

# Swimming performance of adult bighead carp *Hypophthalmichthys nobilis* (Richardson, 1845) and silver carp *H. molitrix* (Valenciennes, 1844)

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## Summary

Although the movement of invasive bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix*) in the Upper Mississippi River system is dependent on their ability to swim through its numerous lock-and-dams, the swimming performance of adults of these species is at present unknown. Using a large (2,935-L) mobile swim tunnel, the swimming performance of adult bighead and adult silver carp was quantified at water velocities that challenged them to exhibit either prolonged and/or burst swimming (76–244 cm/s) with fatigue times of less than 10 min. Simple log-linear models best described the relative swim speed to fatigue relationships for both species. Under these conditions, the swimming performances of adult bighead and silver carp were similar to several species of adult fishes native to the Mississippi River system, but relatively low (<3 total body lengths per second, TL/s) compared to previously studied juveniles and sub-adult bigheaded carps (3–15 TL/s). The decline in endurance with water velocity was three times greater in bighead carp (slope = -2.98) than in silver carp (slope = -1.01) and the predictive ability of the bighead model was appreciably better than the silver carp model. The differences in adult swimming performance between the two species were coincident with behavioral differences (e.g. breaching in silver carp but not in bighead carp). The swimming performance data of adult bighead and silver carp can now be used to evaluate whether their passage through man-made river structures including the gates of lock-and-dams in the Upper Mississippi River might be reduced.

## 1 | INTRODUCTION

Bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix*), collectively referred to as bigheaded carp, comprise one of the most invasive fish taxa introduced into European and North American inland waters (Savini et al., 2010; USFWS, 2012). In the United States, both species have spread rapidly throughout the Lower and Middle Mississippi River since being introduced in the 1970s, and if left unchecked could have adverse ecological and economic impacts in the Upper Mississippi River and Great Lakes (Sass et al., 2014; Schrank, Guy, & Fairchild, 2003). The current range of bigheaded carp extends as far north as Pool 18 near Burlington, Iowa in the

Mississippi River and Dresden Island Pool near Morris, Illinois in the Illinois River (USFWS, 2014). The 29 navigational lock-and-dam structures in the Mississippi River are already known to inhibit passage of native migratory fish (Knights, Vallazza, Zigler, & Dewey, 2002; Zigler, Dewey, Knights, Runstrom, & Steingraeber, 2003, 2004) and may also restrict movement of bigheaded carp by producing velocities through the gates that exceed the swimming abilities of these fish. To date, management decisions in the Mississippi River to control bigheaded carp passage have conservatively assumed that bigheaded carp swimming performance is in the same category as Pacific salmonids (*Oncorhynchus* spp.), based on their size and leaping ability (Stanley Consultants, 2011). If true, bigheaded carp should be readily passing

through most dams; however, the apparent rarity of bigheaded carp in the upper reaches of the Mississippi River and Illinois River suggests otherwise. The objective of this swim tunnel study was to address the knowledge gap between the presumed and actual swimming performance of adult bigheaded carps.

Fish swimming performance is often categorized by one of three modes: sustained, prolonged, and burst swimming (Beamish, 1978). Sustained swimming is aerobically fueled and can be maintained for indefinite periods of time (typically more than 200 min), albeit at slow speeds. Burst swimming is anaerobically fueled and while fast, is brief (<30 s). Prolonged swimming is the transition between sustained and burst swimming that is partly aerobic and partly anaerobic, and can be maintained for moderate periods of time (1–200 min). Depending on the species, prolonged swimming may not be distinguishable from burst swimming. Both burst and prolonged swimming ultimately cause fish to fatigue, which limits their endurance and terminates in exhaustion (inability to swim). All of these characteristics vary greatly by species (muscle type, body morphology) and size, as well as numerous other abiotic and biotic factors. The range of velocities through a typical gated spillway in a Mississippi River lock-and-dam is thought to be approximately 1.5–5 m/s (i.e. 2–7 total body lengths per second, TL/s in large fish) and extend as far as 35 m downstream from the gates (Markussen & Wilhelms, 1987; Zigler et al., 2004), which would likely require fish to employ prolonged and burst swim speeds to pass. Accordingly, quantifying the swimming performance of adult bigheaded carp at prolonged and burst swimming speeds would be useful to understanding whether, how, and when fish can pass lock-and-dams and how this might be managed.

