

Critical swimming speed associated with body shape of Chinese sturgeon *Acipenser sinensis* under different rearing conditions

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Abstract

It was hypothesized that differences of body shape between pond-reared and tank-reared juvenile Chinese sturgeon *Acipenser sinensis* may influence their swimming ability, and thus may play an important role in their stocking into the native population. In this study, morphological characters and critical swimming speed (U_{crit}) of the pond-reared (body weight, $BW = 1426.0 \pm 53.8$ g, $n = 6$) and tank-reared ($BW = 1201.6 \pm 91.4$ g, $n = 6$) size-matched juvenile Chinese sturgeon were measured and compared. The U_{crit} of pond-reared sturgeon was 81.3 ± 3.2 cm/s (relative critical swimming speed, $U_{crit}' = 1.32 \pm 0.04$ SL/s), which was not significantly higher ($P > 0.05$) than that of the tank-reared cohort ($U_{crit} = 76.2 \pm 1.9$ cm/s, $U_{crit}' = 1.40 \pm 0.03$ SL/s). Rearing condition had some significant effects on 12 of morphological characters of the Chinese sturgeon at their early life stage ($P < 0.05$), but there was only a tendency to be difference between the body shape variations as defined by PC1 (body and caudal length, body depth and caudal filament length) from the principal component analysis (PCA) with 12 size-adjusted morphological characters of the two different cohorts ($P = 0.051$). There was a significant negative relationship between $Lg(U_{crit})$ (y) and PC1 (x), which could be described by the equation as follows: $y = 1.897 - 0.002x$ ($r^2 = 0.372$, $P = 0.035$). These results indicated that rearing condition could not significantly influence the swimming ability associated with body shape of the juvenile Chinese sturgeon, but we should select streamline-bodied juveniles when releasing them into nature. Furthermore, the findings may be useful for a fish way and culvert design due to stringent regulatory requirement.

Keywords: Swimming performance, Body shape, Rearing condition, Chinese sturgeon, *Acipenser sinensis*

Introduction

Chinese sturgeon *Acipenser sinensis*, a class I endangered species by the Chinese government (Wei et al. 1997), is an anadromous protected species that presently spawns only in the Yangtze (Changjiang) River, China. As a result of overfishing and construction of Gezhouba Dam in 1981 at Yichang, Hubei Province, 1,766 km from the river

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estuary, which blocked the spawning migration of Chinese sturgeon to the Yibin spawning reach, populations of Chinese sturgeon have greatly declined in abundance (Wei et al. 1997). Commercial fishing for Chinese sturgeon was prohibited after 1983, and as many as 100 adults have been removed annually to support a culture and restocking program (Xiao et al. 1999), but recruit population quantity of Chinese sturgeon decreased by 80% during 1981 to 1999 (Chang and Cao 1999). Research on Chinese sturgeon has focused on artificial culture, spawning, and population dynamics. Zhao et al. (1986) and Yi (1994) found that juveniles concentrated at the river estuary during the period May-September, and almost all the young sturgeon found in the estuary were younger than 1 year old. To date, the major measure for restoring the natural population of Chinese sturgeon was artificial breeding and restocking its juveniles into the midstream and downstream of the Yangtze River, directly. But people often ignore the selection of the individual fitness of the releasing fish.

Swimming performance is considered as a main character determining survival in many species of fish and other aquatic animals (Plaut 2001). Most fishes lack other weapons against predators, and thus swimming is their main way to avoid and survive their attack. Moreover, it is assumed that the maximal swimming performance maintained aerobically may strongly influence the ability of a fish to obtain food, find a mate, avoid unfavorable conditions, and so on. Thus, although rarely proven, it is suggested that swimming capability is a major trait affecting Darwinian fitness (Reidy et al. 2000; Plaut 2001). To evaluate the effects of different environmental conditions or pollutants on fish fitness or survival in an ecological system, a reliable, ecologically relevant measurement of swimming capability is required (Plaut 2001). As morphological diversity, the differences of swimming performance within and among species always contain the morphological inducements. Swimming ability among fishes can vary with differences in anatomy (e.g. position of fins and type of tail), physiology and behaviour (Webb 1993; Peake and Farrell 2006). While a relatively large amount of performance data has been collected for various salmonid species, comparatively little information exists for migratory nonsalmonids, such as Acipenseridae (sturgeons) (Peake 2004). Many studies on sturgeons reveal that burst exercise may not appear to play a large role in the swimming performance of juvenile sturgeons, but the aerobic swimming may be more important at this life-history stage (Belanger et al. 2001; Kieffer et al. 2001; Lankford et al. 2003; Baker et al. 2005; Kieffer et al. 2009). To date, how body size affect the swimming performance of sturgeons has not been entirely understood (Allen et al. 2006), and the swimming performance of Chinese sturgeon *Acipenser sinensis* is unknown.

