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RESEARCH ARTICLE

Swimming activity and energetic costs of adult lake sturgeon during fishway passage

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ABSTRACT

Fish migrations through riverine systems can be energetically demanding, and the presence of fishways to facilitate upstream passage can add an additional energetic cost that may directly affect fitness. Successful fishway passage is a function of the ability of fish to select appropriate paths and swimming strategies that do not exceed their swimming capacity. Triaxial accelerometers were used to estimate the energetic expenditure of adult lake sturgeon (*Acipenser fulvescens*) swimming through a vertical slot fishway, to determine whether individual behaviour or path selection, resulting in differences in cumulative energy use, explain fishway passage success. Most individuals attempted to pass the fishway (n=30/44; 68%), although successful passage only occurred for a subset of those attempting (n=7/30; 23%). High-speed swimming was rarely observed during upstream passage through fishway basins, and was of short duration. Two turning basins delayed passage, subsequently resulting in a higher energetic cost. The rate at which energy was expended did not differ among successful and unsuccessful individuals, although successful sturgeon exhibited higher costs of transport (42.75 versus 25.85 J kg^{-1} m^{-1}). Energy expenditure metrics were not predictive of successful fishway passage, leading us to conclude that other endogenous or exogenous factors influence passage success. In a practical application of field measurements of energy expenditure, we demonstrate that fishway passage through a structure designed to facilitate migration does result in an energetic loss for lake sturgeon (3249–16,331 J kg^{-1}), equivalent to individuals travelling 5.8–28.2 km in a lentic system.

KEY WORDS: *Acipenser fulvescens*, Energy use, Cost of transport, COT, Accelerometer

INTRODUCTION

The rate at which animals expend energy is a key component to understanding how they interact with their surrounding environment (McNab, 2002). The allocation of time and energy to different behaviours across the landscape affects individual survival and fitness (Morales et al., 2010; Wilson et al., 2012). In fish, locomotor activity can account for a considerable portion of an energy budget (Boisclair and Leggett, 1989), thus energetic cost optimisation through the evolution of morphological (e.g. body form and fin shape), physiological (e.g. muscular efficiency) or behavioural (e.g. schooling) traits is often observed (Weihs and Webb, 1983). In lotic systems, and where positive rheotaxis occurs, drag and water velocity typically govern energetic expenditure. Position can be maintained and energy expenditure minimised through behavioural strategies including benthic station-holding by some species at high water velocities (Webb et al., 1996) or simply occupation of less demanding microhabitats (McLaughlin and Noakes, 1998). However, behaviours including migrations that require a net directional upstream movement can be energetically demanding (Lucas et al., 2001).

The energy expended by fish during upstream spawning migrations results in a net energy loss for species that cease feeding, thus the amount of metabolic reserves that fish allocate to their spawning migrations is therefore not available for spawning itself (Brett, 1995). Further, where challenging hydraulic conditions are encountered, individuals are often required to make behavioural adjustments that affect energetic expenditure and, ultimately, fitness. For example, migrating sockeye salmon (*Oncorhynchus nerka*) that select paths resulting in slow swimming speeds are more likely to successfully pass through a challenging river reach (Hinch and Bratty, 2000). In comparison, individuals that exhibit hyper-activity via inappropriate path selection likely deplete energy stores or reach metabolic acidosis and subsequently fail to pass the same reach (Hinch and Bratty, 2000). McElroy et al. (2012) demonstrated that pallid sturgeon (*Scaphirhynchus albus*) exhibited energetic optimisation by selecting migration pathways through sections of a river with the lowest water velocities. A trade-off often exists, however, between the allocation of time and energy during migrations. Standen et al. (2002) observed that sockeye and pink salmon (*O. gorbuscha*) adopted one of two strategies; they either swam slowly and took more time searching for lower velocity areas, thus increasing passage time (cost optimisation strategy), or swam quickly through higher velocity areas (time optimisation strategy). The time optimisation strategy is clearly beneficial if energy is not a limiting factor and/or the timing of arrival at spawning grounds governs fitness. As energy is not replenished, the cost optimisation strategy may be preferable for poor swimmers or through particularly demanding areas. A third possibility is that the total energy used to traverse a given location may be similar between the two strategies, as low energy use over a longer period of time may amount to the same total energetic cost as high energy use over a short period of time. In this example, the advantage would be with the individual adopting the time optimisation strategy.

To add further complexity, many key migratory pathways have been blocked by anthropogenic barriers, such as dams (Lucas et al.,

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List of symbols and abbreviations

COT	cost of transport
D_{max}	maximum distance of ascent
D_{total}	total distance
D_{up}	cumulative upstream distance
E_{rate}	rate of energy use
E_{total}	total energy use
FL	fork length
g	gravitational acceleration
LME	linear mixed effects
$\dot{M}_{O_2}$	rate of oxygen consumption
ODBA	overall dynamic body acceleration
PIT	passive integrated transponder
TL	total length
TMR	total metabolic rate
U_{crit}	critical swimming speed
U_g	ground speed
U_s	swimming speed

2001). Fishways are increasingly being installed at these barriers and represent one solution to facilitate upstream passage of migrating fish, requiring volitional entry and passage through the structure by active swimming (Clay, 1995). To be effective, fishways must allow for the upstream passage of fishes with minimal energy expenditure to reduce potential fitness consequences (Castro-Santos and Haro, 2010). As such, considerable effort has been devoted to linking species-specific swimming ability with fishway design (e.g. Peake et al., 1997). However, fishways that are uniformly successful at passing all individuals or species are rare (Bunt et al., 2012), and individuals that are successful may still exhibit delayed mortality (Roscoe et al., 2011). Recent evidence suggests that laboratory-derived data from forced swimming trials are not indicative of volitional performance (Castro-Santos et al., 2013; Peake, 2004). Further, fishways often represent dynamically turbulent environments (Tarrade et al., 2008), and increases in turbulence generally increase the cost of locomotion (Enders et al., 2003) and decrease fishway efficiency (Silva et al., 2011). Individual differences in path selection can also result in a higher cost of passage for some individuals (Khan, 2006), and although this may explain differential success, it typically remains unknown.

Sturgeon represent a group of fishes for which barriers to migration often limit access to upstream spawning areas and subsequently threaten population persistence (Rochard et al., 1990). Sturgeon have a relatively limited capacity for high-speed swimming, resulting from high profile drag (Webb, 1986) and poor aerobic capacity (Peake et al., 1997). Considerable attention has been devoted to facilitating upstream passage of sturgeon at fishways via laboratory-derived swimming models (Peake et al., 1997), observations of captive sturgeon ascending experimental

fishways (Cheong et al., 2006; Cocherell et al., 2011; Kynard et al., 2011; Webber et al., 2007) and field observations of passage behaviour including quantification of fishway efficiency (Parsley et al., 2007; Thiem et al., 2011). Given their poor aerobic swimming ability, it is possible that fishways impose a particularly high energetic cost to migrating sturgeon, and that energetic expenditure may explain differences in passage success.

