# Swimming performance and behaviour of bighead carp (*Hypophthalmichthys nobilis*): Application to fish passage and exclusion criteria

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## Abstract

The bighead carp (*Hypophthalmichthys nobilis*) is one of the most commercially important freshwater fish species in China, but their abundance has declined considerably in recent decades, partly due to river regulation. In other countries it is invasive, posing an ecological and economic threat. To improve fish pass effectiveness at impediments to migration in its native range, and create velocity barriers to reduce range expansion where it is invasive, an improved understanding of swimming ability and behaviour is needed. The burst, prolonged, and sustained swimming performance of juvenile bighead carp were quantified experimentally through constant acceleration trials (*U*max), fixed velocity tests, and volitional passage efficiency trials through three consecutive constrictions. The effects of fork length (*FL*), temperature, swimming speed and method (swim chamber / open channel flume section) on endurance in fixed velocity trials were evaluated. The utilisation of low velocity areas close to the flume edge and floor at different mid-channel velocities was also explored. The mean sustained swimming speed in endurance tests was 3.84 *FL* s-1 (range equivalent to 0.37-0.78 m s-1), and burst speeds reached 12.78 *FL* s-1 (up to 1.22 m s-1 for larger fish). The mean *U*max was 6.81 *FL* s -1 (0.51 m s-1). In fixed velocity trials, method did not influence endurance and fish rarely utilised low velocity areas in the corners of the flume when water velocity exceeded sustained swimming ability. Passage efficiency decreased at successive flume constrictions, possibly indicating a poor repeat burst swimming performance. Field validation is required to verify wild bighead carp behaviour and passage in the hydraulic conditions created by fish passes.

**Keywords:** Asian carp; dams; migration barriers; invasive control; performance methodologies.

## 1. Introduction

Bighead carp (*Hypophthalmichthys nobilis*), silver carp (*H. molitrix*), grass carp (*Ctenopharyngodon idella*) and black carp (*Mylopharyngodon piceus*) (herein collectively referred to as Asian carp) are the most commercially important freshwater fish species in China, particularly in the Yangtze River basin. They contributed 60% to China’s freshwater fisheries catch in the 20th century (Wu *et al.*, 1992) and 80 to 90% of the mid Yangtze River catch in the 1960s (Chen *et al*., 2004). Although commercial harvest continues, recruitment and catch has declined considerably (Liu *et al.*, 2004; Duan *et al*., 2009; Yi *et al*., 2010), contributing only 0.52 to 5% of the mid Yangtze catch in the 1990s (Chen *et al*., 2004). The decline in recruitment is likely a result of numerous pressures, including overfishing, pollution, land reclamation, and construction of dams and sluice gates (Xie and Chen, 1999; Fu *et al.*, 2003; Yi *et al*., 2010). Impoundments have flooded spawning grounds, altered flow and temperature regimes, and caused longitudinal and lateral habitat fragmentation (Jennings, 1988; Wei *et al*., 1997; Duan *et al.*, 2009). Larval abundance of Asian carp at Sanzhou on the Yangtze River decreased from between 1.9 and 3.6 billion between 1997 and 2002, to 0.34 billion in 2004 and 0.11 billion in 2005, following flooding of spawning grounds due to the construction of the Three Gorges Dam (Duan *et al*., 2009). After spawning, the eggs and larvae drift downstream and juveniles move to side channel rearing habitat and lakes (Jennings, 1988; Hu *et al*., 2015). This lateral migration has been restricted by widespread sluice gate installation for water conservation projects and all lakes, except Dongting and Poyang, have been isolated from the main Yangtze River channel (Fu *et al*., 2003; Chen *et al*., 2004). Sluice gates proposed for Poyang Lake outlet further threaten the sustainability of these potamodromous fish, unless effective mitigation is provided (Hu *et al*., 2015).

Fish passes are increasingly being considered at new barriers in China to mitigate for impeded migration (Shi *et al.*, 2015). Evaluation of their efficiency is rare (see Zhili *et al.*, 1990 for exception), but anecdotal evidence suggests many old structures were ineffective because they were based on Western designs not developed for Asian species (Dudgeon, 1995; Dudgeon, 2005; Fu *et al*., 2003; Zheng *et al.*, 2010). Although a range of variables contribute to determine fish pass efficiency, including location of the fish pass and barrier and watercourse characteristics (reviewed in: Clay, 1995; Marmulla, 2001; FAO and DVWK, 2002), the hydraulic conditions at the entrance and within a fish pass can have a large impact on passage success (reviewed in: Larinier, 2002; Castro-Santos and Haro, 2008). Therefore, to adapt designs to native fish species there is a need to improve understanding of the target species’ swimming performance and behaviour (Clay, 1995; Larinier, 2002; Katopodis, 2005). Performance data help determine suitable velocity criteria, which in turn define optimal pass dimensions, slope, and frequency of resting pools (Clay, 1995; Rodriguez *et al*., 2006), while understanding behavioural response to hydraulic stimuli can improve attraction and passage efficiency (Silva *et al.*, 2009; Piper *et al.*, 2012; Vowles and Kemp, 2012). For the majority of Chinese fish species, quantification of swimming performance is limited and behaviour in non-uniform flow unexplored.

Asian carp have been introduced to many countries for biological control and aquaculture, and have had a negative impact on many native species and ecosystems (Lehtonen, 2002; Nico *et al.*, 2005; Wittmann *et al.*, 2014). For example, invasive silver and bighead carp became established in the U.S. in the 1980s (Kolar *et al.*, 2005; Conover *et al.*, 2007). They may outcompete native species due to their fast growth rate and efficient filter feeding, and are linked to a decline in body condition of native gizzard shad (*Dorosoma cepedianum*) and bigmouth buffalo (*Ictiobus cyprinellus*) (Irons *et al.*, 2007; Sampson *et al.*, 2009). In addition, high densities of silver carp leaping from the water can damage boats and harm anglers (Stokstad, 2010). In response to the threat to native species and the recreational fishing industry, federal agencies released $75.8 million in 2010 for control and research to prevent further spread of silver and bighead carp, particularly to the Laurentian Great Lakes (Stokstad, 2010; ACRCC, 2012). Hydraulic barriers that constrict the channel to elevate water velocity above the swimming ability of the target species are a potential method for reducing the spread of invasive fish (Hoover *et al.*, 2003; Neary, 2012; Noatch and Suski, 2012), including Asian carp.

Fish swimming speeds are commonly categorised into three modes based on endurance time: 1) sustained, which can be maintained for long periods (> 200 min) primarily using energy derived from aerobic processes to power red muscles; 2) burst, which is powered by anaerobic metabolic processes and contraction of white muscle fibres resulting in fatigue within 20 s; and 3) prolonged, which uses both aerobic and anaerobic processes to power red and white muscle fibres for 20 s to 200 min (Brett, 1964; Brett *et al*., 1958; Beamish, 1978).