It is known that rearing environment can affect many aspects of the fishes. Before releasing, the Chinese sturgeon may be stocked in large outdoor earthen ponds and indoor tanks. It was hypothesized that rearing conditions may influence the morphology, and thus affect their swimming capacity associated with the body shape. It is the first study to measure the critical swimming speed associated with body shape of the juvenile Chinese sturgeon reared under different conditions in a large swimming test flume, which will help us to improve the strategy to be more suitable and effective when releasing them into nature.

Materials and methods

Fish and rearing conditions

The Chinese sturgeon juveniles used here were propagated during November 2008, at the Gezhou dam Chinese sturgeon research institute, Hubei, China. A month later, sixty fry were transferred to an earthen pond (area 1500 m², water depth 1.8 m, pond-reared), where they were daily fed commercial diets (comprised of 42.2% protein, 10.3% lipid, 18.4% ash) at random. Another 40 Fry were transferred to an indoor laboratory at East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences (ECSFRI, CAFS), where they were raised in two 1000 l oval tanks with 20 in each (tank-reared) in an indoor re-circulating system. The fish were also daily fed commercial diets described above at random. After 20 months, ten juvenile pond-reared individuals were transferred to one of another two 1000 l oval tanks at ECSFRI, where they were fed commercial diets described above at random daily. All of the pond- and tank-reared sturgeon were not fed on the day before the start of the experiment.

Incoming non-chlorinated water was automatically filtrated, sterilized and constantly aerated to ensure high water quality. Throughout the outdoor reared period, the water temperature, dissolved oxygen and pH were maintained at 21.8 ± 1.5 °C, 7.8 ± 0.5 mg/l and 8.1 ± 0.7 (mean \pm SE), respectively. While during the indoor reared period, the water temperature, dissolved oxygen and pH were maintained at 22.8 ± 0.4 °C, 7.3 ± 0.1 mg/l and 8.8 ± 0.4 (mean \pm SE), respectively.

Morphological data collection

Before introduction into the swim-tunnels, fish (pond-reared sturgeon, $n = 6$; tank-reared sturgeon, $n = 6$) were anesthetized slightly with clove oil and measured for body weight (BW, g), maximum body depth (D_{Bmax} , cm) and maximum body width (W_{Bmax} , cm). For each individual fish, it was placed on a piece of blue polystyrene board, and a photograph was taken using a Sony H20 digital camera. The camera was set at about 1.5 m from the object to minimize potential wide-angle artefacts. Digital photographs were imported into TpsDig (Rohlf 2006), and thereafter the x and y co-ordinates of 13 homogenous points on the left side of each fish were digitized and captured (Fig. 1a), which was followed the truss method (Strauss and Bookstein 1982) modified by Taylor and Foote (1991). They consisted of one head depth, three body depths, one caudal depth, and seven distances between the 13 truss network landmark points (Fig. 1b). For each fish in total, 12 morphological measurements were collected including standard length ($M10 = SL$, cm).