We examined the energetic costs of upstream passage through a vertical slot fishway by lake sturgeon [*Acipenser fulvescens* (Rafinesque 1817)], a locally abundant species endemic to North America that undertake comparatively short-distance spawning migrations that are typically less than 200 km (Auer, 1996). Using a combined tagging approach to determine both spatial location and indirect measures of energy expenditure, our objectives were to determine whether: (1) ground speed, swimming speed or energy use differ among locations within the fishway, (2) energetic costs differ among successful and unsuccessful individuals and (3) the probability of successful passage is a function of energy expenditure, with a view to elucidate the factors that govern effective fishway designs for sturgeon.

MATERIALS AND METHODS
Study site
This study was conducted at the Vianney-Legendre Fishway, a vertical slot fishway located on the Richelieu River adjacent to the St Ours dam (45°51′48″N, 73°08′60″W) in southwestern Quebec, Canada. The fishway was installed in 2001 to facilitate upstream passage for migrating fish past a low level dam (3.4 m height), and is an 85 m long concrete structure with an elevation rise of 2.65 m that includes large entrance and exit basins on gentle slopes. The remainder of the fishway is divided into 12 uniform rectangular basins (3.5×3.0 m) connected by two resting/turning basins with horizontal floors and curved walls (2.75 m radius; Fig. 1) that potentially provide low-velocity resting areas for upstream migrating fish during passage. The uniform basins have successive floor drops of 0.15 m for a total rise of 2.4 m and are each separated by a 0.6 m wide vertical slot (2.3–4.0 m height range). The fishway passes approximately 1 m³ s⁻¹ of water, with a capacity for an additional 6.5 m³ s⁻¹ attraction flow near the entrance basin via a pass-through chamber beneath the fishway (although attraction flow was not used in this study). Maximum water velocities of 1.72 m s⁻¹ occur at the vertical slots. A more detailed description of the fishway and the Richelieu River is provided in Thiem et al. (2011) and Thiem et al. (2013b).

Capture and tagging
Lake sturgeon [*n*=44, 1222±21 mm total length (TL) (939–1555 mm TL range) and 10.56±0.68 kg (4.40–24.61 kg range)] were captured between 18 April and 4 May 2012 downstream of the
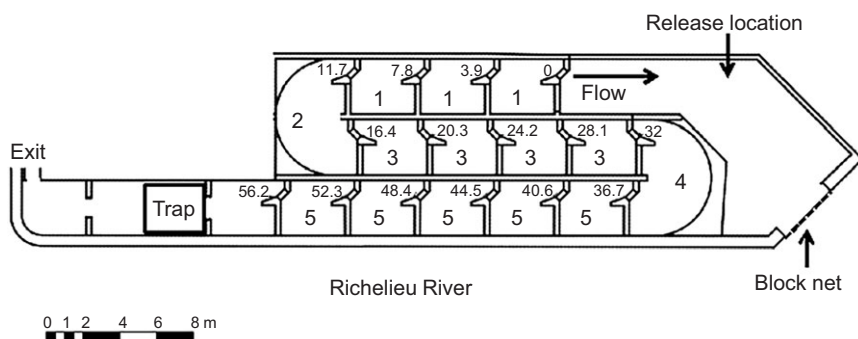

Fig. 1. Schematic of the Vianney-Legendre vertical slot fishway on the Richelieu River in Quebec, Canada. Numbers 1–5 indicate fishway sections and corresponding basins. Distance metrics, corresponding to locations of PIT antennas, indicate the cumulative minimum transit distance between successive fishway basins (beginning at 0 m) and were used in calculations of distance moved and location.

St Ours dam using monofilament gill nets. The methods and capture locations were identical to those previously used, and lake sturgeon congregate at this location prior to spawning at this site or passing upstream via the fishway to spawn (Thiem et al., 2011, 2013b). Captured sturgeon were immediately transferred to on-site indoor holding facilities adjacent to the fishway and held in 2250 litre flow-through hatchery tanks (with water pumped directly from the river replaced at a rate of ca. 50 l min^{-1}) at a density of no more than 20 kg per 1000 litres for 1–3 days prior to release to ensure adequate sample sizes. There was no mortality associated with capture, handling or holding, and fish were not fed during holding. Immediately prior to release, sturgeon were measured, weighed and had a uniquely coded passive integrated transponder (PIT) tag (32×3.85 mm half duplex; Texas Instruments, Dallas, TX, USA) inserted into the coelomic cavity using the methods described by Thiem et al. (2011). Each sturgeon was also fitted with an external package at the base of the dorsal fin (Thiem et al., 2015) comprising a tri-axial accelerometer data storage tag (model G6a, 40×28×16.3 mm, 7.3 g in air, CEFAS Technology, Suffolk, UK) and a coded radio tag to facilitate accelerometer retrieval (149 MHz, 30×8 mm, 8 g mass in air, burst rate 2 s, 90 day battery life; Sigma Eight, Newmarket, ON, Canada). Total package weight was 32 g and never exceeded 0.8% of total fish mass. No anaesthetics or sutures were used and the entire handling process took <5 min, with care taken to minimise air exposure. Accelerometers were programmed to record acceleration in units of gravity (**g**), equivalent to 9.8 m s^{-2}, in separate x, y and z planes (measurement range: ±2 **g**) at user defined intervals of 20 Hz. Device output was calibrated by rotating the device through known angles to real **g** (Gleiss et al., 2010).

A PIT array consisting of 15 complete pass-through antennas [beginning at antenna 15 downstream (0 m) and ending at antenna 1 upstream (56.2 m); Fig. 1] was installed within the fishway during a dewatering period in early April 2012. The antenna array was identical to that described by Thiem et al. (2013a). A multiplexer allowed the antennas to be scanned sequentially at high speed (i.e. each antenna was scanned 2.5 times s^{-1}) and upon positive detection stored a unique tag identification number, antenna number and the date and time of detection to the nearest second. Detection efficiency of the system was 97±1.5% for 32 mm tags, based on a separate study undertaken at this site (Burnett et al., 2013). Sturgeon were released into the entrance basin of the fishway immediately following tag attachment and in three separate groups to minimise the number of sturgeon in the fishway at any time whilst maintaining adequate sample sizes. Trials ran for 72 h [trial 1 ($n=15$): 20–23 April, average water temperature 9.2±0.1°C; trial 2 ($n=14$): 27–30 April, average water temperature 7.8±0.0°C; trial 3 ($n=15$): 4–7 May 2012, average water temperature 10.4±0.1°C], and sturgeon were able to enter the fishway from the entrance basin volitionally, and pass to the upstream section of the fishway. Sturgeon were prevented from exiting the fishway by a block net that was added to the entrance (downstream) gate and a fish trap operating upstream of antenna 1 (Fig. 1). Following cessation of each trial, a slow dewatering of the fishway enabled recapture of sturgeon, removal of external tag packages and release at the point of capture.