Fish swimming performance is commonly quantified using swim chambers which reduce flow heterogeneity (Hammer, 1995). However, the confined conditions in which fish are forced to swim prevent exhibition of natural performance enhancing behaviours, such as burst-and-coast swimming (Peake and Farrell, 2004; Tudorache *et al.*, 2007). Cessation of swimming in chamber based performance tests may reflect a behavioural response to the unnatural conditions, rather than physiological exhaustion (Peake and Farrell, 2006). Longer test sections can increase the time spent using burst-and-coast swimming, resulting in higher swimming speeds than short chambers (Tudorache *et al*., 2007; Deslauriers and Kieffer, 2011). Direct comparisons of swimming speeds within swim chambers and large open channel flumes are limited, as the former are predominantly used to measure prolonged swimming speeds and flumes to evaluate burst speeds (Katopodis and Gervais, 2012). However, two studies with European Eel (*Anguilla anguilla*) found higher burst swimming speeds were reached in volitional flume experiments than had been previously recorded in swim chamber burst swimming trials (Russon and Kemp, 2011; Newbold *et al*., 2014). Furthermore, the uniform flow created in swim chambers prevents utilisation of low velocity areas commonly available under more hydraulically diverse natural conditions. It is assumed that fish use areas of low velocity to minimise the energetic cost of upstream movements, and that this behaviour can enable small and weak swimming fish to pass man-made structures even when the average bulk flow exceeds swimming ability (House *et al.*, 2005; Richmond *et al.*, 2007). Yet attempts to verify this assumption through behavioural observation are uncommon (Katopodis, 2005).

This study focused on bighead carp as a model species to improve the understanding of Asian carp swimming ability. Data for bighead carp swimming performance are limited; one recent report evaluates swimming endurance (Hoover *et al.*, 2012), although no attempt was made to investigate behaviour, while previous *in situ* and laboratory studies are based on few replicates and poorly defined performance criteria (Zhao and Han, 1980; Layher and Ralston, 1997). The data obtained will aid efforts to design more effective fish passes within the native range, and may help to reduce their spread through the development of velocity barriers where they are invasive. The primary aim of this study was to quantify the sustained, prolonged, and burst swimming speeds of juvenile bighead carp, a critical life stage during which migration to lakes occur. This was achieved through: i) fixed velocity trials in a swim chamber and section of open channel flume to quantify performance in all three swimming modes; ii) a constant acceleration test to evaluate anaerobic capacity; and iii) evaluation of repeat burst swimming performance during volitional passage through three consecutive channel constrictions. A secondary aim was to evaluate bighead carp behaviour and its influence on performance, by comparing: a) endurance during swim chamber (homogeneous flow) and flume based (heterogeneous flow) fixed velocity trials; and b) passage predictions based on forced swimming tests with those obtained during volitional ascent of the channel constrictions. It was hypothesised that: 1) fish would utilise the low velocity areas of the flume section during fixed velocity tests, and therefore performance at equivalent mid channel velocity would be higher for the flume than for the swim chamber; and 2) based on the results of the forced swimming performance tests, volitional passage of the constrictions would be possible.

## 2. Methods

### 2.1. Fish maintenance

Experiments were conducted during two experimental periods in 2010 and 2011.

In May and June 2010, 120 bighead carp (mean ± S.E. fork length [*FL*] = 181 ± 37 mm, mass = 114.3 ± 5.5 g) were net caught at Longquan aquaculture pond, Jiangxia District, and transported 3 h in aerated bags to the Institute of Hydroecology, Ministry of Water Resources, Wuhan, China (30° 30’ 17.01”N, 114° 22’ 36.04”E). Fish were held in two 1430 L outdoor tanks sterilised with potassium permanganate to minimise the risk of disease. Constant water exchange with an adjacent large fish pond was used to stabilise water temperature (mean ± S.E. = 23.8 ± 2.1 °C).

In April and May 2011, 184 bighead carp (mean ± S.E. *FL* = 103 ± 30 mm, mass = 28.5 ± 2.3 g) were transported 2 h in aerated bags from the Dangyang hatchery to the China Three Gorges University, Yichang (30° 43’ 47.38”N, 111° 18’ 26.04”E). A 5300 L filtered and aerated outdoor tank was used to hold fish at a mean (± S.E.) temperature of 19.5 (± 3.4) °C.

During both experimental periods water quality was monitored daily and partial water changes were conducted weekly to ensure low nitrate (< 50 mg L-1) and nitrite (< 1 mg L-1) concentrations. Fish were fed daily and all trials were conducted between 3 and 14 days after fish were delivered to experimental facilities. Test facilities were maintained at water temperatures (18-27°C) representative of those found in the Yangtze River during juvenile bighead carp migrations, and within the preferred range for bighead carp activity (Jennings, 1988). After trials, fish were anaesthetised in tricaine methanesulfonate (MS-222), weighed (grams) and measured (*FL:* mm).

### 2.2. Swimming performance during fixed velocity tests

Fixed velocity tests were conducted in a swim chamber at the China Three Gorges University between 6 and 13 April 2011 (*n* = 145, *FL* = 52 - 190 mm) and a test section of open channel outdoor flume at the Institute of Hydroecology between 5 May and 26 June 2010 (*n* = 120, *FL* = 102 - 251 mm).

Flow was driven through the centre of a 93 L Steffensen type swim chamber (Steffensen *et al.*, 1984) by a three phase electric motor and returned through two test sections (0.80 m long, 0.15 m wide and 0.15 m deep) on opposite sides. Temperature (mean ± S.E. = 21.5 ± 0.2 °C) was controlled by constant water exchange with an aerated and regulated buffer tank. A cross vane baffle and flow straightener homogenised flow conditions. Homogeneous velocity conditions permit the assumption that fish swimming speed is equal to mid-channel water velocity (Nikora  *et al.*, 2003). The linear relationship between motor frequency and velocity (calibrated using an impeller flow meter: NTK71-Vectrino, Qingdao Nortek Measuring Equipment Co., Qingdao) was used to determine test water velocity, which had a maximum of 0.82 m s-1.The cross-sectional area of the largest fish was less than 10% of that of the channel. Therefore, increased water velocity due to partial blocking of the flow by the fish was deemed negligible, and following standard practice (e.g. Bell and Terhune, 1970), no adjustment to swimming speeds were made.

A re-circulatory open channel flume (13 m long, 0.6 m wide and 0.8 m deep) was used for fixed velocity trials in heterogeneous flow conditions, within a central 1 m long test section created using 15 mm square mesh screens (Fig. 1). Mean (± S.E.) water temperature was 22.4 (± 0.2) °C. A honeycomb flow straightener was installed at the inlet. Water velocity was controlled by three (5.5, 7.5 and 18.5 KW) pumps to adjust discharge and an outlet weir to regulate water depth. Mid-channel water velocity and depth ranged from 0.38to 1.25 m s-1 and 0.20 to 0.36 m, respectively. For initial analysis, swimming speed was considered equal to mid channel velocity (*V*mid), which was recorded at 60% water depth after each trial using an impeller flow meter for 10 seconds.

Test section length = 1m

Flume length = 13m

Flume depth = 0.8m

Flow

Water depth = 0.2-0.36m

Mesh screens

Figure 1. Side view of the open channel recirculating flume test section used to measure Bighead carp swimming endurance.

Individual fish were tested once under a single velocity. Following 1 h acclimatisation at approximately 1 *FL* s-1 (within known sustained speeds: Hoover *et al*., 2012), velocity was increased to the test level within 1 min and 1 - 2 min in the swim chamber and flume section, respectively. Test velocities represented the fish’s sustained to burst swimming speed range, but varied between the chamber and flume due to differences in the subjects *FL* and the equipment’s maximum capacity (Table 1). Resting on the downstream screen was discouraged by gently tapping the glass or caudal fin. Individuals were classified as swimming at burst, prolonged, or sustained speeds, based on endurance (Beamish, 1978). Endurance was defined as the time interval between reaching the test velocity and impingement on the downstream screen for 3 s. In the flume, trials were ended after 200 min whereby it was assumed fish were swimming at a sustained speed (methods reviewed in Hammer, 1995). The maximum trial length was reduced to 120 min for the swim chamber tests as pilot experiments and data from the flume study indicated no fatigue occurred after this period.

