 22). In all treatments, flume corners had the largest areas of low velocity (Fig. 1).

SWIMMING TESTS

Fish were highly motivated to enter and ascend the flume from the downstream holding areas in the 39, 64 and 78 cm s^{-1} treatments, with 97% (183 of 189) of fish making passage attempts and the percent of fish making passage attempts differing little

TABLE I. Summary of hydraulic conditions for the *Rhinichthys cataractae* swimming tests in the experimental flume. Reynolds (R_e) and Froude (F) numbers are dimensionless

Mean velocity ($cm\,s^{-1}$)		Bottom velocity ($cm\,s^{-1}$)		Flow ($m^3\,s^{-1}$)	Depth (cm)		R_e	F	
Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Mean ± S.D.	Range	Mean ± S.D.	Mean ± S.D.	Range
39 ± 8	27–54	30 ± 7	21–45	0·022 ± 0·003	15 ± 2	12–18	30 000 ± 2600	0·32 ± 0·09	0·20–0·50
64 ± 7	53–75	48 ± 7	37–62	0·061 ± 0·004	26 ± 2	23–29	68 200 ± 10 400	0·40 ± 0·06	0·31–0·50
78 ± 9	65–98	58 ± 8	47–73	0·082 ± 0·000	25 ± 2	22–29	81 100 ± 7900	0·50 ± 0·08	0·39–0·68

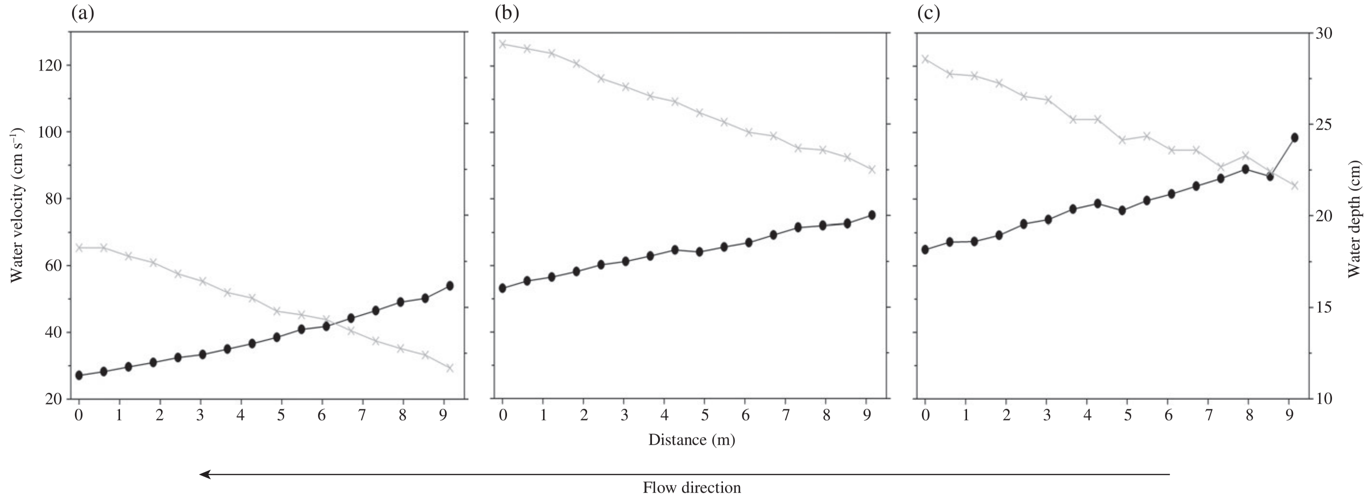

FIG. 2. Mean water velocity (–●–) and depth (–×–) measurements along the length of the 9·2 flume test section for the (a) 39, (b) 64 and (c) 78 cm s^{-1} treatments.