Both bighead and silver carp employ carangiform locomotion (Breder, 1926), a type of swimming in which body and caudal fin undulations across a third-to-half of their body length generates forward thrust that typically translates to higher burst swimming speeds than those seen in more undulatory swimmers (Sfakiotakis, Lane, & Davies, 1999). Both adult bighead and silver carp typically spend the majority of their time in slow moving waters although they seem to spawn in more turbulent areas (Calkins, Tripp, & Garvey, 2012; DeGrandchamp, Garvey, & Csoboth, 2007). Hoover, Southern, Katzenmeyer, and Hahn (2012) examined the swimming performance of juvenile and sub-adult bigheaded carps and observed that bighead carp swim speeds exceed those of silver carp across a range of sizes (TL 36–334 mm), despite having a less streamlined morphology. However, adult bigheaded carp can reach sizes four times the size of the small fish that Hoover et al. (2012) studied [i.e. up to 1,350 mm TL for bighead (Schrank & Guy, 2002) and 900 mm TL for silver carp (Seibert et al., 2015)], and swimming performance data cannot be extrapolated from small fish to large fish because swim speeds relative to total length typically change with size (Videler & Wardle, 1991). The exact relationship between relative swimming speed and size for both adult bighead and adult silver carp is currently unknown.

Swimming performance of fish is typically determined using laboratory swim tunnels in which fish are exposed to a range of water velocities so that endurance (time-to-fatigue) can be determined (Brett, 1964). Tests conducted in the field with mobile swim

tunnels are advantageous because they minimize confounding influences from acclimatization, laboratory conditions, and water quality (Ellerby & Herskin, 2013). Although rarely used because of their high expense, mobile swim tunnels have been effective at measuring swim speeds for a variety of large riverine and marine fishes (Farrell et al., 2003; Graham, DeWar, Lai, Lowell, & Arce, 1990; Jones, Kiceniuk, & Bamford, 1974; Schmulbach, Tunnink, & Zittel, 1982). For the present experiments with large adult bigheaded carps, a custom-built 2,935-L mobile swim tunnel was used to test fish in the field. Similar in concept to a previously built 1,200-L laboratory swim tunnel (Hoover, Collins, Boysen, Katzenmeyer, & Killgore, 2011), this new swim tunnel was portable and larger than a 2,400-L ocean-going tunnel used for sharks (Graham et al., 1990), perhaps making it the largest ever used.

The study was designed to allow for direct comparisons of swimming performance and behavior of adult bighead and adult silver carp at prolonged and burst swim speeds to explore the possibility of hydraulic containment of invasive bigheaded carp at lock-and-dam structures. Specific objectives included determining: (i) the swimming performances of the adult bighead and silver carp and whether these species have different swimming abilities; (ii) if, and to what extent, body length, gender, and water temperature influence carp swimming performance; and (iii) how bigheaded carp swimming performance compares with that of fish native to the Mississippi River system as well as smaller conspecifics, and how that understanding might then lead to the possibility of managing the spread of these invasive carps.

## 2 | MATERIALS AND METHODS

### 2.1 | Test apparatus

Swim tests were conducted in a specially designed 2,935-L mobile Brett-type swim tunnel (Fig. 1). The tunnel was mounted on a 5.5 × 2.0 m trailer and pulled with a truck so that fish could be tested near their point of capture. The trailer was equipped with four leveling jacks, which enabled the vertical position of the tunnel to be adjusted. A 10 horsepower Varidrive US Electrical Motor, capable of 1,740 rpm, 678 g centrifugal force, drove a stainless steel shaft attached to a



**FIGURE 1** Mobile swim tunnel with adult bighead carp *Hypophthalmichthys nobilis* inside

40 cm diameter (40 cm pitch), three-blade propeller, which provided thrust. The motor could be run at shaft speeds of 50–750 rpm and direction of flow could be reversed. The tunnel was made from thermoplastic components, principally Lexan, reinforced with stainless steel frames and perimeters. Components consisted of a 2,029-L test chamber (2.4 m L × 0.9 m W × 0.9 m H), and a 44 cm diameter, 907-L, circulation tube that received outflow from the rear of the tank and propelled it back into the front of the tank as inflow. The propeller was housed in the bottom of the circulation tube and could be viewed through a polycarbonate window. A hinged lid was attached along the length of the tank and secured using pivoting aluminum lock-downs at each end while C-clamps were used to tightly seal the lid against a gasket along the top edges of the tank and minimize water loss. Polycarbonate grids with pores (1.3–5.0 cm) functioned as collimators (flow filters) reducing turbulence, and were positioned at the front and rear ends of the tank. Slots positioned 30 cm from the inflow and outflow ports allowed additional collimators to be inserted to further reduce turbulence, but restricted the working section to 1,525-L. The working section of tank could be used with or without a polycarbonate box that created boundary-layer flow along the bottom and reduced waves at the surface. This box was a double platform with a lower platform (false bottom) and upper platform (false top), having the same footprint as the working section of the tank. Spacers attached to the lower platform elevated it 23 cm off the bottom and submerged the upper platform 23 cm below the lid. The false top and bottom created a functional working section volume of 934-L.