Table 1. The number (*n*) and fork length (*FL*) of bighead carp (*Hypophthalmichthys nobilis*) tested for endurance over a range of water velocities, during fixed velocity tests in a section of open channel flume and a swim chamber. Water velocity was measured at 60% depth in the centre of the test section. Maximum water velocity was limited to 0.82 m s-1 in the swim chamber. The maximum velocity applied in the flume was 1.25 m s-1,as beyond this the test subjects could not maintain active swimming.

|  |  |  |
| --- | --- | --- |
| **Water velocity (m s-1)** | **Swim chamber** | **Flume section** |
| ***N*** | ***FL* (mm)** | ***n*** | ***FL* (mm)** |
| 0.36 - 0.45 | 12 | 75 – 105 | 9 | 102 – 138 |
| 0.46 - 0.55 | 41 | 60 – 180 | 12 | 102 – 168 |
| 0.56 - 0.65 | 40 | 60 – 170 | 14 | 112 – 221 |
| 0.66 - 0.75 | 40 | 52 – 183 | 26 | 145 – 229 |
| 0.76 - 0.85 | 12 | 113 – 190 | 18 | 150 – 246 |
| 0.86 - 0.95 | 0 | NA | 12 | 141 – 213 |
| 0.96 - 1.05 | 0 | NA | 10 | 160 – 247 |
| 1.06 - 1.15 | 0 | NA | 8 | 182 – 251 |
| 1.16 - 1.25 | 0 | NA | 11 | 147 – 242 |
| **Total values/range** | **145** | **52 - 190** | **120** | **102 - 251** |

The combined (swim chamber and flume) data were divided into representatives of the three swimming speed modes based on endurance. The relationship between sustained swimming speed (*U*S [ms-1]), water temperature (*T* [°C]), method (*M*: flume section or swim chamber) and fork length (*FL* [m]) was assessed using the linear regression model:

*U*S= *b*0 + *b*1*T* + *b*2*FL* + *b*3*M*

where *b*iare the regression coefficients. This equation was used to predict the mean (± 90% C.I.) maximum sustained speed for fish of a known *FL*, at a specific temperature.

For prolonged swimming speeds there was insufficient data to construct an accurate model when endurance exceeded 10 min. Therefore, only individuals swimming for between 20 s and 10 min were included in the prolonged swimming regression analysis, which evaluated the relationship between endurance (*E* [min]), prolonged swimming speed (*U*P [FL s-1]), temperature and method:

ln(*E*) = *b*0 + *b*1*U*P + *b*2*T* + *b*3*M*

Fish with an endurance less than 0.33 min (i.e. 20 s) were included in the burst swimming (*U*B [*FL* s-1]) regression analysis:

ln(*E*) = *b*0 + *b*1*U*B + *b*2*T* + *b*3*M*

The maximum speeds reached and those exceeded by 85% of 50-100 mm long fish swimming in burst and prolonged modes were reported to compare performance results between the endurance, constant acceleration and volitional passage trials.

### 2.3. Constant acceleration test

The maximum swimming speed (*U*max;e.g. Farrell, 2008), a measure of anaerobic performance, was calculated for 10 bighead carp using a constant acceleration test. Trials were conducted in the swim chamber described for fixed velocity tests, at the China Three Gorges University, on 15 April 2011. After 1 h acclimatisation at 1 *FL* s-1, velocity was increased by 0.02 m s-1 every minute until fatigue to determine the *U*max. Water temperature was 23.1 °C during all trials. Fish were selected to minimise variation in *FL* (mean ± S.E. = 76.4 ± 2.3 mm) and correlation between individual *U*max and *FL* was assessed using Spearman’s rank correlation (*Rs*). The mean *U*maxwas compared to: (a) the predicted maximum sustained speed for 76 mm fish; (b) predicted endurance at *U*max for 76 mm fish; and (c) burst speeds reached by 50-100 mm long fish in fixed velocity tests.

### 2.4. Swimming behaviour during fixed velocity tests

A sub-sample (*n* = 64) of the fixed velocity tests conducted within the 1m section of open channel flume were filmed to enable analysis of swimming behaviour in response to flow heterogeneity. Following each trial the mean longitudinal velocity was recorded at 60% of water depth in the centre of the test section (*V*mid), and 0.02 m from walls and floor (*V*refugia) using an impeller flow meter for10 seconds. For a range of water velocities a more detailed velocity profile was created by recording mean longitudinal water velocity at 45 sample points and interpolating these using spline methods in ArcGIS (e.g. Figure 2). The length of time spent *utilising flow refugia* (swimming in low velocity areas close to the flume wall and floor) was recorded and subtracted from the total trial duration, and the difference deemed to be allocated to *free swimming*. The relationship between percentage of time spent utilising flow refugia and swimming speed (relative to fish length)was explored using Spearman’s rank correlation. Swimming speeds were corrected (*U*cor) for the time spent utilising flow refugia by:

$U\_{cor}=( t\_{1}×V\_{refuge})+( t\_{2}×V\_{mid})$ where *t1* and *t2* are the proportion of time spent utilising flow refugia and free swimming, respectively. This correction provides an approximation of mean fish swimming speed during the trial. The Wilcoxon signed-rank test was used to evaluate the difference between *V*mid and *U*cor during trials for fish swimming in sustained and prolonged or burst modes.

Low: 0.80

High: 1.39

**Velocity (m s-1)**

Water depth = 0.26 m

Channel width = 0.60 m

Water depth = 0.26 m

Figure 2. Example velocity cross-section (viewed looking upstream) of the 1m flume section used to assess the swimming performance of bighead carp (*Hypophthalmichthys nobilis*) in fixed velocity tests (see section 2.2). Velocity was recorded at each sample point (small dots) using an impeller flow meter and interpolated in ArcGIS. In this example *V*mid (large dot) was 1.08 m s-1 and *V*refugia (triangle) 0.8 m s-1.

0.6 m

### 2.5. Volitional burst swimming performance and behaviour

To evaluate the volitional repeat burst swimming performance of bighead carp, passage efficiencies at three consecutive constrictions (vertical slots) were evaluated in a 4.5 m long test section of an open channel, oval, recirculating raceway (6.50 m long, 0.37 m wide, 0.70 m deep; Fig 3a), at the China Three Gorges University. Trials were conducted on the 18 and 19 May 2011. Four electrically powered, in channel, centrifugal pumps, controlled the velocity while depth remained constant at 0.22 m. Honeycomb flow straighteners delineated the 4.5 m test section, which began 1.4 m downstream of the first constriction approached by upstream moving fish. Constrictions, created from 3 mm width Plexiglass panels, reduced the flume width to 0.14 m, and divided the test area into three sections, including two low velocity pools (1.15 m and 1.25 m long; Fig. 3a). Trials were conducted under two velocity treatments (maximum velocity = 0.50 m s-1 and 0.57 m s-1 for low and high velocity treatments, respectively; Fig. 3b and 3c) by altering the number of pumps in use. Based on the endurance and *U*max results it was predicted that anaerobic swimming would be required to pass the velocities encountered downstream of the constrictions, but that passage would be possible. An Acoustic Doppler Velocimeter (ADV; Nortek +, Nortek AS, Oslo, Norway) was used to measure mean longitudinal velocity at 60% water depth, sampling at 50 Hz for 60 s (sample locations shown in Fig. 3 b and 3c). Data spikes were removed using a maximum / minimum threshold filter (Cea *et al.*, 2007) prior to interpolation in ArcGIS.