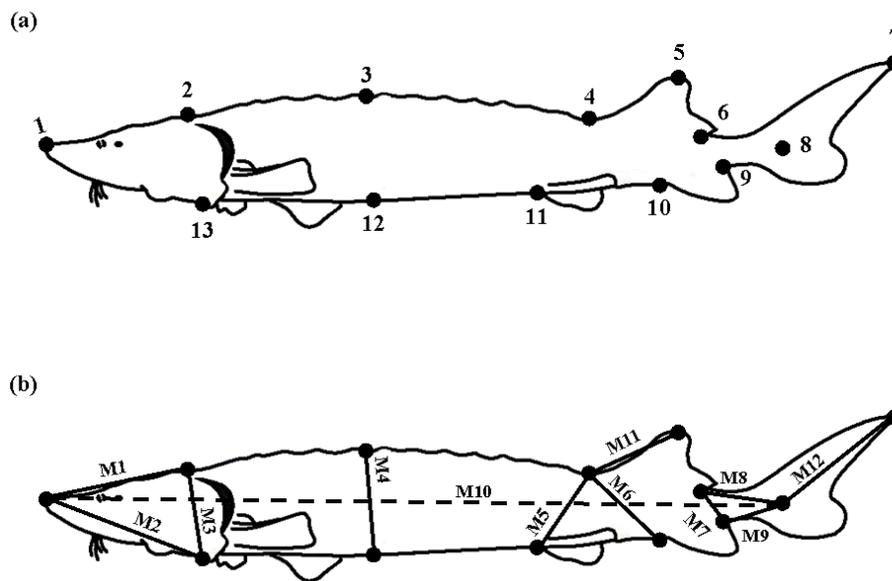


Fig. 1. Morphological Characters taken on the swimming pond-reared and tank-reared juvenile Chinese sturgeon *Acipenser sinensis* tested in swimming trials. (a) Locations for 13 landmarks identified on each sturgeon photograph. (b) Solid lines indicate the head length (M1 and M2), head depth (M3), body depth (M4, M5, M6), caudal depth (M7), caudal length (M8, M9), body length (standard length, M10), dorsal fin length (M11), caudal filament length (M12).

Swimming test

As an estimate of swimming performance, we measured critical swimming ability (U_{crit}) using a modified Brett-type swim chamber (Brett 1964). The swimming chamber consisted of a clear acrylic flume, which comprised of a rectangular swimming channel ($190 \times 50 \times 50$ cm). An impeller powered by a variable-speed motor (15 KW) cycled water through the flume. Each test fish was contained within the swim flume by 2×2 cm screening on its ends. To ensure laminar flow through the swim flume, two rectifier grids were placed at the upstream and downstream ends of the swimming flume. At the end of the flume, there was a stainless steel electrode (0-12 V) to drive the fish to swim against the water flow if necessary. Eight 15 W fluorescent lights were fixed 1 m above the flume to provide even illumination. Prior to the start of the experiment, each test fish was starved for 24 h. After being placed into the flume, the experimental fish was acclimated to a water velocity of 10 cm/s for 2 h. Thereafter, the sturgeon was forced to swim against a water velocity that increased by 10 cm/s every 10 min until fatigue velocity (when fish ceased swimming against a downstream electrified grid). Visual observation ensured that no erratic swimming behaviour or premature fatigue occurred during the swimming trial. During this period, the water temperature, dissolved oxygen and pH were maintained at 22.3 ± 0.9 °C, 7.0 ± 0.5 mg/l and 8.6 ± 0.3 , respectively.

U_{crit} was calculated according to the formula described by Brett (1964) as follows: $U_{crit} = u_i + (t_i/t_{ii}u_{ii})$, where u_i is the highest velocity maintained for the prescribed period (cm/s), u_{ii} is the velocity increment (10 cm/s), t_i is the time (min) fish swam at the 'fatigue' velocity and t_{ii} is the prescribed period of swimming (10 min). Each absolute value of the U_{crit} was converted to relative critical swimming speed in standard body lengths per second (U_{crit}' , SL/s). Cross-sectional area (a) of the sturgeon was calculated based on the equation: $a = \pi \times (0.5 D_{Bmax}) \times (0.5 W_{Bmax})$. Since the cross-sectional area of six pond-reared sturgeon and six tank-reared sturgeon were < 5% of the cross-sectional area of the swimming flume, we did not consider solid blocking effects that sometimes occur when fish of a given size swim in the flume (Bell and Terhune 1970).

Data analysis

All statistical analyses were performed with SPSS 15.0. Differences with $P < 0.05$ were considered significant. Values were expressed as mean \pm standard error (SE) in all cases. ANOVA was used to analyze the difference between pond-reared and tank-reared Chinese sturgeon for BM, SL and CF (condition factor, calculated as $CF = 100 BW SL^{-3}$) while ANCOVA was used for U_{crit} and U_{crit}' with water temperature (WT) during the test and individual SL as covariates, which were confirmed to meet the assumption of normality and equality of variance by Kolmogorov-Smirnov test and Levene's test, respectively. To remove size-dependant variation, all morphological variables were \log_{10} transformed and were corrected for size effects using Burnaby's method (Burnaby 1966; Rolf and Bookstein 1987). This correction method removed the isometric growth related variation by performing a principal component analysis (PCA) of data, setting the first principal component (PC) scores to zero and then reserving the PCA processes, back-transforming the principal component scores to a size-free data set so that patterns in allometric growth variation (i.e. shape) among the groups could be detected (Sheehan et al. 2005). Multivariate analysis of variance (MANOVA) was performed to assess body shape differences between the two sturgeon populations using the size-adjusted morphological characters. A PCA on the covariance matrix of size-adjusted morphological characters was carried out to summarize body shape differences between the two sturgeon populations.