TABLE II. Participation, passage success proportions and maximum ascent distances (D_{max}) of *Rhinichthys cataractae* for 39, 64 and 78 cm s^{-1} treatments conducted in an experimental flume in relation to temperature, velocity and fish length (L_F). Sample size (N) is the number of fish that attempted upstream passage

Velocity (cm s^{-1})	T (°C)	N	L_F (mean ± S.D.; cm)	Participation	Success	D_{max} (mean ± S.D.; m)
39	10·6	19	6·8 ± 0·9	0·90	0·84	8·8 ± 1·0
	15·1	20	7·0 ± 1·7	0·95	1·00	9·2 ± 0·0
	19·4	20	5·7 ± 0·7	0·95	1·00	9·2 ± 0·0
64	10·6	20	6·8 ± 0·8	0·95	1·00	9·2 ± 0·0
	15·4	21	6·8 ± 1·2	1·00	0·95	8·9 ± 1·1
	19·4	21	5·5 ± 0·6	1·00	0·90	8·9 ± 0·9
78	10·9	20	6·7 ± 0·7	0·95	0·55	8·1 ± 1·8
	15·4	21	6·9 ± 1·7	1·00	0·81	8·8 ± 1·0
	19·5	21	5·7 ± 0·4	1·00	0·62	8·6 ± 0·9

among treatments (Table II). The majority of fish quickly exited the downstream holding area, with 30% beginning their ascent in <10 s, 50% in <20 s and 80% in <400 s after release. Fish commonly entered the open channel in groups of two or three but rarely remained in groups for their entire ascent. Multiple attempts were uncommon and fish rarely re-entered the downstream holding area after their initial attempt. Fish successfully ascending the test section were often found in the upstream holding area or below the upstream retention grate. Fish that failed to successfully ascend the flume were typically found holding position in the corners of the flume. Position holding was rarely observed in the lower velocity treatments (39 and 64 cm s^{-1}) but was frequently observed in the 78 cm s^{-1} velocity treatment, with most fish holding for extended periods (>5 min) multiple times during an ascent attempt. When holding position, fish ceased swimming movements and bent their bodies to simulate a hydrofoil, creating negative lift, by pressing their snout, pelvic fins and caudal fin against the flume bottom. Fish were able to hold position at all water velocities (27–98 cm s^{-1}) experienced in 39, 64 and 78 cm s^{-1} treatments. In the supercritical zone of the 90 cm s^{-1} treatment, 70% of fish were observed holding position but did so with difficulty and the average holding time was only 16 s. In all treatments fish ascended the flume using areas of lower velocity associated with the bottom and corners of the open-channel (Fig. 1). Burst–glide swimming was the primary swimming gait used at all water velocities experienced in 39, 64 and 78 cm s^{-1} treatments but only continuous sprint swimming was observed in the test section of the 90 cm s^{-1} treatment.

Logistic regression indicated that water velocity, body length and temperature were associated with passage success in the 39, 64 and 78 cm s^{-1} treatments. The relationships among passage probability, L_F and temperature can be estimated using the following equation:

$$P\,(\text{success} = 1) = \left(e^{\beta_0+\beta_{1x_{i1}}+\dots\,\beta_{kx_ik}}\right) \times \left(1 \;+\; e^{\beta_0+\beta_{1x_{i1}}+\dots\,\beta_{kx_{ik}}}\right)^{-1} \qquad (2)$$

where P is the probability of successful passage and β_0 is the intercept and β values are the coefficients for each explanatory variable (x_i) included in the model (Table III).

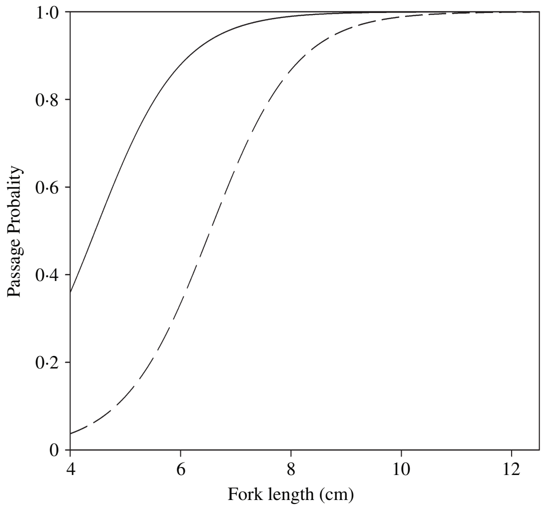

FIG. 3. Estimated logistic regression relationships between passage probability of success of *Rhinichthys cataractae* and fork length (L_F) in a 9·2 m flume section for 39 and 64 cm s^{-1} treatments (——) and the 78 cm s^{-1} (----) at 10·7° C.