Individual fish (*n* = 29, mean ± S.E. *FL* = 101.0 ± 1.7 mm) were allowed at least 1 h to acclimatise to flume conditions in a perforated container downstream of the test section (mean ± S.E. temperature = 25.3 ± 0.1 °C) before release at the downstream screen. Trials were ended after the whole body of the fish passed upstream through the final constriction (passage success) or after 30 min. Three cameras (1.5 m above the channel floor) recorded fish behaviour.

The number of approaches to constriction 1 (movement into the high velocity area 0.05 m downstream; Fig. 3) was recorded and converted to a rate dependent on the time available to individuals before ascent. The effect of velocity treatment on approach rate was evaluated using an exact Mann-Whitney test. The number of passes at each constriction was recorded for each individual. Passage efficiency was calculated as the percentage of the total fish tested that successfully moved upstream of each constriction. Exact Mann-Whitney tests were used to evaluate the effect of *FL*, mass, and water temperature on passage success. Qualitative observations of swimming behaviour in terms of swimming gait, depth in the water column, and utilisation of high and low velocity areas were recorded.

All statistical analysis was completed in IBM Statistics v. 19 (IBM Corp, Armonk, USA).

a)

1.25 m

Flow

Honeycomb

screen

1.40 m

0.14 m

Honeycomb

screen

0.37 m

1.15 m

constriction 1

**Water velocity (ms-1)**

Figure 3 a) Plan view of the open channel recirculating oval raceway used to assess bighead carp volitional burst swimming performance through three constrictions under two velocity treatments: b) low, and c) high velocity. The mean longitudinal water velocity was recorded at each sample point (arrow locations) using an Acoustic Doppler Velocimeter and interpolated using a spline method in ArcGIS. Arrows show the direction of flow, calculated from the longitudinal and lateral velocity components. Fish were recorded as approaching a constriction when they reached 0.05 m downstream (area outlined in red).

Flow direction

constriction 3

constriction 2

b)

c)

##

## 3. Results

### 3.1. Swimming performance during fixed velocity tests

The mean (± S.E.) sustained swimming speed for bighead carp was 3.84 (± 0.12) *FL* s-1 (range equivalent to 0.37 – 0.78 m s-1). As method (flume section or swim chamber) had no effect on sustained speeds (*t* = -1.08, *P* = 0.29) it was excluded from further analysis. Maximum sustained swimming speed (ms-1) was positively related to both *FL* (m) and temperature (°C) (*R*2 = 0.72, *F*2,46 = 58.41, *P* < 0.001, Fig. 4):

 $U\_{S}=-0.268+\left(0.026×T\right)+\left(1.640×FL\right)$

Endurance was short when water velocity exceeded sustained swimming ability in both the flume section and swim chamber, with only 12 fish swimming for longer than 10 min but less than 200 min. Neither temperature nor method had an effect on endurance at prolonged swimming speeds (*T*: *t* = -0.11, *P* = 0.91, *M*: *t* = 0.70, *P* = 0.49) and were excluded from further analysis. Endurance was negatively related to prolonged swimming speed (*FL* s-1), but with high variability (*R*2 = 0.26, *F*1,155 = 54.70, *P* < 0.001):

$lnE =1.74- \left(0.24×U\_{P}\right)$

Mean (± S.E.) burst swimming speed was 7.80 ± 0.41 *FL* s-1. Burst speeds within the section of open channel flume were highly variable and there was no relationship between swimming speed and endurance (*F*2,14 = 2.33, *P* = 0.13). Therefore, only swim chamber data were analysed. Endurance was not influenced by temperature (*t* = 0.78, *P* = 0.44). Although endurance was negatively related to burst swimming speed (*FL* s-1), there was high individual variability and the correlation was weak (*R*2 = 0.19, *F*1,30 = 6.86, *P* = 0.01):

$lnE =-0.90- \left(0.08×U\_{B}\right)$

Due to high individual variation in performance there was considerable overlap of prolonged and burst swimming speeds; speeds reached in the presumed prolonged mode (endurance > 20 s < 10 min) ranged from 2.43 to 11.31 *FL* s-1 (equivalent to 0.30 - 1.23 m s-1) and burst speeds (endurance < 20 s) from 3.41 to 12.78 *FL* s-1 (equivalent to 0.41- 1.22 m s-1). Swimming speeds of 0.60 and 0.49 m s-1 were exceeded by 85% of 50-100 mm *FL* bighead carp swimming in burst and prolonged modes, respectively.

Figure 4. The raw data for bighead carp swimming within the sustained mode in a swim chamber (open circles) and flume section (solid circles), at temperatures between 19.0 and 26.6 °C, and the estimated sustained swimming speed (dashed line) for fish of different fork lengths predicted from regression analysis at a temperature of 22°C.

### 3.2. Constant acceleration test

There was no correlation between *U*max*­*and *FL* over the small size range tested (*Rs* = -0.35, *P* = 0.32). The mean (± S.E.) *U­*max was 6.81 (± 0.45) *FL* s -1 (equivalent to 0.51 m s-1). Using the *U*S regression model, a 76 mm long fish at 23 °C had a predicted mean sustained speed of 0.45 m s-1. Endurance at the *U*max for a 76 mm fish swimming in the prolonged mode was estimated as 67 s. The *U*max was exceeded by 89% of 50 to 100 mm fish with an endurance time of less than 20 s (burst swimming).

### 3.3. Swimming behaviour during fixed velocity tests

The *V*refugia was up to 40% lower than *V*mid. The proportion of time fish spent utilising flow refugia was negatively correlated to *V*mid (*n* = 64, *Rs* = 0.42, *P* < 0.001; Fig. 5). Of the 18 fish swimming in the sustained mode, 11 spent over 50% of the time utilising flow refugia, compared to only 2 of the 46 fish swimming in burst or prolonged modes. The *Vmid* was significantly higher than the *Ucor* for fish swimming in the sustained mode (*T* = 0, *P* = 0.001) but not for fish swimming in burst or prolonged modes (*T* = 0, *P* = 0.07).

Figure 5. Relationship between mid-channel flume velocity (*V*mid) and the percentage of trial time individual bighead carp spent utilising flow refugia near the flume wall and floor. Data was split into fish swimming at sustained (endurance > 120 min; solid circles) and prolonged or burst (endurance < 120 min; crosses) speeds.

### 3.4. Volitional burst swimming performance and behaviour

All fish approached constriction 1 and there was no effect of treatment on approach rate (Mann-Whitney *U* = 94, *P* = 0.64). Fish passed constriction 1 up to eight times under both velocity treatments and constriction 2 a maximum of two and four times under the high and low velocity treatments, respectively. Passage efficiency decreased from 87 and 100% at constriction 1, to 67 and 71% at constriction 3, under the high and low velocity treatments, respectively (Fig. 6). Under the high velocity treatment, successful fish had a greater length and mass (median = 98 mm and 16.5 g) than those that failed (94 mm, 14.7 g) (*FL,* *U* = 8, *P* = 0.04; mass, *U* = 6, *P* = 0.02). There was no difference under low velocity (*P* > 0.05). There was no effect of water temperature during either treatment (*P* > 0.05).