Table 1. Summary information for lake sturgeon ($n=30$) attempting to pass a vertical slot fishway

Fish ID	TL (mm)	Mass (kg)	Attempts	Maximum upstream location (basin)	Pass/ fail	Time in fishway (h)	Time exceeding U_{crit} in fishway (%)	Total swimming energy expenditure in fishway (E_{total}; J kg^{-1})	Rate of energy expenditure (E_{rate}; J kg^{-1} h^{-1})
1	1214	8.54	2	2	1	2.86	11.4	5974	2088.8
2	1330	14.66	3	13	0	2.49	8.5	5563	2234.1
3	1295	12.52	8	2	1	6.25	5.8	13,230	2116.8
4	1209	10.80	5	14	0	0.58	13.9	1215	2094.8
5	1124	9.16	1	13	0	0.82	7.7	1579	1925.6
6	1398	18.03	1	14	0	0.03	52.5	87	2900.0
7	1100	6.50	3	14	0	0.45	4.5	848	1884.4
8	1337	16.21	5	12	0	0.41	17.3	945	2304.9
9	1379	16.71	2	15	0	1.93	2.0	4172	2161.7
10	1075	6.50	12	9	0	2.90	6.5	5549	1913.4
11	1361	13.63	1	15	0	0.17	8.1	388	2282.4
12	1267	9.80	1	15	0	0.08	5.0	162	2025.0
13	1072	6.05	5	10	0	7.89	5.4	14,976	1898.1
14	1386	13.07	6	2	1	1.45	8.6	3249	2240.7
15	1555	24.61	6	4	0	12.26	8.7	29,814	2431.8
16	1092	5.93	1	14	0	0.03	31.1	71	2366.7
17	1221	8.76	5	9	0	6.94	6.0	14,111	2033.3
18	1343	14.56	2	6	0	1.63	7.8	3595	2205.5
19	1206	10.43	16	2	1	7.89	9.0	16,331	2069.8
20	1417	16.23	2	2	1	4.53	10.0	10,403	2296.5
21	1116	6.84	7	3	0	2.31	11.5	4573	1979.7
22	1234	10.52	1	15	0	0.04	21.1	90	2250.0
23	1351	16.16	22	13	0	2.28	4.9	5040	2210.5
24	1471	19.21	1	15	0	0.10	10.3	244	2440.0
25	1144	8.03	1	12	0	0.32	8.7	632	1975.0
26	1216	9.91	3	13	0	1.79	3.1	3592	2006.7
27	1379	13.55	3	2	1	3.59	12.4	8208	2286.4
28	1197	9.11	12	2	1	5.58	8.2	11,538	2067.7
29	975	4.40	2	9	0	2.14	5.8	3732	1743.9
30	1099	6.17	2	13	0	0.53	7.0	1045	1971.7

This project was conducted in accordance with the guidelines of the Canadian Council on Animal Care administered by the Carleton University Animal Care Committee (B10-12).

Data analysis

Sturgeon movements through the fishway over time were reconstructed by converting antenna locations to distance metrics beginning at the first antenna (antenna 15, 0 m) and ending at the most upstream vertical slot (antenna 1, 56.2 m; Fig. 1) (Thiem et al., 2013a). This enabled calculation of the multiple movement metrics for each individual. Minimum cumulative distance moved throughout the fishway (D_{total}) was defined as the cumulative movements in both upstream and downstream directions by an individual within the fishway until successful passage, termination of the trial or no further passage attempts were made. Maximum distance of ascent (D_{max}) represents the maximum upstream location achieved by an individual across all combined attempts and ranged from 3.9 to 56.2 m corresponding to locations of antenna 14 and antenna 1, respectively (Fig. 1). Cumulative upstream distance moved (D_{up}) was defined as the cumulative movements in only an upstream direction (Thiem et al., 2011). As 14 fish were either not detected within the fishway ($n=4$) or were detected beyond the most downstream antenna ($n=10$) (and could not be confirmed to have actually entered the fishway; a minimum of two antennas are required to determine direction), all subsequent analyses were conducted on the remaining 30 sturgeon (Table 1). A passage attempt was defined as any movement into the fishway (to at least the second antenna encountered; antenna 14) and terminated upon either successful passage or return to the downstream staging area. Successful passage was defined as the first detection of an individual on the most upstream antenna (antenna 1), which was located one basin downstream of a fish trap. As the trap was present to prevent complete passage of individuals (and subsequent loss of tags), and aversion to fish traps at fishways has been documented by others (e.g. Stuart et al., 2008), this removed any potential bias the trap may have had on behaviour. To test whether individual variability in fishway passage success was related to condition (e.g. Cocherell et al., 2011), individual length–weight data were used to calculate Fulton's condition factor (Anderson and Neumann, 1996). We compared the condition of lake sturgeon that entered the fishway with that of those that did not, and the condition of lake sturgeon that entered and successfully ascended the fishway with those that entered but were unsuccessful. We used unequal variances t-tests performed on ranked data because of non-normality (Ruxton, 2006).

Accelerometer output for each tag was time calibrated with the PIT antenna system manually by applying a linear correction factor to account for time drift between systems. 'Static' and 'dynamic' acceleration components (for definition, see Shepard et al., 2008) were separated using a weighted smoothing interval of 1.5 s (Shepard et al., 2008) in Igor Pro (version 6.0, WaveMetrics, Lake Oswego, OR, USA) (Fig. 2A). Absolute values of dynamic acceleration from each acceleration axis were summed to yield instantaneous overall dynamic body acceleration (ODBA) (Wilson et al., 2006). We used ODBA as it represents a single integrated measure of body motion in all three spatial dimensions and is generally considered more indicative of total work output than tail beat frequency during unsteady swimming behaviours such as those comprising frequent turns or bursting and coasting (Gleiss et al., 2010, 2011).

To determine location-specific behaviour among lake sturgeon during upstream passage, each individual was assigned a location (basin) for each second during upstream movements. Upstream