Passage success in the 39 and 64 cm s^{-1} treatments was high (95%) and did not differ. Data for these two treatments were therefore combined into a single low-velocity treatment. Passage success decreased significantly to 66% in the 78 cm s^{-1} treatment (DiD = 31·6, d.f. = 1, $P < 0{\cdot}0001$). There was strong evidence for a positive relationship between passage success and L_F (DiD = 12·8, d.f. = 1, $P = 0{\cdot}0003$). The estimated relationship between passage success and L_F for the low velocity and 78 cm s^{-1} treatments at 10·7° C is depicted in Fig. 3. The 10·7° C treatment was chosen to provide conservative estimates, as passage success was lowest at this test temperature. Passage success in the 10·7° C treatment (80%) was significantly lower than the 15·3° C treatment (92%; DiD = 6·5, d.f. = 1, $P = 0{\cdot}01$) and 19·3° C treatment (84%; $D_{iD} = 5{\cdot}0$, d.f. = 1, $P = 0{\cdot}02$). There was no evidence for there being a difference in predicted passage success between the 15·3 and 19·3° C treatments (DiD = 0·2, d.f. = 1, $P = 0{\cdot}16$).

TABLE III. Estimated parameters for the selected logistic model describing associations among passage success, water velocity, temperature and fork length (L_F) of *Rhinichthys cataractae* for the 39, 64 and 78 cm s^{-1} water velocity treatments in an experimental flume

Parameter	β	S.E.	P
β_0 intercept	−5·71	2·64	0·03
β_1 velocity (78 cm s^{-1})	−2·68	0·55	<0·0001
β_2 temperature (15·3° C)	1·42	0·66	0·03
β_3 temperature (19·3° C)	1·68	0·68	0·01
β_4 L_F (cm)	1·28	0·42	0·002

N.B.: Velocity and temperature are categorical variables equal to 1 for the treatment denoted in parentheses and 0 otherwise. The reference level is the 10·7° C × low velocity (39 and 64 cm s^{-1}) treatment.

TABLE IV. Regression model of covariate effects on the ln maximum distance of ascent (ln D_{max}) of *Rhinichthys cataractae* for the 2·7 m supercritical flume test section in the 90 cm s^{-1} treatment. A Weibull distribution was selected to fit the data

Parameter	β	S.E.	P
β_0 intercept	1·84	0·49	0·0002
β_1 temperature (19·3° C)	0·55	0·13	<0·0001
β_2 fish fork length (cm)	0·37	0·07	<0·0001
Scale (K)	2·91		

N.B.: Temperature is a categorical variable equal to 1 for the 19·3° C treatment and 0 for the 10·7 and 15·3° C treatments (grouped together as the reference level).

The median ascent distance (D_{max}) did not differ among the 39, 64 and 78 cm s^{-1} treatments and was equal to the length of the test section: 9·2 m. The majority of fish (86%) ascended the 9·2 m test section of the flume across these treatments, resulting in a large number of censored D_{max} observations that prevented more advanced analysis of the D_{max} data. Ninety-five percent of test fish could ascend at least 9·2 m in the 39 and 64 cm s^{-1} treatments. The majority of fish (90%) were able to traverse 7·0 m in the 78 cm s^{-1}, but the percent traversing declined to 66% by 9·2 m (Fig. 4).