Individuals tended to utilise low velocity areas between the constrictions, until moving into the channel centre, where velocity was highest, on approach to each constriction. Throughout ascent, fish predominantly remained close to the flume floor. Although an unsteady gait was occasionally observed for some fish in lower velocity areas, all maintained high speed steady swimming to pass the constrictions.

Figure 6. The passage efficiency of bighead carp (% of total tested fish) at three consecutive vertical slot constrictions in an open channel flume at the China Three Gorges University, under low (solid bar, *n* = 14) and high (clear bar, *n* = 15) velocity treatments. Constrictions numbered from most downstream (1) to upstream (3).

## 4. Discussion

Loss of connectivity between essential freshwater habitats, due to the construction of anthropogenic structures such as dams, is one of the key causes of Asian carp population decline (Yi *et al*., 2010). Fish passes provide an important means to mitigate for this environmental impact, but design must be based on understanding the swimming ability and behaviour of the target species or guilds (Zheng *et al*., 2010). By using a variety of methods, this study enhanced understanding of juvenile bighead carp swimming performance and provided the first data on their behaviour. This gives a basis on which to inform fish pass design for Asian carp in China, and potential development of velocity barriers in regions where they are invasive.

### 4.1. Swimming ability

The use of multiple methodologies to quantify fish swimming performance and behaviour enhances confidence in the accuracy of results and application to fisheries management (Bestgen *et al.*, 2003). As anaerobic metabolism presumably contributed to swimming during a number of the one minute velocity increments during the constant acceleration tests (Webb, 1971; Hudson, 1973), and the total protocol lasted approximately 20 min, it is likely that *U*max described prolonged rather than burst swimming ability. Indeed, burst speeds for 50 to 100 mm length fish ranged from 0.45 to 0.74 m s-1, with 89% exceeding the *U*max. Furthermore, the *U*max (mean = 0.51 m s-1) was equivalent to speeds that equal sized fish could maintain for approximately one minute in the fixed velocity test. This similarity suggests that anaerobic metabolism contributes to swimming at speeds above 0.5 m s-1. In addition, although most bighead carp could ascend the flume constrictions, where swimming speeds in excess of the highest water velocities (0.5 - 0.57 m s-1) may have been required, there were some that failed. Together, the findings suggest that bighead carp 50 to 100 mm in length exhibit poor anaerobic swimming performance at speeds above 0.5 m s-1. A recent study of swim chamber based fixed velocity performance (Hoover *et al.*, 2012) further supports the findings presented; although burst speeds were slightly lower in the current study, the maximum sustained and prolonged swimming speeds were comparable between the two datasets for fish of equal length.

The capacity of fish to stage successive bursts of locomotion is rarely examined (Castro-Santos, 2004, but see Kemp *et al.*, 20009 for an exception). Yet an inability to negotiate multiple velocity barriers successfully during fish pass ascent could lead to fall back and repeated attempts, thus delaying migration, elevating the energetic cost of passage and increasing fatigue (Quintella *et al.,* 2004). During ascent of the flume, the passage efficiency was reduced at each consecutive constriction where anaerobic swimming was presumed to occur. The incremental passage failure in this study indicates that the design of technical fish passes should consider cumulative passage success at high velocity areas. The methodology described here provides a more realistic means of evaluating burst swimming ability to be applied to fish pass design than fixed velocity trials which induce high speed movement from a resting state. Detailed hydraulic measurements alongside tracking of fish movements within a flume would allow evaluation of the actual velocity and turbulence conditions experienced by fish moving upstream, providing additional useful data for effective fish pass design (e.g. Silva *et al*., 2011; Newbold and Kemp, 2015).

The endurance limits commonly applied to define swimming modes (i.e. burst < 20 s, sustained > 200 min) are somewhat arbitrary values and in reality the transitions may be variable between species (Peake *et al.*, 1997a; Castro-Santos, 2005). For example, 200 minutes is not always a biologically relevant point for assuming a switch from prolonged to sustained swimming speeds (Peake *et al.*, 1997a), and for juvenile Atlantic salmon (*Salmo salar*) the transition appeared to occur at 15 to 20 min (Bernatchez and Dodson, 1985). In this study, endurance of bighead carp between 10 and 200 min was rare. In addition, there was considerable overlap between the swimming speeds presumed, based on endurance, to be in the prolonged and burst modes. Similarly, Lake sturgeon (*Acipenser fulvescens*) showed no change in the swim speed – endurance slope between prolonged and burst speeds (Peake *et al.*, 1997a). However, the lack of defined prolonged and burst swimming modes for bighead carp and Lake sturgeon may not be realistic for volitional open channel swimming. The correlation between bighead carp swimming speed and endurance was weak at burst and prolonged speeds and fish were observed swimming erratically in the test section. Whereas at slow, sustained swimming speeds, fish swam steadily and there was a stronger relationship between sustained swimming speed, body length and temperature. The confined conditions in which trials were conducted, may have induced unnatural behaviour during anaerobic swimming and prevented fish from reaching maximum burst speeds (Tudorache *et al*.,2007), thus potentially contributing to the high variation between individuals. Therefore, although swim chambers may be suitable for the evaluation of steady sustained swimming, open channel flumes are preferable for quantifying burst swimming ability.

### 4.2. Swimming behaviour

As passage of the flume constrictions was volitional, behaviour, motivational status, and attractiveness of the conditions encountered, in addition to swimming ability, could have influenced passage success (Weaver, 1965; Peake and Farrell, 2004; Castro-Santos *et al*., 2012). While unconstrained, fish could exhibit burst-and-coast swimming and exploit low velocity areas available within the flume to conserve energy. Compared to that observed in the swim chamber trials, performance may have been expected to be higher as a consequence (Peake and Farrell, 2004; Hoover *et al*., 2011). During fixed velocity tests burst speeds of 0.60 m s-1 were exceeded by 86% of 50 - 100 mm fish. As fish in the constriction trials were at the upper limit of this size range, passage of the constrictions was predicted to be possible, yet several individuals failed to ascend under both test conditions. A lack of motivation to ascend flumes can influence volitional passage and may be evident as limited upstream progress against velocities that do not exceed swimming ability (Mallen-Cooper, 1992). However, as fish were generally active in both treatments, exploring the flume throughout the trials and passing the first and second constrictions up to eight and four times, respectively, motivation was unlikely to be the sole determinant of success. The higher passage success under low flow and the positive relationship between success and fish length, a known predictor of swimming ability (Bainbridge, 1960), indicates the potential influence of swimming ability on ascent. Further research with higher water velocities is recommended as this study had relatively low velocity treatments. In addition, turbulence within the flume was not assessed in this study, which is known to regularly cause instability (Tritico and Cotel, 2010), increase the cost of swimming (Enders *et al.*, 2005), reduce swimming performance (Lupandin, 2005; Tritico and Cotel, 2010) and influence fish swimming behaviour (Smith *et al*., 2005; Silva *et al*., 2011). Large variation in performance independent of body length was observed during all swimming performance tests in this study. A more holistic understanding of how individual behaviour as well as physiological capacity can influence fish pass efficiency is required to optimise designs.