movements were categorised as any upstream directional movement determined from records on sequential antennas. When this occurred, a location was assigned based on the time of the last
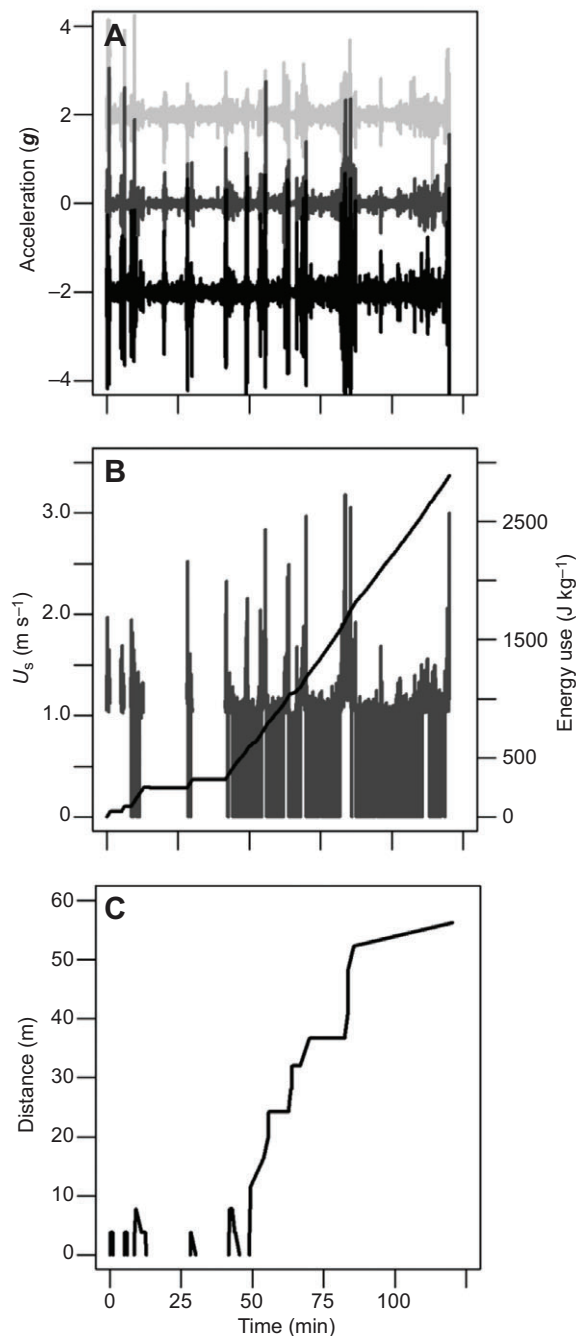

Fig. 2. Time series passage profile of one lake sturgeon (ID 14; 1386 mm TL, 13.07 kg) ascending a vertical slot fishway. (A) The dynamic component of acceleration [presented for separate x (light grey), y (dark grey) and z (black) axes], with +2 g and −2 g added to x and z axes, respectively, for graphical purposes only. (B) Swimming speed (U_s) and cumulative energy use for times when the sturgeon was within the fishway, where swimming speed was derived from the linear relationship between speed and the absolute sum of the dynamic component of all three acceleration axes (overall dynamic body acceleration; ODBA). (C) Approximate spatial location within the fishway, expressed as distance from fishway entry (0 m) until successful passage (56.2 m), with location determined using PIT antennas located on each vertical slot baffle ($n=15$).

detection of the downstream antenna and the time of the first detection on the upstream antenna. Ground speed (U_g; m s^{-1}) during upstream movements through basins was determined by the time difference between the two antennas divided by the minimum distance travelled (3.9 m for regular basins and 4.7 m for turning basins), although the actual distance travelled is unknown. A corresponding median swimming speed (U_s; m s^{-1}) estimate was also allocated for upstream passage through each basin, derived from the median ODBA value during ascent based on the ODBA–U_s relationship previously identified for this species and tag type (Thiem et al., 2015):

$$U_s = 0.7072 + 0.5435(\text{ODBA}) \times \text{TL}, \qquad (1)$$

where total length (TL) is in m. Median ODBA values always fell within the range of those previously used for ODBA–U_s calibrations for this species (Thiem et al., 2015). An estimate of the total energetic cost to pass upstream through any given basin was also calculated and used to express the cost of transport (COT; J kg^{-1} m^{-1}). One second U_s values were first derived from ODBA (as above), and values below the previously calibrated minimum ODBA value of 0.06 g (Thiem et al., 2015) were conservatively allocated a value of 0 m s^{-1}. Values above the previously calibrated maximum ODBA of 3.96 g were not recorded in this study. Swimming speeds were subsequently converted to an oxygen consumption rate ($\dot{M}_{O_2}$; mg kg^{-1} s^{-1}) using the equation from McKinley and Power (1992) for a lake sturgeon swimming at 10°C (which represents the approximate water temperatures observed during this study), where U_s was first converted to cm s^{-1} and 3600 represents the number of seconds in an hour:

$$\dot{M}_{O_2} = \frac{43 + 1.1(U_s)}{3600}. \qquad (2)$$

Total metabolic rates (TMR; the sum of energy consumed within a fishway basin) were determined by summing $\dot{M}_{O_2}$ for total duration (in seconds) within a fishway basin and multiplying this by an oxycalorific coefficient of 13.598 J mg^{-1} O$_2$ (Brett and Groves, 1979). COT (J kg^{-1} m^{-1}) through a fishway basin was determined as:

$$\text{COT} = \frac{\sum^{\text{TMR}}}{D}, \qquad (3)$$

where D is the minimum distance required for a fish to travel through a basin (3.9 or 4.7 m). These COT estimates assume purely aerobic respiration during passage through fishway basins (where location is defined above), thus an estimate of the proportion of time each individual exceeded its critical swimming speed (U_{crit}) was also determined. The use of U_{crit} is widely recognised in laboratory experiments as a transitional phase from the use of purely aerobic red muscle fibres to the recruitment of anaerobic white muscle fibres that result in muscle fatigue and an oxygen debt (Beamish, 1978; Burgetz et al., 1998). We calculated the proportion of time individuals spent exceeding U_{crit} during their entire time within the fishway, as well as the continuous duration (bout length) for which U_{crit} was exceeded when traversing fishway basins. We determined U_{crit} from the equation provided by Peake (2005) encompassing three species of sturgeon (including lake sturgeon):

$$U_{crit} = 21.05 + 0.84 \times \text{FL} \qquad (4)$$

where U_{crit} is in cm s^{-1} and fork length (FL) is in cm. Total length (TL) of sturgeon was first converted to FL by rearranging the

equation provided by Fortin et al. (1996) for St Lawrence lake sturgeon as follows (and where FL and TL are in mm):

$$\text{FL} = \frac{\text{TL} - 35.97}{1.06}. \qquad (5)$$

To determine location-specific differences in U_g, U_s and COT among fishway locations (basins), we used a linear mixed effects (LME) model selection approach (Zuur et al., 2009) using the package nlme (Pinheiro et al., 2012) in R (version 2.14.2; R Development Core Team, 2012). Initially, fishway basins (n=14) were grouped into five fishway sections (Fig. 1). Included as covariates were: fishway section, TL, mean trial water temperature (collected hourly from within the fishway; DS1921Z iButton, Maxim Integrated, San Jose, CA, USA) and a binary pass/fail response depending upon whether the entire attempt resulted in successful or unsuccessful passage. Initially, a full model including all covariates was fitted using generalised least squares and compared with an LME model that included a random intercept term of attempt number nested within fish ID. In all cases, inclusion of a random intercept significantly improved model fit and we proceeded with model selection using LME. A variance structure to account for heterogeneity of variance among fishway sections for models of U_g and U_s improved model fit and residual spread, although a log transformation was required for the COT model. Temporal auto-correlation of residuals was assessed visually using semi-variograms because of irregularly spaced data (Zuur et al., 2009). The optimal fixed structure of models was assessed using likelihood ratio tests applied to models fitted using maximum likelihood estimation based on sequential removal of covariates. Final models were subsequently refitted using restricted maximum likelihood estimation. *Post hoc* tests for differences among fishway sections were conducted using a Bonferroni correction in the package multcomp (Hothorn et al., 2013). For graphical purposes, predictions of U_g, U_s and COT along with corresponding confidence intervals were computed using AICcmodavg (Mazerolle, 2012), with covariates held at their average value where applicable.