With this ordination technique, the correlated multivariate data set was reduced into a smaller set of composite variables (PC) with a limited loss of information (McGarigal et al. 2000). For PCA, scores of factors with eigenvalue greater than the mean eigenvalue of all factors were used in further analysis. As there is no absolute rule for factor loading cut offs, the cut off value 0.6 was used to determine if a component-loading coefficient was strong. The differences in mean factor scores between the two cohorts were examined by ANOVA. A general linear model (GLM) with U_{crit} as dependent variable, cohort as a categorical factor and the PC axes which the differences were detected in mean factor scores between cohorts as independent variables, was used to reveal possible effects of morphology on swimming performance. The relationship between morphological characters and swimming abilities was explored by regressing $Lg(U_{crit})$ from each sturgeon on its corresponding factor score from the principal axes.

Results

Swimming performance

The fish used in the present study were size-matched in BM (ANOVA, $P > 0.05$), but pond-reared (R_p) sturgeon was much longer in SL than the tank-reared sturgeon (R_t) (ANOVA, $P < 0.01$), the R_p was much thinner than the R_t (ANOVA, $P < 0.01$) (Table 1). There was no significant difference in U_{crit} and U_{crit}' between the two different rearing cohorts (ANCOVA, for all $P > 0.05$) (Table 1).

Morphological comparison

The analysis based on 12 size-adjusted morphological characters indicated that there was significant difference in body shape between R_p and R_t (MANOVA, $P < 0.05$). Using PCA, 12 morphological characters were condensed into four PCs, which were extracted accounting for 86.3% of the total variance (Table 2). There was no significant relation between any principal axis and SL (for all correlations, $r^2 < 0.07$, $P > 0.05$), indicating that the effects of size were removed effectively by Burnaby's method. PC1 accounted for 28.6% of variance and summarized variation in body and caudal length, body depth and caudal filament length (Table 2). The R_p were not essentially separated from the R_t on PC1, but had a tendency to be different (ANOVA, $P = 0.051$). PC2, PC3, PC4 were not effective to identify difference between the two cohorts (ANOVA, for all $P > 0.05$; Fig. 2).

Table 1. Standard length (*SL*), Body weight (*BW*), Condition factor (*CF*), absolute critical swimming speed (U_{crit}) and relative critical swimming speed (U_{crit}') of pond-reared (R_p) and tank-reared (R_t) juvenile Chinese sturgeon *Acipenser sinensis* used in the swimming test (mean \pm SE).

	n	<i>SL</i> (cm)	<i>BW</i> (g)	<i>CF</i> (g cm ⁻³)	U_{crit} (cm/s)	U_{crit}' (<i>SL</i> /s)
R_p	6	61.6 \pm 0.8	1426.0 \pm 53.8	0.61 \pm 0.03	81.3 \pm 3.2	1.32 \pm 0.04
R_t	6	54.6 \pm 1.2	1201.6 \pm 91.4	0.73 \pm 0.02	76.2 \pm 1.9	1.40 \pm 0.03

	ANOVA			ANCOVA	
<i>F</i>	23.178	4.484	10.935	0.022	1.047
df	1, 10	1, 10	1, 10	1, 8	1, 8
<i>P</i>	0.001	0.060	0.008	0.887	0.336

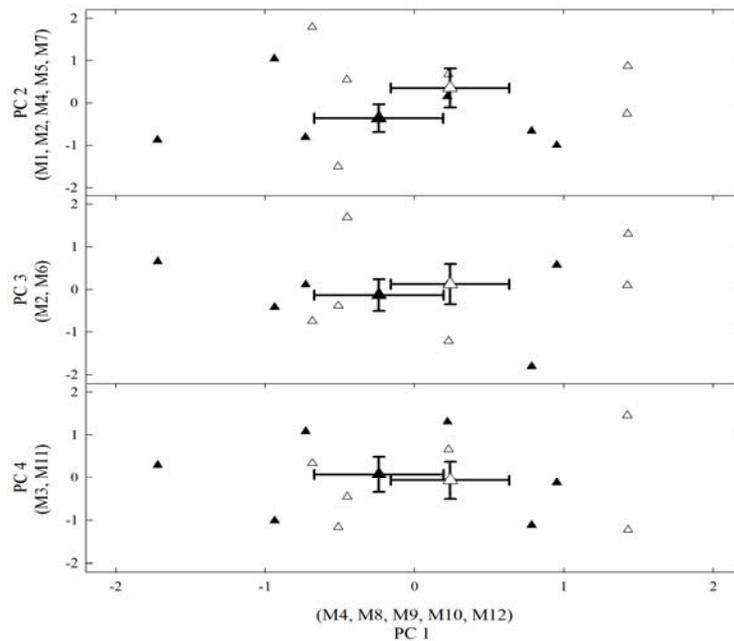


Fig. 2. Principal component (PC) scores from a principal component analysis (PCA) with 12 size-adjusted morphological characters (see Fig. 1) of pond-reared (\blacktriangle) and tank-reared (\triangle) juvenile Chinese sturgeon *Acipenser sinensis* used in the swimming tests for PC1 vs. PC2, PC3, PC4. The mean PC score for each cohort is indicated by larger solid symbol (SE of mean, horizontal and vertical bars).