To enhance performance, exploitation of low velocity areas within the flume section used for fixed velocity trials was expected. Indeed the lower velocities experienced by fish utilising these flow refugia is highlighted through the estimations of *U*cor. Yet utilisation of flow refugia was common only at relatively low *V*mid*.* Other species have been observed swimming close to the channel centre during flume ascent at high speeds, despite occupying edge areas at low bulk velocity (Castro-Santos, 2005; Haro *et al.*, 2004; Castro-Santos *et al.*, 2012). For example, brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) burst swimming upstream remained close to the channel floor but away from the walls, possibly to avoid an unequal pressure distribution across the body, which may cause instability (Castro-Santos, 2005). When sustained swimming speeds were exceeded in the current study, fish were more likely to swim erratically in the centre of the channel, avoiding both the walls and floor, therefore not reducing their mean swimming speed. The comparable endurance times achieved in the flume and swim chamber may therefore have been due to exhibition of this behaviour at high bulk velocities. In addition, although this study did not quantify turbulence, higher intensities of turbulence in the open channel may have influenced endurance at all swimming speeds and had the potential to displace fish from low velocity areas. It has been suggested that culvert velocity criteria for small fish could be based on low velocity areas rather than the mean cross-sectional velocity, under the assumption that small fish will utilise these regions of the channel (e.g. Ead *et al*., 2000; Clark *et al*., 2014).However, this study does not support this assumption and further research is required before such velocity criteria are implemented.

### 4.3. Management recommendations

Based on the results of this study, to allow passage of a high proportion of small bighead carp (50 - 100 mm) upstream, velocities below 0.40 m s-1 (lower 90% C.I. of the mean predicted sustained speed for 80 mm fish at 22 °C) are recommended where anaerobic swimming should be avoided (e.g. in fish pass pools, Armstrong *et al.*, 2010). This speed was surpassed by 94% of individuals swimming at sustained speeds across the temperature range tested (18 – 27 °C).

Further research into bighead carp swimming performance at high water velocities is required to confirm the results of this study. However, the data indicates that if a short burst of high speed swimming is required without the need to maximise distance, then routes with velocities not exceeding 0.60 m s1 (surpassed by 85% of 50 - 100 mm fish) may be appropriate. Due to the highly variable relationship between swimming speed in burst and prolonged modes and endurance, the subsequent regression models may not provide accurate swimming ability predictions, and their application to management decisions should be cautioned. Other swimming performance studies have also reported high variability in performance during endurance trials. For example, Peake *et al*. (1997a) analysed the endurance of lake sturgeon, and using similar regression methods to this study reported an adjusted R2 value of 0.85, whereas using the same methods for various salmonid species, Peake *et al*. (1997b) reported R2 values ranging from 0.33 to 0.66 at prolonged and burst swimming speeds. Where variation in fish swimming performance is so high and statistical analysis demonstrates a weak relationship between swimming speed and endurance, using the mean swimming ability and linear regression methods may not be an appropriate method to design passable velocities for a high proportion of a population.

Utilisation of low velocity areas available along channel boundaries should not be assumed, as fish may move into the higher velocity are in the mid-channel, depending on bulk flow and potentially turbulence. Passage of velocity barriers longer than a single sluice or vertical slot, will depend on both the swimming ability and speed selected by the individuals (Castro-Santos, 2005), and cannot be predicted based on the findings of this study. Of the existing fish pass designs, vertical slot or nature like fish passes may be the most suitable options for Asian carp passage, as predicted for other weak swimming benthic fish (Mallen-Cooper, 1992; Bestgen *et al*., 2003). However, further tests and subsequent monitoring are required to optimise these designs due to the variable efficiencies of current fish pass facilities (Noonan *et al.*, 2012).

Invasive bighead carp less than 200 mm long may be blocked if velocities exceed 1.30 m s-1 over 50 m (based on maximum swimming speeds reported) at temperatures between 18 and 27 °C. The same criteria could also be appropriate for silver carp which are reported to have a slightly weaker swimming performance (Hoover *et al.*, 2012). Smooth high velocity culverts may have potential, alongside other devices (e.g. electric barriers and sound and bubble screens; Taylor *et al.*, 2005), to impede Asian carp movement as part of an integrated management programme.

This study provides a platform for further iterative research on Asian carp swimming behaviour and performance to guide management practices. Prior to the installation of fish passes for bighead carp, further experimental research employing volitional ascent at a range of high velocities is recommended to evaluate anaerobic performance, swimming speed selection, refuge utilisation, and the influence of turbulence. In addition, validation of performance with wild fish in the field is recommended to ensure fish pass attraction is not compromised by setting conservative water velocity criteria. Further, robust quantification of fish response to potential behavioural deterrents (e.g. hydrodynamic and acoustic cues), in isolation and in combination, is also suggested.

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## References

The Asian Carp Regional Coordinating Committee [ACRCC]. FY 2012 Asian Carp Control Strategy Framework, 2012.

Armstrong, G.S., Aprahamian, M.W., Fewings, G.A., Gough, P.J., Reader, N.A., Varallo, P.V., 2010. *Environment Agency Fish Passage Manual: Guidance Notes on the Legislation, Selection and Approval of Fish Passes in England and Wales*. Environment Agency, Bristol.

Bainbridge, R., 1960. Speed and stamina in three fish. *J. Exp. Biol.* **37** (1), 129–153.

Beamish, F.W.H., 1978. *Swimming capacity*. Fish Physiol. Vol. VII, 101–187.

Bell, W.H., Terhune, L.D.H., 1970. Water tunnel design for fisheries research. *Fish. Res. Board Can*., **69** (Technical Report no 195).

Bernatchez, L., Dodson, J.J., 1985. Influence of temperature and current speed on the swimming capacity of lake whitefish (Coregonus clupeaformis) and cisco (C. artedii). *Can. J. Fish. Aquat. Sci*. **42** (9), 1522–1529.

Bestgen, K.R., Mefford, B., Bundy, J., Walford, C., Compton, B., Seal, S., Sorensen, T., 2003. *Colorado State University, Larval Fish Laboratory Contribution70*.

Brett, J.R., Hollands, M., Alderdice, D.F., 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Board Can*. **15** (4), 587–605.

Brett, J.R., 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can*. **21** (5), 1183–1226.

Castro-Santos, T., Haro, A., 2008. Fish guidance and passage at barriers. In: Domenici, P., Kapoor, B.G. (Eds.), *In Fish Locomotion: An Eco-Ethological Perspective*. Science Publishers, Enfield New Hampshire, pp. 48–62.

Castro-Santos, T., Sanz-Ronda, J., Ruiz-Legazpi, J., 2012. Breaking the speed limit-comparative sprinting performance of brook trout (*Salvelinus fontinalis*) and brown trout (Salmo trutta). *Can. J. Fish. Aquat. Sci*. **70** (2), 280–293.

Castro-Santos, T., 2004. Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. *Can. J. Fish. Aquat. Sci*. **61** (9), 1602–1615.

Castro-Santos, T., 2005. Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. *J. Exp. Biol.* **208** (3), 421–432.

Cea, L., Puertas, J., Pena, L., 2007. Velocity measurements on highly turbulent free surface flow using ADV. *Exp. Fluids* **42** (3), 333–348.