To determine overall differences in the rate of energy use and COT among successful and unsuccessful individuals, we calculated total energy use by lake sturgeon during fishway passage. Total energy use (E_{total}; J kg^{-1}) was calculated using Eqns 1, 2 and 3, and represents a cumulative value for each second a sturgeon was within the fishway, regardless of location (Fig. 2B). The rate of energy use (E_{rate}; J kg^{-1} h^{-1}) was determined as E_{total} divided by the duration of time (hours) in the fishway. Total COT (J kg^{-1} m^{-1}) was calculated as per Eqn 3, where distance was the total distance moved (D_{total}) within the fishway defined by movements between PIT antennas. Differences in E_{rate} and total COT were compared among successful and unsuccessful individuals using unequal variances t-tests performed on ranked data because of non-normality (Ruxton, 2006). Linear regressions were used to describe relationships between E_{total} and time in the fishway, D_{max}, D_{up} and D_{total}. Passage success or failure was modelled as a binary response variable with E_{total}, E_{rate} and COT using logistic regression, to determine whether any of these three variables alone could adequately predict the probability of fishway passage success.

RESULTS
A total of 30 lake sturgeon made at least one attempt to pass the fishway, and seven fish successfully passed, resulting in a passage efficiency estimate of 23%. There was no difference in the condition of sturgeon making no attempt to enter the fishway and that of those that entered ($t_{27.203}$=−1.439, P=0.162), nor any difference in
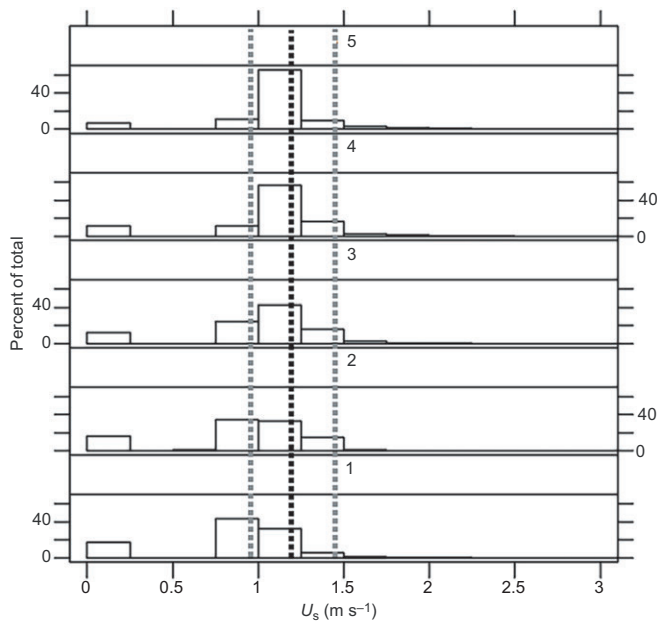
Fig. 3. Frequency distribution of lake sturgeon (n=30) swimming speeds (U_s; m s^{-1}) through pooled basins located in different sections (1–5) of a vertical slot fishway. The black dashed line indicates the critical swimming speed (U_{crit}) of the average sized sturgeon in this study, and grey dashed lines indicate minimum and maximum U_{crit} values for the smallest and largest individuals, respectively.

condition between successful and unsuccessful individuals ($t_{15.934}$=0.955, P=0.354). Individuals typically made multiple attempts to pass the fishway (up to 22 attempts; Table 1), with successful passage requiring two to 16 attempts. The amount of time sturgeon spent in the fishway ranged from 0.03 to 12.26 h, and individuals successfully passing the fishway occupied the fishway for 1.45–7.89 h (Table 1). Sturgeon most frequently swam at speeds ≤1.25 m s^{-1} during passage through fishway basins (Fig. 3). Critical swimming speed for an average sized sturgeon in this study was 1.17 m s^{-1}, and U_{crit} ranged from 0.96 to 1.41 m s^{-1} for minimum and maximum sized individuals, respectively. Sturgeon exceeded their respective U_{crit} whilst within the fishway a median of 8.4% of the time (range 2.0–52.5%), and all of the highest records of U_{crit} exceedance were associated with short (≤0.04 h) total periods of time within the fishway (Table 1, Fig. 3). Where U_{crit} was exceeded during passage through basins, bout lengths were typically of short duration (i.e. ≤3 s continuous exceedance of

U_{crit} accounted for 83% of exceedance records). Twenty seconds was the maximum length of time U_{crit} was continuously exceeded, although continuous exceedance of U_{crit} for ≥10 s accounted for only 1% of exceedance records.

During upstream passage, U_g was higher through regular basins than in turning basins (Table 2). The final model comparing U_g among fishway basins was best described through the inclusion of the covariate water temperature and the fixed factor pass/fail (Table S1). Estimates of U_g positively covaried with water temperature, and U_g was slower during successful passage attempts (Table S1). In addition, sturgeon exhibited significantly higher U_g when passing upstream through regular basins in comparison with turning basins (Table 2, Fig. 4A). Estimates of U_s during upstream passage were higher in regular basins in comparison with turning basins (Table 2, Fig. 4B). The final model included TL and water temperature, which both covaried positively with U_s (Table S1). Swimming speed was significantly higher in section 5 than in other sections, and also significantly higher in section 3 than in all other sections (except section 5) (Table 2). Sturgeon U_s was significantly higher in section 1 compared with section 2, although sections 1 and 4 were similar, as were sections 2 and 4 (Table 2). The final model describing COT through different fishway sections included the covariate water temperature, which covaried negatively with COT (Table S1). COT estimates were significantly higher through turning basins (sections 2 and 4) than in regular basins (sections 1, 3 and 5; Table 2, Fig. 4C). Passing upstream through turning basins in section 2 and 4, lake sturgeon used a median of 34.39 and 30.31 J kg^{-1} m^{-1}, respectively, in comparison to 4.57, 5.91 and 4.19 J kg^{-1} m^{-1}, respectively, for sections 1, 3 and 5 (Table 2).