Relationship between swimming performance and morphology

GLM analysis revealed that the morphology defined by PC1 had no significant effects on U_{crit} ($P > 0.05$). But there was a significant negative relationship between U_{crit} and PC1, which could be described by the equation as follows: $Lg(U_{crit}) = 1.897 - 0.002 \times PC1$ ($r^2 = 0.372$, $P = 0.035$; Fig. 3).

Discussion

This is the first study to examine the swimming performance associated with body shape of the juvenile Chinese sturgeon by measuring their critical swimming speeds and their body shapes, although there have been some research on the ontogenetic behaviour and migration of this species (Zhuang et al. 2002). It was clear that U_{crit} of the

Chinese sturgeon was $72 \sim 95$ cm/s (R_p , 81.3 ± 3.2 cm/s; R_t , 76.2 ± 1.9 cm/s), while the U_{crit} was $1.17 \sim 1.50$ SL/s (R_p , 1.32 ± 0.04 SL/s; R_t , 1.40 ± 0.03 SL/s). It corroborates what has been seen in other acipenserids. For example, U_{crit} values for sturgeons are low relative to other species of fishes (Peake 2004; McKenzie et al. 2007).

Table 2. Loading coefficients and percentage of total variance from a principal component analysis with 12 size-adjusted morphological characters (See Fig. 1) of the 12 juvenile Chinese sturgeon *Acipenser sinensis* used in the swimming tests (strong loadings indicated in bold).

Morphological character	Landmarks	Component loadings				
		PC 1	PC 2	PC 3	PC 4	
M1 (Head length 1)	1-2	0.205	-0.821	-0.486	-0.050	
M2 (Head length 2)	1-13	-0.138	-0.603	-0.715	0.192	
M3 (Head depth)	2-13	0.529	-0.053	0.195	0.739	
M4 (Body depth 1)	3-12	0.643	0.680	0.213	-0.042	
M5 (Body depth 2)	4-11	0.550	0.633	-0.369	-0.232	
M6 (Body depth 3)	4-10	0.029	-0.084	0.895	0.251	
M7 (Caudal depth)	6-9	0.152	0.810	-0.413	-0.076	
M8 (Caudal length 1)	6-8	-0.940	0.187	0.103	0.067	
M9 (Caudal length 2)	8-9	-0.759	0.120	0.471	-0.123	
M10 (Body length)	1-8	-0.695	0.414	-0.158	0.270	
M11 (Dorsal fin length)	4-5	0.042	-0.385	0.394	-0.667	
M12 (Caudal filament length)	7-8	0.637	-0.350	0.514	-0.015	
Eigenvalue		3.4	3.1	2.6	1.2	Total
Variation (%)		28.6	25.5	21.8	10.4	86.3