The tunnel was calibrated three times corresponding to its three test configurations with no insert, a false bottom and top, and false bottom only (see below). Velocity was measured in the middle of the tank at three vertical positions (20% from surface, 50% from surface, and 80% from surface), at three distances along the length of the tank (at inflow, 1 m from inflow, at outflow), resulting in nine points for each velocity and 72 points for each configuration for each of eight motor speeds (50–700 rpm). At each point 5–10 measurements were taken using a Marsh-McBirney Flo-Mate 2000 with the probe mounted on a wading rod. All measurements were taken with the tunnel lid closed and the tank filled to the lid. Because values for the mid-length vertical profile were intermediate between those of the inflow and outflow profiles and were more uniform, they were averaged and the mean value was used. Simple linear regressions were performed with motor speed as independent variable and mean water velocity as dependent variable resulting in the following rating curves:

$$\text{Velocity}_{\text{No Insert}} = 0.3279 [\text{rpm}], R^2 = .9982$$

$$\text{Velocity}_{\text{False Top and Bottom}} = 0.3329 [\text{rpm}], R^2 = .9973$$

$$\text{Velocity}_{\text{False Bottom Only}} = 0.3052 [\text{rpm}], R^2 = .9950$$

## 2.2 | Study site and field collection

This study took place at Forest Home Chute (32°45.340'N; 91°01.440'W), Warren County, Mississippi (Pongruktham, Ochs, & Hoover, 2010), a long, narrow river scar that parallels the main channel of the Mississippi River just north of river km 724–729. At

low river stages, it functions as a backwater lake and at high river stages as a secondary channel. The reach of Forest Home Chute sampled is 3.5 km long and is the middle section of the chute. More than 20 species of fish have been documented from the middle reach and both bighead and silver carps are significant components of the fish community (Varble et al., 2007). We tested fish in the spring (17–31 March 2015) and summer (04–19 June 2015). Water was moderately conductive ( $373 \pm 26$  and  $385 \pm 8$   $\mu\text{S}$ , respectively), slightly alkaline ( $7.76 \pm 0.26$ ,  $8.30 \pm 0.36$  pH), and normoxic ( $10.6 \pm 2.3$ ,  $9.2 \pm 1.7$  mg/L). Turbidity was higher and water temperature lower in March ( $24.1 \pm 15.8$  NTU,  $12.1 \pm 1.4^\circ\text{C}$ ) than in June ( $5.0 \pm 1.9$  NTU;  $27.5 \pm 0.9^\circ\text{C}$ ). Channel depth was 7–10 m in March, 5–6 m in June.

The test fish were collected in Forest Home Chute and transported to the swim tunnel, which was located on shore. Carp were collected each sampling period by a commercial fisherman using wide-mesh (7.5–12.5 cm) surface gillnets of variable length. Surface gillnets were used to avoid hypoxia at greater depths. Gillnets were monitored during sets and every 30 min thereafter. Time of capture was noted for each fish while being removed from the netting, then lifted into the boat and placed in an aerated 350-L live-well filled with fresh river water and immediately taken to shore. Fish were removed by hand from the live-well, wrapped in a soft nylon body sling, hand-carried to the swim tunnel, and immediately placed in the tank by unrolling the sling underwater. If more than one fish was caught, 1–2 representatives were selected for later tests, tethered in shady water using waxed nylon twine looped snugly around the caudal peduncle. If more than three fish were caught, all extra fish were immediately released. Average time from capture to testing was 49.3 min for bighead carp and 62.0 min for silver carp.

The swim tunnel was operated at a single shoreline position approx. 30 m distant from the water's edge. Prior to tests each morning, the tunnel was filled with untreated well water that was circulated at 35 cm/s, treated with API Stress Coat (Mars Fishcare North America, Inc., Chalfont, PA), and aerated with compressed oxygen. Throughout each day of testing, water was partially exchanged and re-aerated to maintain normoxia ( $>7.00$  mg/L), pH ( $>7.3$ ), and clarity ( $<5$  NTU). Test temperatures varied daily and throughout the day during each period but were cooler in March ( $13.1$ – $19.3^\circ\text{C}$ ) than in June ( $20.8$ – $25.9^\circ\text{C}$ ). After completion of tests each evening, the tunnel was drained.

## 2.3 | Testing

Adult carp of both species were tested over a range of constant water velocities (75–244 cm/s) with several replicates for each water velocity. For a test, a freshly captured carp was carefully placed into the working section of the swim tunnel and allowed to habituate to a water velocity of 7 cm/s for 10 min, then 28 cm/s for another 10 min, and lastly 42 cm/s for another 10 min. At the end of the habituation period, water velocity was increased over a 2–3 s interval to one of 12 test velocities (76–244 cm/s), and the fish was observed until it fatigued. Each fish was tested only once. During testing, three aspects of swimming were evaluated: (i) rheotaxis—head-first orientation into the direction of water flow, (ii) endurance (or time-to-fatigue)—length