Chen, D., Duan, X., Liu, S., Shi, W., *Status and Management of Fishery Resources of the Yangtze River.* In: R. Welcomme, T. Petr (Eds.), Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume I. RAP Publication 2004/16, FAO Regional Office for Asia and the Pacific, Bangkok, Thailand, 2004. 173–182.

Clark, S.P., Toews, J.S., Tkach, R., 2014. Beyond average velocity: modelling velocity distributions in partially filled culverts to support fish passage guidelines. *Int. J. River Basin Manage*. **12**, 101–110.

Clay, C.H., 1995. *Design of Fishways and Other Fish Facilities*, 2nd edition. Lewis Publishers, Florida.

Conover, G., Simmonds, R., Whalen, M., 2007. *Management and Control Plan for Bighead, Black, Grass, and Silver Carps in the United States*. Asian Carp Working Group, Aquatic Nuisance Species Task Force, Washington, D.C.

Deslauriers, D., Kieffer, J.D., 2011. The influence of flume length and group size on swimming performance in shortnose sturgeon *Acipenser brevirostrum*. *J. Fish Biol*. **79**, 1146–1155.

Duan, S., Liu, M., Huang, S., Qiu, Z., Li, K., Wang, D., 2009. Changes in abundance of larvae of the four domestic Chinese carps in the middle reach of the Yangtze River, China, before and after closing of the Three Gorges Dam. *Environ. Biol. Fish.* **86** (1), 13–22.

Dudgeon, D., 1995. River regulation in Southern China: ecological implications, conservation and environmental management. *Regul. River* **11** (1), 35–54.

Dudgeon, D., 2005. River rehabilitation for conservation of fish biodiversity in monsoonal Asia. *Ecol. Soc*. **10** (2), 15–34.

Ead, S.A., Rajaratnam, N., Katapodis, C., Ade, F., 2000. Turbulent open-channel flow in circular corrugated culverts. *J. Hydraul. Eng*. **126**, 750–757.

Enders, E.C., Boisclair, D., Roy, A.G., 2005. A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci*. **62** (5), 1079–1089.

FAO, DVWK, 2002. *Fish Passes -Design, Dimensions and Monitoring*. Food and Agricultural Organization of the United Nations, Rome.

Farrell, A.P., 2008. Comparisons of swimming performance in rainbow trout using constant acceleration and critical swimming speed tests. *J. Fish Biol*. **72** (3), 693–710.

Fu, C., Wu, J., Chen, J., Wu, Q., Lei, G., 2003. Freshwater fish biodiversity in the Yangtze River basin of China: patterns, threats and conservation. *Biodivers. Conserv*. **12** (8), 1649–1685.

Hammer, C., 1995. Fatigue and exercise tests with fish. Comp. *Biochem. Phys*. A **112** (1), 1–20.

Haro, A., Castro-Santos, T., Norelka, J., Odeh, M., 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Can. J. Fish. Aquat. Sci*. **61** (9), 1590–1601.

Hoover, J.J., Adams, S.R., Killgore, K.J., 2003. *Can Hydraulic Barriers Stop the Spread of the Round Goby?* TN ANSRP-03-1, U.S. Army Corps of Engineers, US Army Engineer Research and Development Center (ERDC). Vicksburg, MS.

Hoover, J.J., Southern, L.W., Katzenmeyer, A.W., Hahn, N.M., 2012. *Swimming Performance of Bighead Carp and Silver Carp: Methodology, Metrics, and Management Implications.* Aquatic Nuisance Species Research Program (ERDC/TN ANSRP-12-3).

House, M.R., Pyles, M.R., White, D., 2005. Velocity distributions in streambed simulation culverts used for fish passage. *J. Am. Water Resour. Assoc*. **41**, 209–217.

Hu, M., Hua, Q., Zhou, H., Wu, Z., Wu, X., 2015. The effect of dams on the larval abundance and composition of four carp species in key river systems in China. *Environ. Biol. Fishes* **98**, 1201–1205.

Hudson, C.L., 1973. On the function of the white muscles in teleosts at intermediate swimming speeds. *J. Exp. Biol*. **58** (2), 509–522.

Irons, K.S., Sass, G.G., McClelland, M.A., Tafford, J.D., 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? *J. Fish Biol*. **71**, 258–273 (sd).

Jennings, D.P., 1988. *Bighead carp (Hypophthalmichthys nobilis): a biological synopsis*. U. S. fish and wildlife service washington, DC. U.S. Fish Wildlife Serv. Biol. Rep. 88, 1–47.

Katopodis, C., 2005. Developing a toolkit for fish passage, ecological flow management and fish habitat works. *J. Hydraul. Res*. **43** (5), 451–467.

Katopodis, C., Gervais, R., 2012. Ecohydraulic analysis of fish fatigue data. *River Res. Appl*. **28**, 444–456.

Kemp, P.S., Tsuzaki, T., Moser, M.L., 2009. Linking behaviour and performance: intermittent locomotion in a climbing fish. *J. Zool*. **277** (2), 171–178.

Kolar, C.S., Chapman, D.C., Courtenay, W.R., Housel, C.M., Williams, J.D., Jennings, D.P., 2005. *Asian carps of the genus Hypophthalmichthys (Pisces, Cyprinidae)—a biological synopsis and environmental risk assessment*. Report to U.S. Fish Wildlife Serv. Interag. Agreem. (94400-3-0128).

Larinier, M., 2002. Biological factors to be taken into account in the design of fishways, the concept of obstructions to upstream migration. *Bulletin Francais de la Peche et de la Pisciculture* **364**, 28–38 (supplément).

Layher, W.G., Ralston, A.O., *Swimming performance of juvenile bighead carp (Hypophthalmichthys nobilis).* Final report to USDA Forest Service, Ouachita National Forest, Hot Springs, AR. 5, 1997.

Lehtonen, H., 2002. *Alien freshwater fishes of Europe*. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds.), Invasive Aquatic Species of Europe: Distribution, Impacts and Management. Kluwaer Academic Publishers, Dordrecht, The Netherlands, pp. 153–161.

Liu, S.P., Chen, D.Q., Duan, X.B., Qiu, S.L., Huang, M.G., 2004. Monitoring of the four famous Chinese carps resources in the middle and upper reaches of the Yangtze River. *Resour. Environ. Yangtze Basin* **13** (2), 183–186.

Lupandin, A.I., 2005. Effect of flow turbulence on swimming speed of fish. *Biol. Bull*. **32** (5), 461–466.

Mallen-Cooper, M., 1992. Swimming ability of juvenile australian bass, macquaria-Novemaculeata (Steindachner), and juvenile barramundi, lates-Calcarifer (Bloch), in an experimental vertical-Slot fishway. *Aust. J. Mar. Freshw. Res.* **43** (4), 823–837.

Marmulla, G., 2001. *Dams, Fish and Fisheries: Opportunities, Challenges and Conflict Resolution*. Food and Agricultural Organization of the United Nations, Rome.

Neary, S., 2012. Binary fish passage models for uniform and nonuniform flows. *River Res. Appl*. **28** (4), 418–428.

Newbold, L.R., Kemp, P.S., 2015. Influence of corrugated boundary hydrodynamics on the swimming performance and behaviour of juvenile common carp (*Cyprinus carpio*). *Ecol. Eng*. **82**, 112–120.