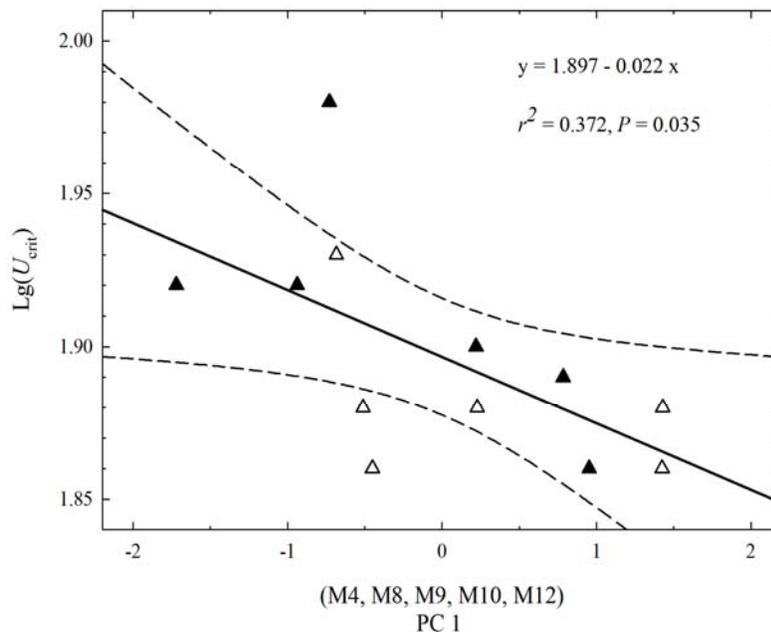


Fig. 3. The relationship between critical swimming speed (U_{crit}) and body shape variations as defined by PC1 from the principal component analysis (PCA) with 12 size-adjusted morphological characters (see Fig. 1) of pond-reared (▲) and tank-reared (△) juvenile Chinese sturgeon *Acipenser sinensis* used in the swimming tests. The curve was fitted (both groups) by $y = 1.897 - 0.022x$ ($r^2 = 0.372$, $P = 0.035$) (broken curves were the $\pm 95\%$ confidence intervals). The regressions for individual treatments tested separately were not significant (for all $P > 0.05$).

Environmental condition and genotype can significantly affect the morphology of fish in respect to the shape (Blaxter 1988; Wimberger 1992), allometric growth of the body (Koumoundouros et al. 1995, 1999), and meristic characters (Lindsey 1988), as well as development of morpho-anatomical abnormalities (Divanach et al. 1996). In the present study, although the rearing condition could only have a tendency to affecting the morphological characters, there was a negative relationship between the critical swimming speed and body shape when pooled the data of pond- and tank-reared juvenile Chinese sturgeon together, indicating that superior swimmers in this species possess longer body and caudal lengths, shallower body depth and shorter caudal filament length. In other words, no matter which rearing conditions this species cultured in, much streamlined shape of Chinese sturgeon may be a superior swimmer, which thus possess much higher survival fitness in nature. However, Swain et al. (1991) argued that deep-bodied fish with large median fins were superior burst swimmers, whereas streamlined fish could sustain swimming for longer periods of time. In the present study, however, size-matched individuals in body weight were selected, and we did not measure the burst swimming speed of the two groups under different rearing conditions, which could only partly represent the rearing condition effects, as well as the size-dependant effects. Further research should focus on effects of different size groups between these two rearing conditions.

Sturgeons have retained many ancestral body characteristics that distinguish them as a 'primitive' fishes. Among these primitive characteristics are the protective armour or scutes, a largely cartilaginous skeleton (Kynard 1997), the presence of a notochord, large and flattened rostrum, rigid pectoral fins and the shark-like heterocercal tail (Scott and Crossman 1973). These anatomical features can influence the swimming ability and the behaviour of sturgeons (Webb 1986; Wilga and Lauder 1999; Liao and Lauder, 2000; Peake 2004). In the present study, poorer performance of Chinese sturgeon may be related to body morphology of the fish like other sturgeons (Adams et al. 1997, 2003; Peake 2004; Allen et al. 2006; Kieffer et al. 2009). For instance, the large pectoral fins, flat ventral surface and large flattened rostrum suggest that sturgeons compensate for low swimming performance by modifying their swimming patterns (Webb 1986; Adams et al. 2003; Peake 2004; Kieffer et al. 2009). Moreover, with direct observations in the present study, like other sturgeons (Wilga and Lauder 1999; Kieffer et al. 2009), Chinese sturgeon used a burst-glide behaviour at higher speeds when challenged to increasing water velocities. Similarly, they also swam in close contact with the floor of the flume, a behaviour that was also shown for pallid sturgeon *Scaphirhynchus albus* (Adams et al. 2003) and shortnose sturgeon *A. brevirostrum* (Kieffer et al. 2009). This substratum appression has been suggested to be an important mechanism for sturgeons maintaining position against water current (Adams et al. 2003).

Maintaining position in high flow may also be partly achieved by fishes alternating between substratum skimming and station holding. In the present study, we observed that during station holding, fish normally pressed their abdomens to the flume floor and angled their fins in a direction that allowed the fish to press itself against the floor of the flume. Station holding became more difficult as water speed increased, and fish began to slide backwards by using their caudal fin for propulsion in the flume. This holding-gliding swimming behaviour was suggestive of an energetic cost-saving measure, as it was noticed in some cases that ventilation frequency would decrease slightly during the holding period. As we observed, once water speeds reached 50 cm/s, some individuals swam on their sides, with one pectoral fin pushed to the floor of the flume. In other cases, fish alternated between burst-glide swimming and then attempted to station hold. It should be noted that this latter behaviour may have been a reflection of the simplicity (i.e. smooth plexiglass floor) of the experimental flume, as water velocity affects substrate preference in Gulf sturgeon *A. oxyrinchus desotoi* Vladykov (Chan et al. 1997) and shortnose sturgeon *A. brevirostrum* (Kieffer et al. 2009). These behaviour patterns appear to be important for reducing the overall energetic costs associated with swimming in sturgeons (Peake 2004). Urgently, the behaviours and velocity preference of juvenile Chinese sturgeon should be quantized by future series studies.