of time that a fish was able to maintain a position in flowing water, (iii) behavior—mode of locomotion used to swim forward or maintain station. If a fish failed to exhibit rheotaxis, it was given 1–2 min rest before flow was again increased to the test velocity, but if after multiple attempts it still did not exhibit rheotaxis, or if it exhibited behavior atypical for the species, it was considered a “non-performer”. Most fish, however, were performers and trials lasted until the fish was exhausted (i.e. became impinged on the downstream grid twice) or 60 min had passed. If exhausted, flow was reversed for 10 s, and the fish was allowed to re-orient for 10 min at 7 cm/s. If the fish was unable to continue swimming, the test was ended and the time of initial impingement recorded. If the fish resumed swimming, the test was restarted and continued until the fish was impinged a second time and unable to extricate itself and the time was then recorded as the endpoint. If the second time-to-fatigue was less than first, the original endpoint was accepted. If the second time-to-fatigue was greater than the first, the fish was classified as a “non-performer”. A total of 80 adult carp were tested including 17 adult bighead carp (760–1040 mm TL, 5.2–12.3 kg, and condition factor,  $K_f = 0.98$ –1.60) and 63 adult silver carp (535–921 mm TL, 1.5–9.0 kg, and  $K_f = 0.85$ –1.30). No fish died as a result of testing. After testing, carp were euthanized with MS-222 and total length and weight recorded, as well as any morphological anomalies (e.g. scarring, missing fins, etc.). Gonads were examined to establish gender.

Initial trials (17/80) at slower speeds were successful without the box insert, but at higher motor speeds ( $\geq 600$  rpm) surface and bottom velocity shadows, or “dead zones”, were found near the inflow and adjustments were made. Subsequent trials (60/80) were conducted using only the false bottom insert, which reduced dead zones while promoting consistent normal behavior and post-test recovery, although three trials also used the false top insert. Black plastic sheeting overlaid on the surface of the lid promoted relaxed swimming and eliminated strikes against the tank lid by leaping silver carp.

## 2.4 | Data analysis

Test speeds, in cm/s, were converted into relative swim speeds, in total lengths/second (TL/s), by dividing absolute water velocity by total length of fish. Endurance (time to fatigue) was transformed using natural logarithm. Data were compiled and analyzed in SAS<sup>®</sup> 9.3 using General Linear Models (SAS Institute, Cary, NC). Non-performers, fish that exhibited conspicuous stress, trials with equipment failure, and fish that did not fatigue were excluded from analyses.

To relate swimming endurance to swim speed (water velocity), we developed three performance models for each species: broken-stick, log-linear (sensu Castro-Santos, 2005), and log-linear plus temperature (sensu Peake, Beamish, McKinley, Scruton, & Katapodis, 1997). The broken-stick model assumed that prolonged and burst swim speeds are discrete responses represented by two different lines with an inflection point and distinct slopes at slower and faster ranges of swim speed. The log-linear model assumed that prolonged and burst speeds are a graded continuous response represented by a single line with no significant inflection or change in slope at slower and faster ranges of

swim speed. Evidence for a mode shift between prolonged and burst swimming in the broken stick model was tested using the model:

$$\text{Ln}[\text{Endurance}] = \beta_0 + \beta_1 [\text{TL/s}] + \beta_2 [x_1] + \beta_3 [x_1] [\text{TL/s}],$$

in which the first and second terms represent the intercept and slope for a line for prolonged swimming, while the third and fourth terms are the adjustment to the intercept and slope for a separate line for burst swimming. For swim speeds considered prolonged,  $x_1 = 0$ ; for burst speeds  $x_1 = 1$ . The model was run iteratively, incrementing maximum prolonged swim speed by 0.01 TL/s. The log-linear model followed the form:

$$\text{Ln}[\text{Endurance}] = \beta_0 + \beta_1 [\text{TL/s}].$$

A third type of model, which evaluated the influence of water temperature on the log-linear model followed the form:

$$\text{Ln}[\text{Endurance}] = \beta_0 + \beta_1 [\text{TL/s}] + \beta_2 [\text{TEMP}].$$

For all three models, fit of model residuals to a normal distribution was tested using Shapiro-Wilks statistic for which  $W > 0.95$  indicates high fit,  $W = 0.90$ –95 indicates a good fit, and  $W < 0.90$ , a poor fit. Magnitude of  $W$  is generally considered a more reliable indicator of fit than tests of significance, which can be strongly influenced by minor departures of kurtosis and skew (Douglass & Douglass, 2004). Predictive power of the respective models, and individual regression coefficients within each of those models, were quantified as  $R^2$  and  $p$  values. Model selection was based on the corrected version of the Akaike Information Criterion (AICC) to select the most parsimonious model (Castro-Santos, 2005). Analysis of covariance (ANCOVA) was used to compare log-linear model coefficients between bighead and silver carp.