Our E_{total} estimates from lake sturgeon whilst in the fishway ranged from 71 to 29,814 J kg^{-1} for unsuccessful individuals and from 3249 to 16,331 J kg^{-1} for successful individuals (Table 1). There were no significant differences in E_{rate} between unsuccessful [median (range): 2094.8 J kg^{-1} h^{-1} (1743.9–2900.0)] and successful individuals [2116.8 J kg^{-1} h^{-1} (2067.7–2296.5); $t_{18.418}$=−1.076, P=0.296]. Unsuccessful lake sturgeon typically exhibited shorter D_{total} values [54.6 m (7.8–289)] than did successful sturgeon [121.8 m (104.6–443.2)]. The COT for unsuccessful sturgeon whilst in the fishway was significantly lower [25.85 J kg^{-1} m^{-1} (4.55–267.44)] than for successful sturgeon [42.75 J kg^{-1} m^{-1} (28.99–111.55); $t_{17.630}$=−2.159, P=0.045]. Estimates of D_{up} were lower for unsuccessful sturgeon [27.3 m (3.9–144.5)] in comparison with successful sturgeon [89.0 m (80.4–245.8)]. There was a strong linear relationship

Table 2. Fishway section characteristics (pooled by similar fishway basin types; see Fig. 1) and corresponding lake sturgeon mean (±s.e.m.) ground speed (U_g; m s^{-1}), swimming speed (U_s; m s^{-1}) and median (range) cost of transport (COT; J kg^{-1} m^{-1}) during passage through a single fishway basin located within each grouped fishway section

	Fishway section				
	1	2	3	4	5
Fishway basins	16, 15, 14	13	12, 11, 10, 9	8	7, 6, 5, 4, 3
Basin type	Regular	Turning	Regular	Turning	Regular
U_g	0.16±0.01	0.02±0.00	0.15±0.02	0.02±0.00	0.21±0.03
Bonferroni contrasts of U_g	A	B	A	B	A
U_s	1.07±0.01	1.00±0.02	1.16±0.02	1.11±0.03	1.35±0.04
Bonferroni contrasts of U_s	C	D	B	C,D	A
COT	4.57 (1.15–155.11)	34.39 (6.13–221.13)	5.91 (1.53–196.71)	30.31 (12.17–82.06)	4.19 (1.63–290.80)
Bonferroni contrasts of COT	B	A	B	A	B

Letters denote significant differences in *post hoc* tests following a linear mixed-effects modeling approach comparing lake sturgeon activity metrics among fishway sections.
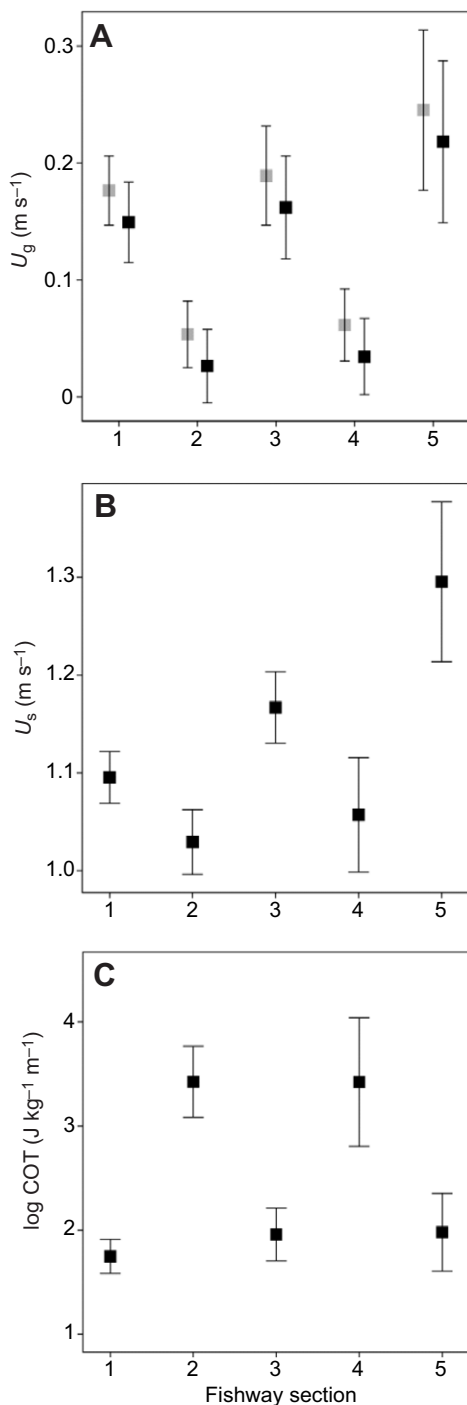
Fig. 4. Model predictions (±95% confidence intervals) resulting from linear mixed-effects model analysis of lake sturgeon (*n*=30) during passage through a single fishway basin nested within sections (1–5) of a vertical slot fishway. (A) Ground speed (U_g; grey squares indicate failed passage attempts; black squares indicate successful passage attempts); (B) median swimming speed (U_s); (C) cost of transport (COT). Water temperature was a significant covariate in models of ground speed and swimming speed (see Table S1), although it was held at its average value in model predictions for graphical purposes only.

between the time sturgeon spent in the fishway and E_{total} (Fig. 5A) for both successful (E_{total}=541.4+2026.2T, where T is time, R^2=0.99) and unsuccessful fish (E_{total}=−266.3+2247.5T, R^2=0.98). A weak linear relationship existed between E_{total} and

D_{max} (E_{total}=564.1+196.2D_{max}, R^2=0.35; Fig. 5B). Estimates of E_{total} increased at differing rates for unsuccessful and successful sturgeon in response to D_{up} (unsuccessful: E_{total}=−192.0+97.6D_{up}, R^2=0.47; successful: E_{total}=4399.2+40.7D_{up}, R^2=0.32; Fig. 5C) and D_{total} (unsuccessful: E_{total}=−192.0+48.8D_{total}, R^2=0.47; successful: E_{total}=5555.9+20.2D_{total}, R^2=0.33; Fig. 5D), although there was limited overlap of data as successful sturgeon typically had greater D_{up} and D_{total} values. The metrics E_{total}, E_{rate} and COT were not predictive of successful passage by sturgeon (Table S2).

DISCUSSION

This study found that a small proportion (23%) of lake sturgeon attempting to pass the fishway were successful. Individual condition, total energy expenditure and the rate of energy expenditure did not differ between successful and unsuccessful lake sturgeon, although COT estimates indicate that successful sturgeon typically expended more energy per unit distance than unsuccessful sturgeon. There was little evidence of cost optimisation exhibited by successful sturgeon; rather, the data presented here support a time-optimising strategy that was linearly related to energy optimisation. This is most likely explained by the physical size of individuals in comparison with the fishway dimensions. Although vertical slot fishways have spatially and temporally heterogeneous hydraulics within basins, any possible cost optimisation strategy may be precluded as all individuals are required to pass through the highest velocities occurring at the vertical slots when travelling upstream. Further, there was considerable variability among successful individuals in terms of the total energy used, and this was likewise linked to passage duration and corresponding distance travelled. Although the sample size of successful individuals was low (*n*=7) and the causal mechanisms for inter-individual variability were not identified, the variability in passage behaviour observed in this study is consistent with previous observations of lake sturgeon at this site by Thiem et al. (2011). Cocherell et al. (2011) likewise identified variability in passage behaviour of white sturgeon (*A. transmontanus*) ascending a laboratory fishway. Unlike the findings of the present study, Cocherell et al. (2011) identified that individual condition, based on a health index that quantified external injuries rather than derived from length and weight, accounted for the observed variability in passage success of white sturgeon.