In the 90 cm s^{-1} treatment, fish were not deterred by the turbulence and unsteady flow profiles in the subcritical zone below the standing wave, with 97% (61 of 63) fish making upstream passage attempts from the downstream holding area. Of these fish, 90% (55 of 61) were observed sprinting in the supercritical zone and included in the data analysis. Video observation showed fish used the area of energy dissipation and low velocity associated with the standing wave to stage upstream passage attempts. Fish generally swam for <10 s in the supercritical zone before returning to a holding position in the critical or subcritical zone.

Twenty-two percent of fish (12 of 55) successfully ascended the 2·7 m of supercritical flow and were treated as censored observations for survival analysis. All fish volitionally swam for a distance of 0·3 m against an average velocity of 108 cm s^{-1} and 59% swam 1·8 m against an average velocity of 116 cm s^{-1}. Only fish >6·7 cm successfully ascended the 2·7 m of supercritical flow and a 1·6 cm difference between successful and unsuccessful fish (mean, 7·8 *v.* 6·2 cm) was observed.

Parametric survival analysis indicated that ascent distances (D_{max}) in the 90 cm s^{-1} treatment were influenced by L_F ($\chi^2 = 31{\cdot}3$, d.f. = 1, $P < 0{\cdot}0001$) and temperature ($\chi^2 = 18{\cdot}2$, d.f. = 1, $P < 0{\cdot}0001$). There was no evidence for a difference in sprint distances between the 10·7 and 15·3° C treatments ($\chi^2 = 0{\cdot}6$, d.f. = 1, $P = 0{\cdot}45$) and data from these two treatments were grouped together in the regression equation (Table IV). Distance of ascent, however, increased by 74% in the 19·3° C treatment in comparison with the 10·7 and 15·3° C treatments. A 1 cm increase in L_F was associated with a 45% increase in D_{max}.

Model selection (AIC) provided strong evidence that the Weibull distribution best described the D_{max} data for the 90 cm s^{-1} treatment. For a Weibull distribution, the survival function is defined as:

$$S\left(D_{max}\right) = \exp\left(-\lambda\ {D_{max}}^{K}\right) \tag{3}$$

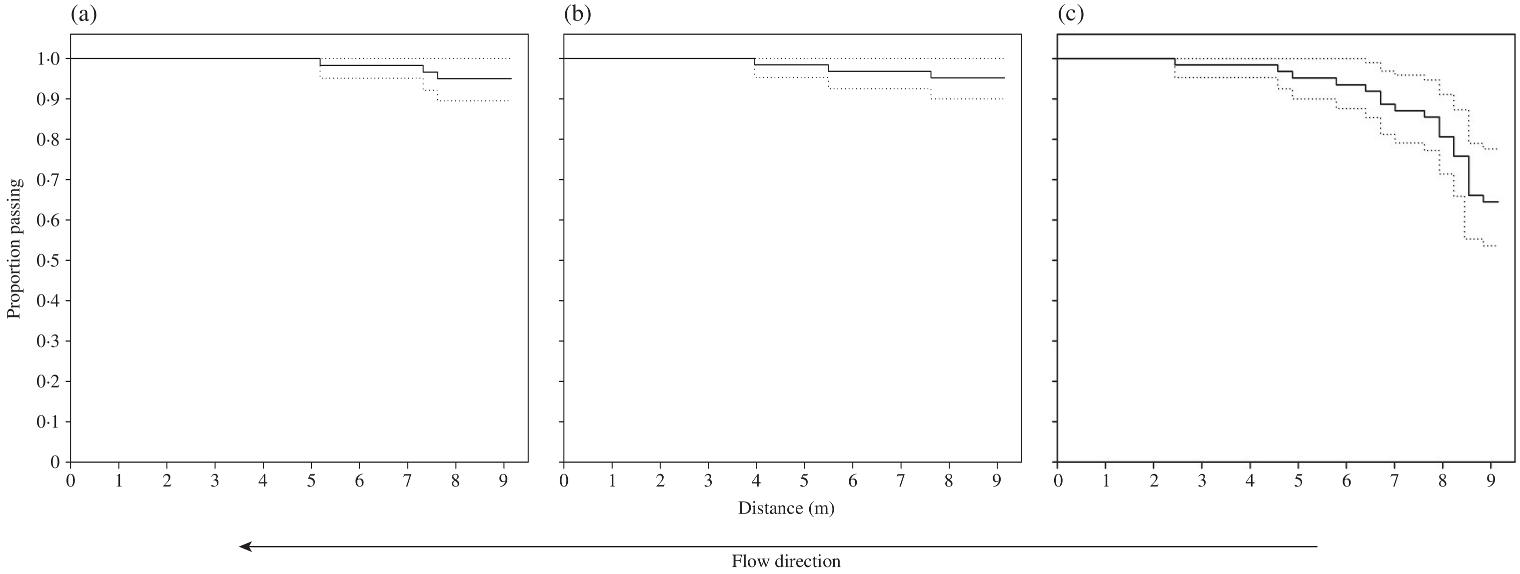

FIG. 4. Estimated probability curves for the maximum ascent distance (m) of *Rhinichthys cataractae* for (a) 39, (b) 64 and (c) 78 cm s^{-1} treatments conducted in an experimental flume. Proportion passing (——) and 95% C.I. (⋯⋯) were estimated using Kaplan-Meier survival analysis. Censoring occurs at 9·2 m.

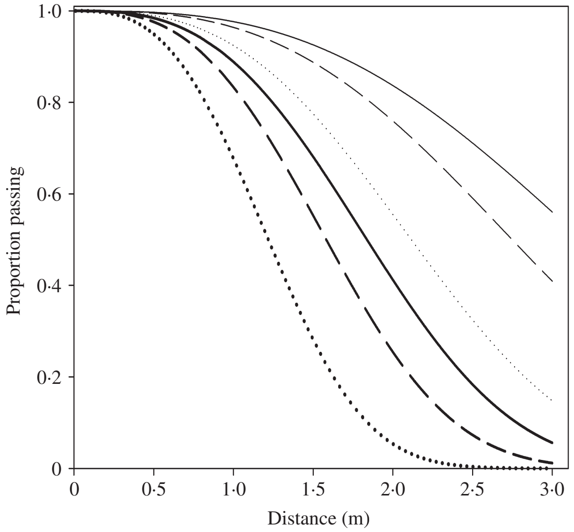

FIG. 5. Estimated probability curves for the maximum ascent distance (m) of *Rhinichthys cataractae* in the $90\,\mathrm{cm\,s^{-1}}$ treatment conducted in a 2·7 m flume section. Bold lines represent survival curves for fish in the 10·7 and 15·3° C treatments; non-bold lines represent the 19·3° C treatment. Curves are provided for small ($L_F = 5{\cdot}8$ cm; ·········), medium ($L_F = 6{\cdot}5$ cm; — —) and large fish ($L_F = 6{\cdot}9$ cm; ——) for both temperature designations. Censoring occurred at 2·7 m.

where λ is the scale parameter and K is the shape parameter. The scale parameter is equal to the natural exponent of the regression equation (equation 1) and depends on covariate values (Table IV). The survival model can be used to predict the proportion of fish able to pass distances up to 2·7 m at a mean velocity of $122\,\mathrm{cm\,s^{-1}}$. Survival curves for small (25th percentile of $L_F = 5{\cdot}9$ cm), medium (50th percentile = 6·5 cm) and large (75th percentile = 6·9 cm) fish for the 19·3° C and the combination of the 10·7 and 15·3° C treatments are depicted in Fig. 5.