Once bighead and silver carp data were evaluated, their swimming performance was qualitatively compared with other river fish and juveniles of the same species. First, swim tunnel data were tabulated for other comparably sized Mississippi River fishes including lake sturgeon (*Acipenser fulvescens*), shovelnose sturgeon (*Scaphirhynchus platyrhynchus*), and smallmouth buffalo (*Ictiobus bubalus*). Swim tunnel data of large (>500 mm TL) sockeye salmon (*Oncorhynchus nerka*) were also tabulated to address the assumption that Pacific salmonids may be used as models for estimating bigheaded carp swimming performance. Second, to evaluate the influence of fish size on swimming performance, endurance data for sizes classes of bigheaded carp previously studied (Hoover et al., 2012) were plotted with the adult carp data from this study. Data were plotted using total length as the independent variable and relative swim speed (TL/s) as the dependent variable. Juvenile carp swim speed values were calculated by dividing the limits for prolonged (1 min) and burst (0.1 min) swimming modes by the range of fish lengths tested (e.g. for a given TL there are two swim speed data points).

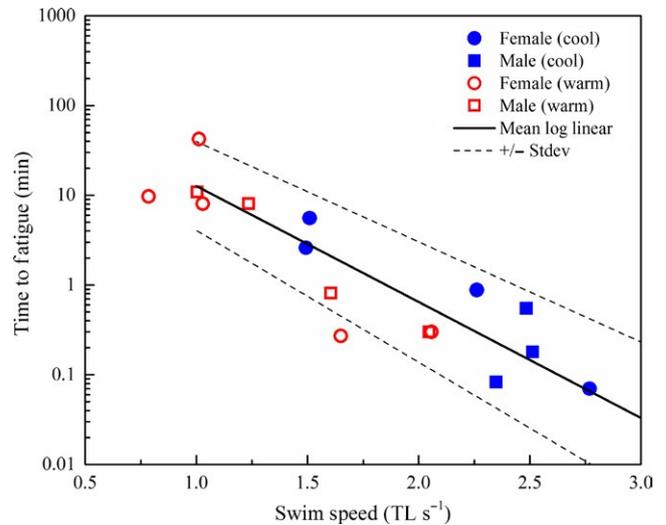
## 3 | RESULTS

All 17 adult bighead carp were performers that exhibited typical and regular swimming movements and their data were used in analyses.

Swimming behavior was dominated by free-swimming in the water column with brief bouts of occasional tail-bracing observed prior to fatigue. The log-linear model fit the bighead carp data best and was a slightly better fit than the broken-stick model for which the mode shift and interaction term were both non-significant, making the model less informative (AICC = 59.40) than the simpler log-linear model (AICC = 55.90; Table 1). The slope of the swim speed to fatigue line was  $-2.98$  and had low point scatter ( $R^2 = .78$ ) for the log-linear model. Adding water temperature as a co-variate to the log-linear model increased  $R^2$  by 7% but was less informative (AICC = 58.66) than the log-linear model. Residuals for both log-linear and log-linear plus temperature models were distributed normally ( $W > 0.95$ ). Estimators of water temperature for bighead carp were negative, indicating that endurance was higher at cooler temperatures. For bighead carp, 94% (16/17) of all observations were within the prediction limits of the log-linear model; males and females were equitably distributed above, on, and below the regression line; and data for warm water tests predominated (6/9) below the line, supporting a negative effect of temperature on endurance (Fig. 2).

For adult silver carp, 43 of 63 individuals performed while exhibiting typical and regular swimming movements and were used in the analyses. Of fish included, swimming behavior was again characterized by free-swimming in the water column with brief bouts of occasional tail-bracing observed prior to fatigue. The broken-stick model was significant and slightly more informative (AICC = 126.85) than the simpler log-linear model (AICC = 129.77; Table 1), but the slope of the burst speed line was slightly positive, thus the log-linear model was considered the best. The slope of the swim speed to fatigue line was three times less than bighead carp at  $-1.01$  for the log-linear

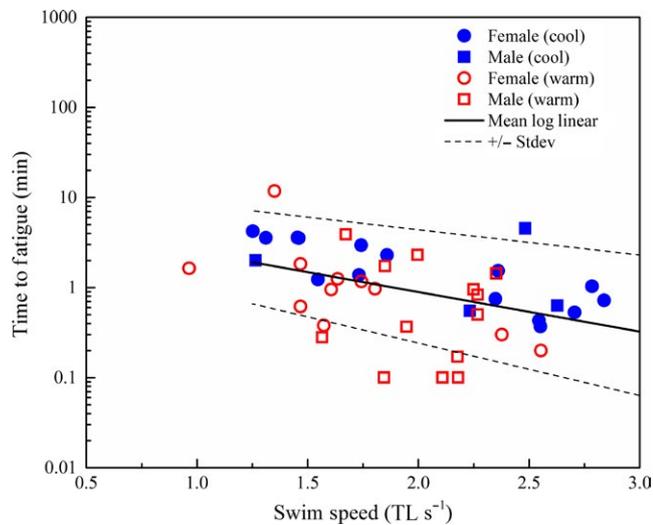
model (ANCOVA:  $F = 14.34, p < .001$ ). The point scatter was greater for silver carp ( $R^2 = .19$ ), which indicated greater predictive power of the bighead carp log-linear model. Adding water temperature as a co-variate to the log-linear model increased  $R^2$  by 9% but was less informative (AICC = 131.90) than the log-linear model. Residuals for both log-linear and log-linear plus temperature models were normally distributed ( $W > 0.95$ ). Estimators of water temperature for silver carp were negative, indicating that endurance was also higher at cooler