Conclusions

The present study was the first research to examine the relationship between swimming performance and morphological characters of the juvenile Chinese sturgeon. Rearing condition in our study could not affect the body form of the Chinese sturgeon. And the critical swimming speed of Chinese sturgeon was lower than other species of fishes, which was negatively influenced by the principal morphological characters. As a result, superior swimmers in this species possessed longer body and caudal length, shallower body depth and shorter caudal filament length, that is, streamline-bodied shape of Chinese sturgeon may be a superior swimmer. Nevertheless, behaviours and velocity preference of this species with different body shape should be study in the near future. From an applied

perspective, we should select streamline-bodied shape of Juvenile Chinese sturgeon when releasing them into nature; moreover, the findings may be useful for a fish way and culvert design due to stringent regulatory requirement.

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References

- Adams SR, Adams GL, Parsons GR. 2003. Critical swimming speed and behaviour of juvenile shovelnose sturgeon and pallid sturgeon. *Trans Am Fish Soc* 132: 392-397.
- Adams SR, Parsons GR, Hoover JJ, Killgore KJ. 1997. Observations of swimming ability in shovelnose sturgeon (*Scaphirhynchus platyrhynchus*). *J Freshwater Ecol* 12: 631-633.
- Allen PJ, Hodge B, Werner I, Cech JJ. 2006. Effects of ontogeny, season, and temperature on the swimming performance of juvenile green sturgeon (*Acipenser medirostris*). *Can J Fish Aquat Sci* 63: 1360-1369.
- Baker DW, Wood AM, Litvak MK, Kieffer JD. 2005. Haematology of juvenile *Acipenser oxyrinchus* and *Acipenser brevirostrum* at rest and following forced activity. *J Fish Biol* 66: 208-221.
- Belanger JM, Son JH, Laugero KD, Moberg GP, Doroshov SI, Lankford SE, Cech JJ. 2001. Effects of short-term management stress and ACTH injections on plasma cortisol levels in cultured white sturgeon, *Acipenser transmontanus*. *Aquaculture* 203: 165-176.
- Bell WH, Terhune LDB. 1970. Water tunnel design for fisheries research. Fisheries Research Board of Canada. Technical report. no. 159, pp. 1-69.
- Blaxter JHS. 1988. Pattern and variety in development. In *Fish Physiology XIA* (Hoar WS. and Randall DJ, eds.), pp. 1-58. London: Academic Press.
- Brett JR. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Can J Fish Aquat Sci* 21: 1183-1226.
- Burnaby TP. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics* 22: 96-110.
- Chan MD, Dibble ED, Kilgore KJ. 1997. A laboratory examination of water velocity and substrate preference by age-0 Gulf sturgeons. *Trans Am Fish Soc* 126: 330-333.
- Chang J, Cao W. 1999. History and prospect of conservation on Chinese sturgeon in the Yangze river. *Acta Hydrobiol Sinica* 23: 712-720.
- Divanach P, Papandroulakis N, Anastasiadis P, Koumoundouros G, Kentouri M. 1997. Effect of water currents during postlarval and nursery phase on the development of skeletal deformities in sea bass (*Dicentrarchus labrax* L.) with functional swimbladder. *Aquaculture* 156: 145-155.
- Drucker EG. 1996. The use of gait transition speed in comparative studies of fish locomotion. *Am Zool* 36: 555-566.
- Kieffer JD, Arsenault LM, Litvak MK. 2009. Behaviour and performance of juvenile shortnose sturgeon *Acipenser brevirostrum* at different water velocities. *J Fish Biol* 74: 674-682.
- Kieffer JD, Wakefield AM, Litvak MK. 2001. Juvenile sturgeon exhibit reduced physiological responses to exercise. *J Experiment Biol* 204: 4281-4289.
- Koumoundouros G, Divanach P, Kentouri M. 1999. Osteological development of the vertebral column and of the caudal complex in *Dentex dentex*. *J Fish Biol* 54: 424-436.
- Koumoundouros G, Kiriakos Z, Divanach P, Kentouri M. 1995. Morphometric relationships as criteria for the evaluation of larval quality of gilthead sea bream. *Aqua Int* 3: 143-149.
- Kynard B. 1997. Life history, latitudinal patterns and status of the shortnose sturgeon, *Acipenser brevirostrum*. *Environ Biol Fish* 48: 319-334.
- Lankford SE, Adams TE, Cech JJ. 2003. Time of day and water temperature modify the physiological stress response in green sturgeon, *Acipenser medirostris*. *Comp Biochem Physiol A* 135: 291-302.
- Liao J, Lauder GV. 2000. Function of the heterocercal tail in white sturgeons: flow visualization during steady swimming and vertical maneuvering. *J Experiment Biol* 203: 3585-3594.
- Lindsey CC. 1988. Factors controlling meristic variation. In *Fish Physiology XIA* (Hoar, WS and Randall, DJ, eds.), pp. 197-274. London: Academic Press.