Energy expenditure metrics were not predictive of successful fishway passage by lake sturgeon. Other factors most likely influence passage success, including individual motivation or navigational ability. The approach used in this study of downstream capture and subsequent release into the fishway provides an artificial measure of passage efficiency (Cooke and Hinch, 2013), as volitional entry into the fishway (attraction) did not occur. Further, one spawning site occurs downstream of the fishway (Thiem et al., 2013b) and thus differentiation between individuals motivated to pass upstream of the dam or spawn downstream remains unknown. Nonetheless, although energy expenditure metrics (E_{total}, E_{rate} and COT) were not predictive of successful passage through the fishway, passage did result in an energetic loss (3249–16,331 J kg^{-1}) that was largely determined by passage duration. Roscoe et al. (2011) demonstrate that for sockeye salmon, passage success does not necessarily transfer directly to reproductive success. The authors identified evidence of delayed post-passage consequences including *en route* mortality or a reduced competitive ability at spawning grounds. Similarly, Caudill et al. (2007) identified that delayed dam passage was indicative of reproductive failure in Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*), with one possible mechanism being premature depletion of energy stores.
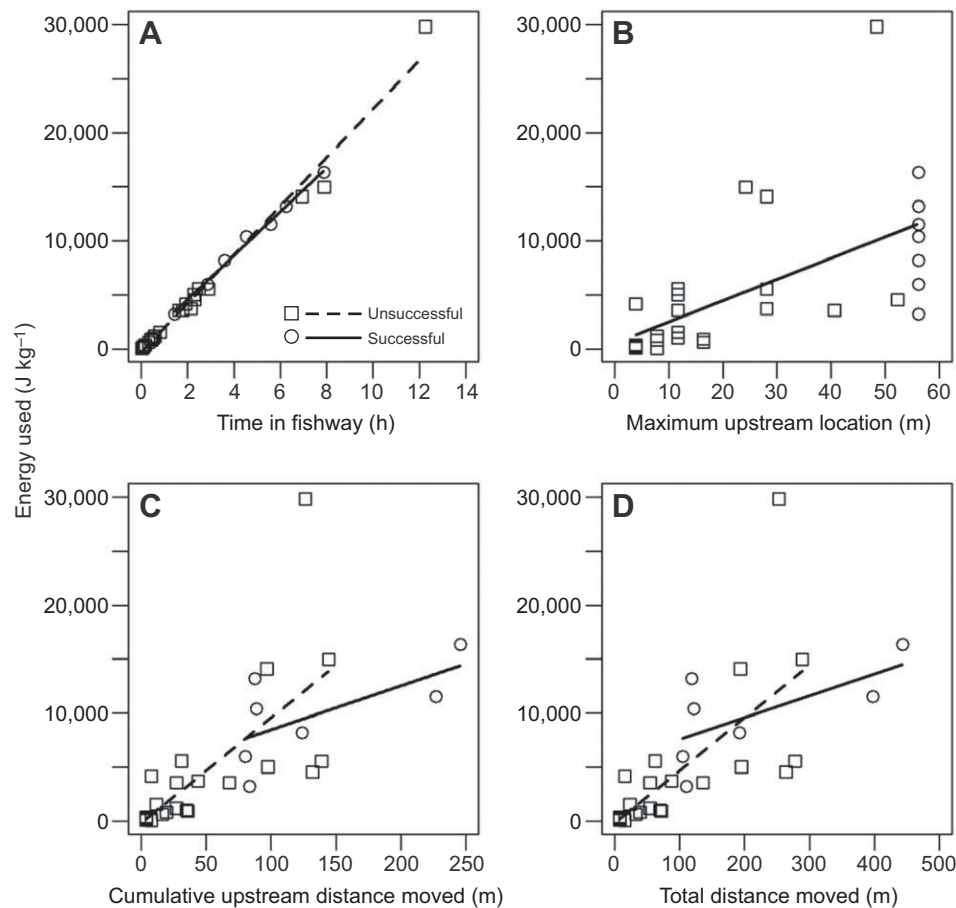
Fig. 5. Linear regression relationships between total energy used and various metrics for lake sturgeon in a vertical slot fishway. (A) Total time in the fishway and total energy used for unsuccessful (n=23) and successful individuals (n=7); (B) maximum upstream location and total energy used within the fishway for unsuccessful and successful individuals, with the solid line indicating the overall best linear fit; (C) cumulative upstream distance moved and total energy used for unsuccessful and successful individuals; and (D) total distance moved and total energy used within the fishway for unsuccessful and successful individuals.

The post-passage reproductive success of lake sturgeon in the present study was not evaluated, and the delayed consequences of energy expenditure resulting from fishway passage remain unknown. Nevertheless, given that lake sturgeon typically undertake comparatively short-distance migrations (Auer, 1996) and may allocate less energy to migrations in comparison to longer-distance migrants (e.g. Crossin et al., 2004), it is possible that any additional energy expenditure could influence migratory or reproductive success. To place the results of this study in the context of migration in general for this species, we compared the total energy used by successful lake sturgeon during fishway passage with the equivalent energy used and corresponding distance travelled for sturgeon swimming at a range of speeds (0.25–1.50 m s^{-1}). For simplicity, we assumed that this movement occurred in a lentic system, which is typical habitat for this species throughout much of the year (Scott and Crossman, 1973). The energy expended by successful lake sturgeon in the present study to swim an estimated 104–443 m through the fishway is equivalent to individuals travelling a distance of 5.8–28.2 km in a lentic system at equivalent swimming speeds (Fig. 6). Thus, while energy expenditure may not be predictive of, or indeed limit, successful passage in lake sturgeon, the evidence presented here suggests that the energy expended during fishway passage may have unintended consequences on individual fitness.