**FIGURE 2** Log-linear model for bighead carp *H. nobilis* ( $n = 17$ ) swimming performance. Boundaries on model are means  $\pm$  SE. Individual data points coded to indicate water temperature (blue = cool water [13.1–19.3°C], red = warm water [20.8–25.9°C]), and gender (o for female, □ for male)

**TABLE 1** Broken-stick, log-linear, and log-linear plus temperature models for swimming endurance of adult bighead and silver carp

Species	Model	Effect	Estimate	Standard Error	df	t-, F value	Pr > t, F	R <sup>2</sup>	Pr > t, F	AICC
Bighead carp	Broken-stick	$\beta_0$	6.746	1.179	13	5.72	<0.0001	.809	<0.0001	59.40
		$\beta_1$	-3.981	0.865		-4.60	0.0005			
		$\beta_2$	-3.178	4.708		-0.68	0.5114			
		$\beta_3$	1.889	2.075		0.91	0.3794			
	Log-linear	$\beta_0$	5.521	0.733	15	7.53	<0.0001	.782	<0.0001	55.99
		$\beta_1$	-2.978	0.406		-7.34	<0.0001			
		$\beta_2$	-0.137	0.054		-2.52	0.0246			
	Log-linear + temperature	$\beta_0$	9.139	1.569	13	5.83	<0.0001	.850	<0.0001	58.66
		$\beta_1$	-3.479	0.401		-8.67	<0.0001			
$\beta_2$		-0.137	0.054		-2.52	0.0246				
Silver carp	Broken-stick	$\beta_0$	3.583	1.221	39	2.93	0.0056	.282	0.0044	126.85
		$\beta_1$	-2.061	0.749		-2.75	0.0090			
		$\beta_2$	-6.429	3.061		-2.10	0.0422			
		$\beta_3$	3.009	1.370		2.20	0.0341			
	Log-linear	$\beta_0$	1.916	0.654	41	2.93	0.0055	.192	0.0033	129.77
		$\beta_1$	-1.015	0.325		-3.12	0.0033			
	Log-linear + temperature	$\beta_0$	4.009	1.104	39	3.63	0.0008	.286	0.0012	131.90
		$\beta_1$	-1.193	0.319		-3.74	0.0006			
		$\beta_2$	-0.088	0.038		-2.30	0.0270			



**FIGURE 3** Log-linear model for silver carp *H. molitrix* ( $n = 43$ ) swimming performance. Boundaries on model are means  $\pm$  SE. Individual data points coded to indicate water temperature (blue = cool water [13.1–19.3°C], red = warm water [20.8–25.9°C]) and gender (o for female,  $\square$  for male)

temperatures (Fig. 3). For silver carp, 79% (34/43) of observations were within prediction limits of the model; females and males were equally distributed above, on, and below the regression line; warm water tests again predominated (14/24) below the line, indicating a possible negative effect of warm water temperature on endurance (Fig. 3). Exclusion of 20 silver carp from the analysis was due to non-performance (8/20), conspicuous stress (7/20), equipment failure (1/20), and lack of fatigue (4/20). Notably, all four silver carp that did not fatigue (trials terminated after 60 min) had been tested at relatively slow speeds ranging from 76 to 107 cm/s (0.9–1.4 TL/s).

Tabulating data from fish native to the Mississippi River, adult bighead and silver carp swim speeds were greater than that of lake sturgeon but less than those of shovelnose sturgeon and smallmouth buffalo (Table 2). Bigheaded carp swim speeds were less than half the swim speeds of sockeye salmon at the same endurance times (Table 2).

**TABLE 2** Predicted water velocities corresponding to three different endurance times based on swimming performance models for species of similar sizes

Species	Mean Total Length (mm)	Water Velocity for Endurance (TL/s)			Reference
		>10 min	1 min	0.5 min	
Bighead carp	908	1.08	1.85	2.09	This study
Silver carp	801	<1.25	1.89	2.57	This study
Lake sturgeon <sup>a</sup>	1,200	1.03	1.31	1.39	Peake et al. (1997)
Shovelnose sturgeon <sup>b</sup>	579	1.77	NA	NA	Hoover et al. (2011)
Smallmouth buffalo <sup>b</sup>	311	2.00	NA	NA	Schmullbach et al. (1982)
Sockeye salmon <sup>c</sup>	541	3.98	4.25	>4.25	Brett (1982)

<sup>a</sup>Data for lake sturgeon derived from a model that used multiple-regression between water velocity, water temperature, and time-to-fatigue at a water temperature of 14°C.