The mean V_{max} observed in the $90\,\mathrm{cm\,s^{-1}}$ treatment was $175\,\mathrm{cm\,s^{-1}}$ (range: 123–231 $\mathrm{cm\,s^{-1}}$) and was positively associated with L_F (ESS F-test: $F_{1,51} = 19{\cdot}1$, $P < 0{\cdot}0001$) and temperature ($F_{2,51} = 11{\cdot}2$, $P < 0{\cdot}0001$). The relationship among mean V_{max}, L_F and temperature was estimated using the regression equation:

$$V_{max} = 93 + \left(5\,T_{15}\right) + \left(30\,T_{19}\right) + \left(11\,L_F\right) \tag{4}$$

where T_{15} and T_{19} are indicator variables denoting the 15·3 and 19·3° C treatments ($T_i = 1$ if $i =$ test temperature and 0 otherwise) and the 10·7° C treatment is the reference level. A 1 cm increase in L_F was associated with an $11\,\mathrm{cm\,s^{-1}}$ increase in mean V_{max} (95% C.I.: 6, 16). Despite fish being the smallest in the 19·3° C treatment, the highest mean V_{max} was observed at 19·3° C ($186\,\mathrm{cm\,s^{-1}}$) and mean V_{max} decreased significantly to $172\,\mathrm{cm\,s^{-1}}$ ($25\,\mathrm{cm\,s^{-1}}$ decrease; 95% C.I.: 11, 38) at 15·3° C ($F_{1,51} = 12{\cdot}5$, $P = 0{\cdot}0009$) and to $165\,\mathrm{cm\,s^{-1}}$ ($31\,\mathrm{cm\,s^{-1}}$ decrease; 95% C.I.: 17, 43) at 10·7° C ($F_{1,51} = 20{\cdot}8$, $P < 0{\cdot}0001$). There was no evidence for a difference between the 10·7 and 15·3° C treatments ($F_{1,51} = 0{\cdot}6$, $P = 0{\cdot}43$).

DISCUSSION

Results from the current study show *R. cataractae* are stronger swimmers than previous studies have indicated. High passage success (>95%) was observed for distances up to 9·2 m and average velocities <64 cm s^{-1}. In comparison, 50% passage success is predicted for a distance of 9·2 m and a velocity of 49 cm s^{-1} for *R. cataractae* based on endurance data collected in a swim chamber (Peake *et al.*, 1997; Billman & Pyron, 2005). The observed ascent distances far exceed estimated passable distances for other minnow species at similar velocities. Specifically, Ficke *et al.* (2011) predicted a maximum ascent distance of 3 and 1·2 m for brassy minnow *Hybognathus hankinsoni* Hubbs 1929 and common shiners *Luxilus cornutus* (Mitchill 1817), respectively, at 60 cm s^{-1} and Adams *et al.* (2000) calculated maximum ascent distances <3 m for Topeka shiners *Notropis topeka* (Gilbert 1884) at 51–61 cm s^{-1}. For *R. cataractae* volitionally swimming in a flume, continuous sprint swimming was not consistently observed until water velocities exceeded 100 cm s^{-1}. In comparison, swim chamber studies reported sprint swimming is induced at water velocities of 60 cm s^{-1} for *N. topeka* (Adams *et al.*, 2000), 32–67 cm s^{-1} for *H. hakinsoni*, Arkansas darters *Etheostoma cragini* Gilbert 1885 and *L. cornutus* (Ficke *et al.*, 2011) and 67 cm s^{-1} for 15 North American minnows, including *R. cataractae* (Billman & Pyron, 2005). Observed sprint speeds (175 cm s^{-1}) exceeded those previously reported for *R. cataractae* from a stimulated sprint test (120 cm s^{-1}; Aedo *et al.*, 2009), a constant acceleration test in a swim chamber (78 cm s^{-1}; Ficke, 2015) and estimates for 31 North American small-bodied species (mean ± S.D. = 60 ± 20 cm s^{-1}; Ficke, 2015).

Individual variation in swimming abilities, which has been observed within other fish species (Nelson *et al.*, 2002; Ficke *et al.*, 2011; Castro-Santos *et al.*, 2013), may explain some of the intraspecific differences in *R. cataractae* swimming performance among the aforementioned studies. Differences in metabolic rates, aerobic and anaerobic capacities and swimming behaviour among individuals can lead to intraspecific differences in swimming performance (Peake & Farrell, 2004; Castro-Santos, 2005; Marras *et al.*, 2010). These differences may be more evident in volitional flume tests than swim chamber tests as volitional tests allow fish to move through the current and select different ground-velocities, behavioural strategies and swimming gaits. If these intraspecific differences affect passage success, passage structures can have evolutionary consequences if passage affects survival or reproduction (Webb, 1994; Castro-Santos, 2005).