- McGarigal K, Cushman S, Stafford S. 2000. Multivariate Statistics for Wildlife and Ecology Research. New York, NY: Springer-Verlag.
- McKenzie DJ, Hale M, Domenici P. 2007. Locomotion in primitive fishes. In Primitive Fishes (McKenzie DJ, Farrell AP and Brauner CJ, eds.), pp. 319-380. Amsterdam: Elsevier Publishers.
- Peake SJ, Farrell AP. 2006. Fatigue is a behavioural response in respirometer confined smallmouth bass. *J Fish Biol* 68: 1742-1755.
- Peake SJ. 2004. Swimming and respiration. In Sturgeon and Paddlefish of North America (LeBreton GTO, Beamish FWH and McKinley RS, eds.), pp. 147-166. Dordrecht: Kluwer Academic Publishers.
- Plaut I. 2001. Critical swimming speed: its ecological relevance. *Comp Biochem Physiol A* 131: 41-50.
- Reidy SP, Kerr SR, Nelson JA. 2000. Aerobic and anaerobic swimming performance of individual Atlantic Cod. *J Experiment Biol* 203: 347-357.
- Rolf FJ, Bookstein FL. 1987. A comment on shearing as a method for 'size correlation'. *Systematic Zool* 36: 356-367.
- Scott WB, Crossman EJ. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin, 184. p. 966. Ottawa, Ontario.
- Sheehan TF, Kocik JF, Cadrin SX, Legault CM. 2005. Marine growth and morphometrics for three populations of Atlantic salmon from eastern Maine, USA. *Trans Am Fish Soc* 134: 775-788.
- Strauss RE, Bookstein FL. 1982. The truss: body form reconstructions in morphometrics. *Systematic Zool* 31: 113-135.
- Swain DP, Riddell BE, Murray CB. 1991. Morphological differences between hatchery and wild populations of Coho salmon (*Oncorhynchus kisutch*): Environmental versus genetic origin. *Can J Fish Aquat Sci* 48: 1783-1791.
- Taylor EB, Foote CJ. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *J Fish Biol* 38: 407-419.
- Webb PW. 1986. Kinematics of lake sturgeon, *Acipenser fulvescens*, at cruising speeds. *Can J Zool* 64: 2137-2141.
- Webb PW. 1993. Swimming. In *The Physiology of Fishes* (Evans, D., ed.), pp. 47-73. Boca Raton, FL: CRC Press.
- Wei Q, Ke F, Zhuang P, Luo J, Zhou R, Yang W. 1997. Biology, fisheries, and conservation of sturgeons and paddlefish in China. *Environ Biol Fish* 48: 241-255.
- Wilga CD, Lauder GV. 1999. Locomotion in sturgeon: function of pectoral fins. *J Experiment Biol* 202: 2413-2432.
- Wimberger PH. 1992. Plasticity of fish body shape: the effects of diet, development, family and age in two species of Geophagus (Pisces: Cichlidae). *Biol J Linnean Soc* 45: 197-218.
- Xiao H, Chang J, Liu Y. 1999. Evaluation on status of artificial propagation and releasing of Chinese sturgeon in the Yangtze River. *Acta Hydrobiol Sinica* 23: 572-576.
- Yi J. 1994. Investigation on the resources of young Chinese sturgeon in the Yangtze River. *J Gezhouba Hydropower* 1: 53-58.
- Zhao Y, Huang X, Yu Z. 1986. Investigation on the status of young Chinese sturgeon in the Yangtze River. *Reservoir Fish* 6: 38-41.
- Zhuang P, Kynard B, Zhang L, Zhang T, Cao W. 2002. Ontogenetic behavior and migration of Chinese sturgeon, *Acipenser sinensis*. *Environ Biol Fish* 65: 83-97.