<sup>b</sup>Data for shovelnose sturgeon and smallmouth buffalo are mean 15 min critical swim speeds (i.e. maximum cumulative water velocity at which swimming for 15 min was predicted).

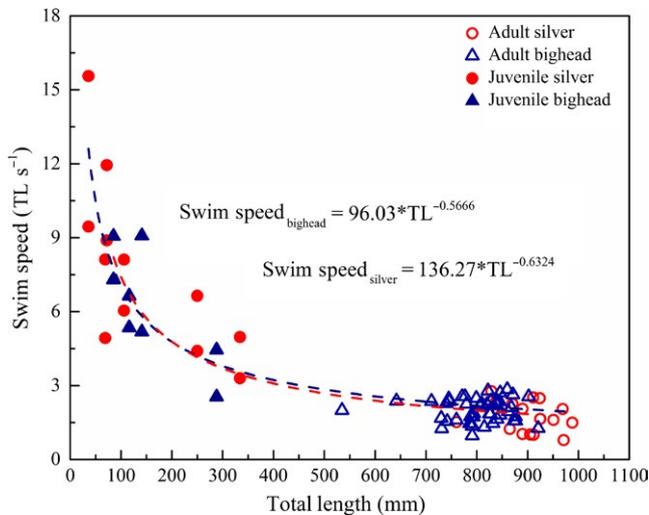
<sup>c</sup>Data for sockeye salmon based on a log-linear relationship between water velocity and time-to-fatigue at a water temperature of 18°C.

When adult bighead and silver data from this study were combined with data from juvenile bigheaded carps previously tested, a power-law decay (with exponents of  $-0.56$  and  $-0.63$ ) could be fit to describe the reduction in relative swim speed with size (Fig. 4). Swim speeds declined from approx. 3–15 TL/s for juvenile bigheaded carps to 1–3 TL/s for adults. Similarly, swim speeds declined from approx. 3–9 TL/s for juvenile silver carp to 1–3 TL/s for adults. Across the size range of adult carp of both species, the response of relative swim speed to length was asymptotic.

## 4 | DISCUSSION

Adult bighead and silver carp exhibited regular and typical swimming movements in a large outdoor swim tunnel. While adult bighead carp showed an ability to swim for about 1 min at 1.85 TL/s (168 cm/s) and about 0.5 min at 2.09 TL/s (189 cm/s), adult silver carp swam about 1 min at 1.89 TL/s (151 cm/s) and about 0.5 min at 2.57 TL/s (206 cm/s). These swim speeds are comparable to three fish species native to the Mississippi River, but far lower in magnitude than those for sockeye salmon (Table 2). Thus Pacific salmonids are poor models for bigheaded carp swimming abilities. Differences between adult bighead and silver carp were evident. The bighead carp had a more pronounced decline in endurance with increasing water velocity than did silver carp. The swimming performance of adult bighead carp was also less variable than that of silver carp. This is consistent with field observations of brief high burst speeds and occasional breaching by silver carp as well as morphological variation (Parsons, Stell, & Hoover, 2016). Together, these swim performance data could be used to evaluate if and how adult bighead and silver carp swim through spillway gates in the Mississippi River lock-and-dams and whether changes to gate operation could hydraulically contain both species.

Log-linear models of both bighead and silver carp best fit our data. Although water temperature was a statistically significant covariate, it provided only marginal improvement in the overall model for bighead and silver carp. The log-linear models were similar in form (low slope,



**FIGURE 4** Relationship of swim speed (TL/s) to total length for juvenile, sub-adult (Hoover et al., 2012), and adult silver ( $n = 43$ ) and bighead carp ( $n = 17$ ). Equation and correlation of least squares for each line are provided

moderate point scatter) to those developed for other species of pelagic planktivores with cruiser morphology, like alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), but were conspicuously lower in magnitude (Castro-Santos, 2005). The measured top-end speeds of adult bigheaded carps of  $\sim 2.8$  TL/s, seemingly representative of burst swimming, are well below the generally assumed maximum burst speed of 10 TL/s for fish (Videler & Wardle, 1991). It also falls well below the maximum burst speed of  $\sim 15$  TL/s previously measured for small ( $< 250$  mm TL) juvenile bighead and silver carp (Hoover et al., 2012; Fig. 4). The relatively slow adult swim speeds documented in this study are counter to perceptions of bigheaded carp as powerful and swift swimmers. Although it also falls below estimates of maximum swim speeds for silver carp from a video-based study of leaping fish (Parsons et al., 2016), such high speeds can easily be accommodated by our models by extrapolating the regression line and prediction boundaries out to a time-to-fatigue less than 1 s. In sum, these data strongly suggest that the swimming performance of adult bigheaded carp is rather typical of other large river fishes.