The magnitude of the differences in average swimming performance metrics among studies on *R. cataractae* suggests that differences in testing methods also contribute to the observed differences in performance. Study results contribute to the growing body of literature that suggest swim-chamber tests may underestimate swimming abilities (Haro *et al.*, 2004; Peake, 2004; Holthe *et al.*, 2009). Comparisons of current test results to previous swim chamber studies on *R. cataractae* parallels the observations of Peake (2004) and Holthe *et al.* (2009), who found swim chamber studies can underestimate swimming abilities by at least 50%. Underestimation of swimming abilities in swim chambers may result from the inability of fishes to express volitional behaviour and utilize different swimming gaits in a limited swimming space (Peake & Farrell, 2005; Tudorache *et al.*, 2007, 2010; Castro-Santos *et al.*, 2013). Observation of volitionally swimming *R. cataractae* in the flume revealed a number of behaviours used to maximize ascent distance that would be inhibited in swim chambers. Specifically, burst–glide and steady-sprint swimming were the only swimming gaits observed for volitionally swimming *R. cataractae*. Swim chambers prevent fishes from maintaining positive ground speeds and fishes must engage in energetically-inefficient oscillations between positive and negative ground speeds in order to use these swimming gaits (Peake & Farrell, 2006; Sanz-Ronda *et al.*, 2015). Additionally, *R. cataractae* were frequently observed holding position in between upstream movements, particularly at high velocities. While swim chambers do not prevent station holding, they are unable to account for how this behaviour affects swimming performance and ascent distances. *Rhinichthys cataractae* were also observed actively selecting low velocity pathways along the flume corners and using the structured turbulence associated with a standing wave to stage upstream attempts. The uniform hydraulic conditions and limited swimming space of swim chambers prevents the selection of efficient pathways and the observation of natural swimming behaviours. Observed behaviour differed substantially from the behaviour reported for other species tested in flumes and represent some of the first behavioural observations of a small-bodied benthic orientated Cyprinidae in an experimental flume (Ficke, 2015). Specifically, in previous studies unsteady swimming has been uncommon, fishes have avoided pathways along the walls and station holding is not reported (Castro-Santos, 2005; Castro-Santos *et al.*, 2013; Sanz-Ronda *et al.*, 2015). Increased use of flumes and other testing apparatus that allow observation of natural swimming behaviours and incorporation of swimming behaviour and path selection into passage design will contribute to more efficient multi-species passage structures.

Study results contribute to the large body of literature that show swimming abilities are positively affected by body size (Brett, 1965; Goolish, 1991; Videler, 1993). Small changes in body size had large effects on traversable distances, especially at the higher velocities experienced in the 90 cm s^{-1} treatment. Thus, body size of migrating fishes is an important consideration for passage design and assessment. A strength of the study is providing models (equations 1–4) that allow managers and engineers to estimate design criteria for fishes of different lengths. Additionally, the results highlight the practicality of designing passage structures for small-bodied fishes, as such designs will probably allow for the passage of larger-bodied species.

Fish passage studies have generally been performed over a narrow range of temperatures, but the current results indicate that temperature can influence swimming abilities. For most species, swimming performance follows a bell-shaped 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 (Randall & Brauner, 1991; Myrick & Cech, 2000; Ojanguren & Brana, 2000). In the current experiments, swimming performance metrics (passage success, $D_{\max}$, $V_{\max}$) increased with temperature, suggesting test temperatures did not exceed the thermal optimum. A larger increase in response metrics between the 15·3 and 19·3° C treatments is probable if fish had not been substantially smaller (1·3 cm) in the 19·3° C treatment. Previous studies on plains minnows have indicated that swimming performance continues to increase at higher temperatures (20–25° C; Bestgen *et al.*, 2010; Ficke *et al.*, 2011; Ficke, 2015) and decrease at temperatures lower than 10·7° C (Randall & Brauner, 1991; Ficke, 2015). Synthesis of knowledge on the effects of temperature on swimming performance, life history, movement patterns and seasonal variation in hydraulics and temperature can facilitate the design and evaluation of passage structures.