Newbold, L.R., Karageorgopoulos, P., Kemp, P.S., 2014. Corner and sloped culvert baffles improve the upstream passage of adult European eels (*Anguilla anguilla*). *Ecol. Eng*. **73**, 752–759.

Nico, L.G., Williams, J.D., Jelks, H.L., 2005. *Black Carp. Biological Synopsis and Risk Assessment of an Introduced Fish.* American Fisheries Society, Bethesda.

Nikora, I., Aberle, J., Biggs, B.J.F., Jowett, I.G., Sykes, J.R.E., 2003. Effects of fish size, time-to-fatigue and turbulence on swimming performance: a case study of *Galaxius maculatus*. *J. Fish Biol*. 63 (6), 1365–1382.

Noatch, M.R., Suski, C.D., 2012. Non-physical barriers to deter fish movements. *Environ. Rev*. **20** (1), 71–82.

Noonan, M.J., Grant, J.W.A., Jackson, C.D., 2012. A quantitative assessment of fish passage efficiency. *Fish Fish*. **13** (4), 450–464.

Peake, S.J., Farrell, A.P., 2004. Locomotory behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass (*Micropterus dolomieu*). *J. Exp. Biol*. **207** (9), 1563–1575.

Peake, S.J., Farrell, A.P., 2006. Fatigue is a behavioural response in respirometer-confined smallmouth bass. *J. Fish Biol*. **68**, 1742–1755.

Peake, S.J., Beamish, F.W.H., McKinley, R.S., Scruton, D.A., Katopodis, C., 1997a. Relating swimming performance of lake sturgeon *Acipenser fulvescens*, to fishway design. *Can. J. Fish. Aquat. Sci*. **54** (6), 1361–1366.

Peake, S.J., McKinley, R.S., Scruton, D.A., 1997b. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *J. Fish Biol*. **51** (4), 710–723.

Piper, A.T., Wright, R.M., Kemp, P.S., 2012. The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecol. Eng*. **44**, 329–336.

Quintella, B.R., Andrade, N.O., Koed, A., Almeida, P.R., 2004. Behavioural patterns of sea lampreys’ spawning migration through difficult passage areas, studied by electromyogram telemetry. *J. Fish Biol*. **65** (4), 961–972.

Richmond, M.C., Deng, Z., Guensch, G.R., Tritico, H., Pearson, W.H., 2007. Mean flow and turbulence characteristics of a full-scale spiral corrugated culvert with implications for fish passage. *Ecol. Eng*. **30**, 333–340.

Rodríguez, T.T., Agudo, J.P., Mosquera, L.P., González, E.P., 2006. Evaluating vertical-slot fishway designs in terms of fish swimming capabilities. *Ecol. Eng*. **27** (1), 37–48.

Russon, J., Kemp, P.S., 2011. Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *J. Fish Biol*. **78** (7), 1965–1975.

Sampson, S.J., Chick, J.H., Pegg, M.A., 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biol. Invasions* **11** (3), 483–496.

Shi, X., Kynard, B., Liu, D., Qiao, Y., Chen, Q., 2015. Development of fish passage in China. *Fisheries* **40** (4), 161–169.

Silva, A.T., Santos, J.M., Franco, A.C., Ferreira, M.T., Pinheiro, A.N., 2009. Selection of Iberian barbel *Barbus bocagei* (Steindachner, 1864) for orifices and notches upon different hydraulic configurations in an experimental pooltype fishway. *J. Appl. Ichthyol*. **25** (2), 173–177.

Silva, A.T., Santos, J.M., Ferreira, M.T., Pinheiro, A.N., Katopodis, C., 2011. Effects of water velocity and turbulence on the behaviour of Iberian barbel (*Luciobarbus bocagei*, steindachner 1864) in an experimental pool-type fishway. *River Res. Appl*. **27**, 360–373.

Smith, D.L., Brannon, E.L., Odeh, M., 2005. Response of juvenile rainbow trout to turbulence produced by prismatoidal shapes. *Trans. Am. Fish. Soc*. **134,** 741–753.

Steffensen, J.F., Johansen, K., Bushnell, P.G., 1984. An automated swimming respirometer. *Comp. Biochem. Phys. A* **79** (3), 437–440.

Stokstad, E., 2010. Biologists rush to protect Great Lakes from onslaught of carp. *Science* **327** (5968), 932.

Taylor, R.M., Pegg, M.A., Chick, J.H., 2005. Response of bighead carp to a bioacoustic behavioral fish guidance system. *Fish. Manage. Ecol*. **12** (4), 283–286.

Tritico, H.M., Cotel, A.J., 2010. The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). *J. Exp. Biol.* **213** (13), 2284–2293.

Tudorache, C., Viaene, P., Blust, R., De Boeck, G., 2007. Longer flumes increase critical swimming speeds by increasing burst-glide swimming duration in carp *Cyprinus carpio* L. *J. Fish Biol*. **71** (6), 1630–1638.

Vowles, A.S., Kemp, P.S., 2012. Effects of light on the behaviour of brown trout (*Salmo trutta*) encountering accelerating flow: application to downstream fish passage. *Ecol. Eng*. **47**, 247–253.

Weaver, C.R., 1965. Observations on the swimming ability of adult American shad (*Alosa sapidissima*). *Trans. Am. Fish. Soc*. **94** (4), 382–385.

Webb, P.W., 1971. The swimming energetics of trout: i—thrust and power output at cruising speeds. *J. Exp. Biol*. **55** (2), 489–520.

Wei, Q.W., Ke, F.E., Zhang, J.M., Zhuang, P., Luo, J.D., Zhou, R.Q., Yang, W.H., 1997. Biology, fisheries and conservation of sturgeons and paddlefish in China. *Envion. Biol. Fish*. **48** (1–4), 241–255.

Wittmann, M.E., Jerde, C.L., Howeth, J.G., Maher, S.P., Deines, A.M., Jenkins, J.A., Whittledge, G.W., Burbank, S.R., Chadderton, W.L., Mahoon, A.R., Tyson, J.T., Gantz, C.A., Keller, R.P., Drake, J.M., Lodge, D.M., 2014. Grass carp in the Great Lakes region: establishment potential, expert perceptions, and re-evaluation of experimental evidence of ecological impact. *Can. J. Fish. Aquat. Sci*. **71** (7), 992–999.

Wu, J., Rao, He, B., 1992. *The history of the Chinese freshwater fisheries*. In: Liu, J., He, B. (Eds.), Cultivation of the Chinese Freshwater Fishes. Science Press, Beijing, China, pp. 5–29.

Xie, P., Chen, Y., 1999. Threats to biodiversity in Chinese inland waters. *Ambio* **28** (8), 674–681.

Yi, Y., Yang, Z., Zhang, S., 2010. Ecological influence of dam construction and river-lake connectivity on migration fish habitat in the Yangtze River basin, China. *Procedia Env. Sci*. **2**, 1942–1954.

Zhao, Z., 1980. Han Experiments on the current overcoming ability of some freshwater fishes. *J. Fish. China* **4** (1), 31–37.

Zheng, J., Han, D., Hu, W., Wang, X., Zhang, X., 2010. Fish swimming performance related to fishway design. *J. Hydroecol*. **3** (5), 104–110.

Zhili, G., Qinhao, L., Keming, A., 1990. *Layout and performance of Yangtang fishway*. In: Proceedings of the International Symposium on Fishways ‘90, Gifu, Japan.