Adult silver carp exhibited slightly higher endurances than adult bighead carp at higher swim speeds but were also more variable. Silver carp are more sensitive to stress than bighead carp and jump, perhaps explaining the much greater variation in silver carp data. In contrast, the bighead carp data were more tightly clustered. If most upstream passage occurs through the spillway gates and not through the lock chamber, as suggested by telemetry data in the Middle Mississippi River (Tripp, Brooks, Herzog, & Garvey, 2014), the fact bighead carp grow larger than silver carp and may yet obtain faster absolute swim speeds might partially explain why few, but mostly large bighead carp are at present found in the Upper Mississippi River above prominent lock-and-dams such as Lock and Dam #5 (MNDNR, 2015). Alternatively, bighead carp may have a more extensive geographic distribution upriver and are available to colonize pools whereas silver carp do not.

Experiments using large fish in enclosed swim tunnels are imperfect, but several factors suggest that our conclusion (i.e. bigheaded carps are average swimmers with relatively low endurance at burst swim speeds) is parsimonious. First, great care was taken in collecting and testing experimental fish and the largest mobile swim tunnel ever employed in the field was used. Notably, no carp died and few showed signs of stress. Second, each fish was re-evaluated after testing to verify initial trial endpoints and fatigue. Third, data from all non-performers were excluded because this would have negatively biased results. Similarly, data from fish that did not fatigue were excluded because they were tested at slow speeds that did not require prolonged or burst swimming. Lastly, several statistical models were evaluated to identify the best one.

One possible explanation for the failure of bigheaded carps to colonize pools of the Upper Mississippi River after their establishment in the Lower and Middle Mississippi River may be that they struggle to swim through the rapidly flowing waters, which pass through the numerous gates that comprise Mississippi River lock-and-dams. If true, then the upstream movement of bigheaded carp might be further impeded by adjusting gate operation, effecting a type of hydraulic containment. Existing data on fish passage and water flow, while limited, support this possibility. For example, the head differential at Lock and Dam #8 (Genoa, Wisconsin, USA) at present exceeds 1 m 90% of the year, and by our calculations generates a uniform jet of water with velocities  $> 4.5$  m/s, a swimming speed that a large 900 mm TL silver carp can only maintain for 2.5 s. Once water velocity is factored in, the distance such a large silver carp can cover is likely to be  $< 1$  m, which would be insufficient to pass through the gates at this particular structure and hydraulic condition. Although these calculations only consider flow fields directly beneath the gates, which is relatively uniform but spatially limited, flows further downstream of the gates are turbulent with eddies that may provide fish a low velocity pathway up to and possibly through the dam. However, data are very limited. Spatially and temporally detailed velocity data obtained through computational fluid dynamics models are now urgently needed to better evaluate if and how bigheaded carp might pass through the variable flows near gates of individual lock-and-dam structures under different flow regimes. This work is now underway.

Alternative pathways for carp passage such as human assisted dispersal (i.e. carp minnows used as bait; Conover, Simmonds, & Whalens, 2007), and possible passage of carps through lock chambers should be factored in. Initial fish tracking data suggest that bigheaded carp do not routinely exploit locks (Tripp et al., 2014), but further study is needed. However, if warranted, bigheaded carp passage through locks could be eventually addressed using behavioral deterrents given the relatively small size and number of such structures (Noatch & Suski, 2012; Zielinski & Sorensen, 2016). Future study should ideally address passage of native fishes. In sum, our study demonstrates that the swimming abilities of adult bigheaded carps appear rather typical of many other large river fishes and that with further study their swimming performance, and associated behaviors, could be exploited to impede the upstream invasion of this invasive genus through some Mississippi River lock-and-dams.

## ACKNOWLEDGEMENTS

Fish were collected by W.E. Lancaster under scientific collecting permit # 1205141, Mississippi Department of Wildlife Fisheries and Parks. Assistance in the field was provided by J.A. Collins, S.G. George, N.M. Hahn, A.W. Katzenmeyer, K.J. Killgore, B.R. Lewis, and W.T. Slack. Site access and logistic support were provided by property owners Wade and Betsy Creekmore. Statistical analyses and advice on model interpretation were provided by C.E. Murphy. Handling of fish was in accordance with experimental protocol # EL-5036-2015-1, Field Studies of Swimming Performance of Large Riverine Fishes, approved by the US Army Engineer Research and Development Center Environmental Laboratory (ERDC-EL) Institutional Animal Care and Use Committee (IACUC) which is accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care International (AAALAC). This study was funded by the Minnesota Environmental and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources (LCCMR). Permission to publish was provided by the Chief of Engineers.

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