A major limitation of laboratory studies is that results are specific to the hydraulics the fish experience, which may differ from the hydraulics in passage structures. Backwatered conditions in the 39, 64 and 78 cm s^{-1} treatments resulted in fish experiencing velocities significantly lower and higher than the reported mean velocities. Thus, test results and predictions from the logistic model (equation 2) are most applicable to structures with similar ramped velocity profiles, such as backwatered culverts (Harvey, 2009). Given the high passage rates and relatively low variation in water velocity in the 64 cm s^{-1} treatment, however, and the results from the 78 cm s^{-1} treatment, it is reasonable to assume most *R. cataractae* should be able to traverse distances up to 9·2 m at water velocities up to 64 cm s^{-1}. Use of the survival model (equation 3) to predict traversable distances at mean velocities up to 122 cm s^{-1}, while accounting for body size and seasonal temperatures, is also reasonable given the low variation in water velocity for the 90 cm s^{-1} test section. Estimates of maximum sprint speeds (equation 4) should be used to identify barriers to passage for fish of different lengths and temperatures. It is important to note that hydraulic characteristics other than velocity can affect fish passage and behaviour. The smooth lining (Manning's coefficient $n = 0{\cdot}010$) of the flume and lack of structured turbulence may have inhibited the position holding abilities of *R. cataractae* and test results are therefore most applicable to smooth concrete structures (Manning's coefficient $n = 0{\cdot}011$–$0{\cdot}015$; Chow, 1959) such as box culverts. Roughness elements and other design features that increase boundary layer thickness and provide structured turbulence may allow *R. cataractae* to pass structures with mean velocities higher than the current recommendations, which has been demonstrated for other species (Pavlov *et al.*, 2000; Liao *et al.*, 2003; Bestgen *et al.*, 2010; Goerig *et al.*, 2016). Owing to limited information on the volitional swimming abilities of *R. cataractae* in conditions that simulate field conditions, results may need to be applied to passage structures with different hydraulic characteristics. Careful thought, however, on how the hydraulics differ from those presented here and their potential effects on fish behaviour and passage is warranted. Additionally, observations of passage failure along with the hydraulic features of a structure should be documented and reported to increase the understanding of fish swimming and contribute to the design of more effective passage structures.

Based on the results of this study, passage structures up to 9·2 m in length with average velocities <64 cm s^{-1} and areas of high velocities ($\geq$100 cm s^{-1}) < 1 m should allow passage of the majority of *R. cataractae* whereas any structure with velocities exceeding 158 cm s^{-1} should be identified as a barrier. Recommendations represent conservative estimates based on regression equations 1–4 for a 5·9 cm (25th percentile) *R. cataractae* swimming at 10·7° C. Coefficient values, however, can be altered by managers to provide acceptable criteria for a variety of water temperatures, fish lengths, water velocities and proportions passing (equation 3; recommendation based on 70% passage). It is important to note that fishway design recommendations, including the present ones, are typically based on average water velocities. Recommendations based on water velocities experienced by *R. cataractae* along the bottom of the channel can be calculated by multiplying recommendations by 0·74, the ratio of bottom to average water velocity. Previous field studies have indicated *R. cataractae* can traverse long distances (14·0–19·7 m) at low velocities (12–16 cm s^{-1}; Rosenthal, 2007). Ficke (2015), however, observed low passage at (31–38%) in a 10·1 m experimental rock ramp at similar velocities (68 cm s^{-1}) at which high passage was observed in the flume, indicating hydraulic characteristics such as turbulence may have a large effect on

R. cataractae swimming abilities. Using field studies to identify structures that either inhibit or promote passage then examining their specific hydraulic characteristics and effects on swimming abilities and behaviour in a laboratory may be an efficient method to progress the ability to design more effective passage structures.

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