Swimming speeds and corresponding U_g were slower when sturgeon were moving upstream through turning basins, and the corresponding COT through these sections was higher in comparison with regular basins. It is worth noting that the methods to determine distance travelled likely result in underestimates as they represent the minimum distance between two locations, and thus COT estimates may be artificially inflated, although path selection and the subsequent distance travelled by individuals through basins remains unknown. Previous studies have identified that the presence of turning basins increases passage failure and delays passage (Bunt et al., 2000; Silva et al., 2015; White et al., 2011), including for this species (Thiem et al., 2011). Webber et al. (2007) recommended the inclusion of lower-velocity areas between higher-velocity passage areas for white sturgeon. Such lower-velocity areas could be used for recovery from the measured metabolic acidosis associated with burst swimming through the higher-velocity areas (Cocherell et al., 2011). We identified that continuous anaerobic swimming was of short duration during passage through basins. Further, the proportion of time spent swimming anaerobically typically represented a small proportion of the total time spent swimming in the fishway and most likely occurred during passage through vertical slots, where velocities are highest. Similarly, Alexandre et al. (2013) identified that high U_s exhibited by Iberian barbell (*Luciobarbus bocagei*) typically occurred only through passage of submerged orifices in a pool-type fishway, and that U_{crit} was rarely exceeded. Hinch and Bratty (2000) found that sockeye salmon exhibiting hyper-activity by exceeding U_{crit} for more than 10 min continuously were more likely to exhibit fallback, although U_{crit} was never exceeded for this length of time in the present study. Further, Burnett et al. (2014) linked burst swimming in areas of high water velocities with delayed mortality in sockeye salmon. We do not advocate against low-velocity areas, but rather it appears that the heterogeneous nature of hydraulics in the basins of the vertical slot fishway studied here
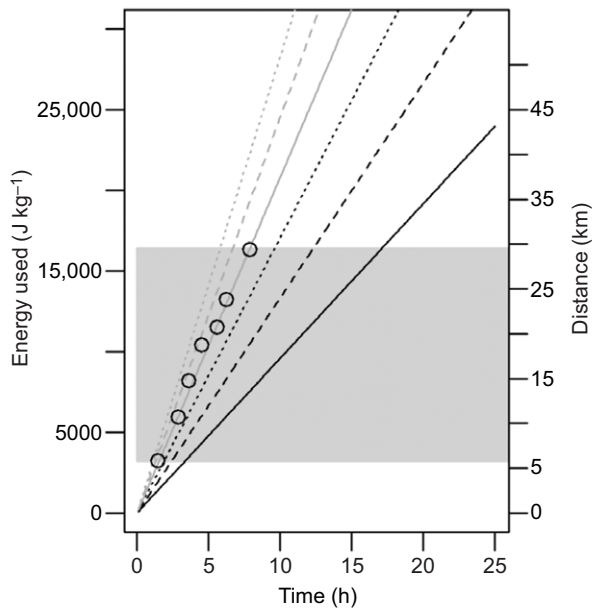
Fig. 6. Comparison of energy expenditure and corresponding distance travelled over time for lake sturgeon swimming in a lentic habitat at constant swimming speeds of 0.25 m s^{-1} (black solid line), 0.50 m s^{-1} (black dashed line), 0.75 m s^{-1} (black dotted line), 1.00 m s^{-1} (grey solid line), 1.25 m s^{-1} (grey dashed line) and 1.50 m s^{-1} (grey dotted line). The range of observations from the present study is indicated (grey shading), as well as specific values for successful fishway passage ($n=7$; black circles).

provides an adequate quantity of low-velocity refuges. Further, sturgeon are capable of station-holding to conserve energy in high-velocity areas (Adams et al., 2003; Geist et al., 2005). In terms of a time optimisation strategy, the absence of turning basins would be beneficial as the addition of large low-velocity regions appears to delay passage, presumably because of the absence of high velocity cues (Marriner et al., 2014). Indeed, the low-velocity range (0.51–0.68 m s^{-1}) recommended by Webber et al. (2007) exceeded that determined to be the threshold (0.45 m s^{-1}) attraction velocity to initiate upstream swimming in white sturgeon.

Lake sturgeon exhibited a range of U_s during fishway passage in this study. This is unsurprising given the range of water velocities likely encountered, although previous data indicate that even when faced with a constant water velocity, U_s also varies over short time scales (Thiem et al., 2015). In a theoretical simulation of the energetic cost of passage through a fishway by Pacific salmon (*Oncorhynchus* spp.), Khan (2006) assumed a constant U_s of 3 m s^{-1} regardless of the velocity encountered. A constant U_s represents a simplistic approach as it does not require any gait adjustment by the individual, although it results in constant changes in U_g based on the velocities encountered. In the present study, this would require that the U_s of any individual was greater than the highest water velocity (~1.7 m s^{-1} through vertical slots) to maintain an overall positive U_g and result in net upstream movement, resulting in U_{crit} being exceeded 100% of the time. Maintaining a constant U_s through varying water velocities likely represents a poor strategy, however, as distance in relation to endurance is not optimised (Castro-Santos, 2005). We were unable to establish whether lake sturgeon in the present study exhibited a distance optimising strategy, as the actual paths selected and water velocities encountered remain unknown, although adaptation of a random movement path scenario (McElroy et al., 2012) represents a potential solution.

For our study we assumed that purely aerobic metabolism of energy stores occurred during swimming by lake sturgeon. There was some evidence to suggest an occasional anaerobic contribution and thus our energy expenditure estimates are likely conservative. We used the proportion of time respective U_{crit} values were exceeded as an approximate indicator of the anaerobic contribution to swimming. Lake sturgeon rarely exceeded U_{crit}, and typically not for extended periods; however, anaerobic contributions to swimming and the corresponding energy expended can add substantial errors to energy budgets. Burgetz et al. (1998) identified that an anaerobic contribution to metabolism is required to support swimming at speeds as low as 70% of U_{crit} in rainbow trout (*O. mykiss*), corresponding to 1.48 body lengths s^{-1}. Using this information, the authors provide values that can be added as an additional anaerobic tax to total energy expenditure. For example, the anaerobic contribution can be as high as 205% of oxygen consumption for 30 min of swimming at 100% of U_{crit} when including the necessary post-swimming recovery phase (i.e. oxygen debt) (Burgetz et al., 1998). Similar values are not available for lake sturgeon, or any sturgeon species, in part because of problems associated with a lack of volitional high-speed swimming in swim tunnels and also the physical size of adults of most species. Accordingly, we used previously determined calibrations of U_s–ODBA based on volitional swimming of lake sturgeon in a large open-channel flume to generate U_s well above those previously determined from forced swimming, and more indicative of field estimates (Thiem et al., 2015). As a result, the $\dot{M}_{O_2}$–U_s relationship was borrowed from a previous study (McKinley and Power, 1992) and linearly extrapolated to the U_s observed in our calibration study. This requires a number of assumptions, and probably represents an underestimate of energy expenditure, particularly at higher U_s, yet this approach maximises the utility of available data.

We used animal-borne accelerometer data loggers in this study in an example application of fundamental science to inform an applied issue. The use of animal-borne accelerometers is rapidly increasing, and although applied applications are lagging, recent examples include determination of energy expenditure by fish in aquaculture to inform feed rations and stocking densities (Yasuda et al., 2012) and examination of locomotor impairment following a recreational fishing simulation (Brownscombe et al., 2013). Here, we provide evidence of the first use of this technology to inform water resource development and specifically fishway design. Although the differences in energy expenditure observed were not typically indicative of fishway passage success in lake sturgeon, we were able to quantify the energetic cost of passage. Considering that fishways should be designed so as to minimise energy expenditure (Castro-Santos and Haro, 2010), we identified that the absence of turning basins in the current fishway design would reduce passage time and correspondingly reduce energy expenditure. Given that lake sturgeon have likely evolved for short-distance migrations that are not typically energetically demanding, supported by evidence of a comparatively reduced ability for high-speed swimming, the energetic costs quantified here have potential fitness consequences.

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