



Oxygen consumption and swimming behavior of juvenile Siberian sturgeon *Acipenser baerii* during stepped velocity tests

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ABSTRACT: Oxygen consumption rate (MO_2) and critical swimming speed (U_{crit}) of juvenile Siberian sturgeon *Acipenser baerii* were measured at 24°C using a step-wise velocity test in a flume-type respirometer. Swimming behavior was video-recorded before and after the swimming experiment in a respirometer and an open tank. The relationship between MO_2 and swimming speed (U) can be accurately described by a power function. The U_{crit} of *A. baerii* was found to be 2.28 ± 0.09 body lengths (BL) s^{-1} or 0.51 ± 0.05 $m s^{-1}$. The standard metabolic rate was calculated to be 149.24 $mg O_2 kg^{-1} h^{-1}$, and measured maximum metabolic rate (MMR) was 385.04 $mg O_2 kg^{-1} h^{-1}$. This is a relatively low MMR, resulting in a low metabolic scope, and is consistent with the low U_{crit} of juvenile sturgeon. Excess post-exercise oxygen consumption, measured over a 60 min recovery period, was 65.20 $mg O_2 kg^{-1}$. Therefore, *A. baerii* possess high fatigue recovery capability. Tail beat frequencies increased significantly with U , but there was very little change in tail beat amplitude, and results differed between respirometer and open tank observations. Our results provide data on the physiology and behavior of *A. baerii* and will help to support conservation of this important species.

KEY WORDS: Siberian sturgeon · Swimming capability · Swimming behavior · Oxygen consumption

INTRODUCTION

The Siberian sturgeon *Acipenser baerii* is mainly distributed in the Siberian region of the Russian Arctic, but a small part of the natural distribution of this species occurs in the Irtysh River in China. During May–June it migrates to the upper reaches of rivers for spawning. Its population is declining, mainly due to a reduction of spawning areas caused by damming, overfishing and environmental pollution (Billard & Lecointre 2000). One of the potential

solutions to the migration problem is to incorporate fishpass facilities into dams and other hydrologic barriers.

Protocols for testing swimming performance are well established and the results are of interest to fish physiologists as they provide design criteria for the construction of fish passages (Brett 1964, Yagci 2010, Fu et al. 2013). Successful fish passage design relies on information on fish swimming performance, specifically, physiological condition and swimming behavior (Thiem et al. 2011, Cooke & Hinch 2013, Hatry et

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al. 2014). To improve the effectiveness of fish passage for larger species, designs can be enhanced by incorporating orifices into the traditional pool and weir design, as reported in previous studies of the swimming performance of sturgeons (He et al. 2013, Cai et al. 2013). For example, the minimal slot width (in the vertical slot model) can be determined by the largest tail beat amplitude (TBA), and the slot velocities of upstream fishways should be lower than critical swimming speed (U_{crit}) of the fish in downstream fishways (Tu et al. 2011). It is easy to evaluate costs of activities such as migrating by measuring tail beat frequency (TBF) and observing body movements of the fish (Ohlberger et al. 2007). Excess post-exercise oxygen consumption (EPOC) can be used to determine recovery time after fatigue, and resting pools should usually be required in fishways (Cai et al. 2013). Other important design considerations include fish physiology, flow velocity and hydraulic conditions (Roscoe & Hinch 2010, Katopodis & Williams 2012).

Measurement of fish swimming performance is based on fish swimming against the flow in a swim channel under specified conditions (Brett 1964). U_{crit} is measured to estimate maximum swimming speed and maximum metabolic rate (MMR) (Marras et al. 2013, Cai et al. 2014a).

The present study focused on swimming performance in a series of laboratory experiments of juvenile *A. baerii*. The objectives of the study were to: (1) examine the effects of a change in flow velocity on oxygen metabolism and swimming behavior, to find a potential predictor for energy expenditure, and (2) monitor post-exercise metabolism and swimming behavior during the recovery period from fatigue after swimming to U_{crit} .

MATERIALS AND METHODS

Test fish

Juvenile Siberian sturgeon *Acipenser baerii* were obtained from the institute of Chinese sturgeon research, China Three Gorges Project Corporation, in Yichang (30°56'N, 111°15'E). The sturgeon ranged in body length from 16.5 to 21.2 cm and in body mass from 21.2 to 37.2 g. Test fish were acclimated for 2 wk in the laboratory in dechlorinated freshwater at ambient temperature (23.0 to 25.0°C), with dissolved oxygen (DO) above 6.5 mg l⁻¹, and under a natural photoperiod. Fish were fed to satiation once daily on a commercial diet (pro-

tein >38%, fat >5%, fiber <5%, ash <12%, moisture <11%) and uneaten food and feces were removed. One-third of the water in each tank was replaced daily after feeding. Test fish were fasted for 48 h prior to testing.

Experimental apparatus

Tests were carried out in a temperature-controlled flume-type respirometer with a 6 l swimming chamber (60 × 10 × 10 cm, length × width × height) with sensor mounts for temperature and DO. The flow velocity was measured with a current meter (Vectrino, Nortek) and DO was measured using a DO meter (Hach). The flow velocity was controlled with a propeller driven by a 350 watt variable-speed motor and current transducer to give a water velocity range of 0.08–1.37 m s⁻¹. A charge coupled device (CCD) video camera (S423C) was placed directly over and perpendicular to the swimming chamber at a height of 0.50 m to record fish swimming behavior. Swimming speed (U) was analyzed with SwisTrack, an open-source tracking tool for biological systems developed at the Swiss Federal Institute of Technology (Corell et al. 2006).

In addition to the respirometer, a 60 l open tank (60 × 40 × 25 cm) was used to test fish swimming behavior, and the tank was equipped with a CCD recorder mounted 0.5 m above the surface.

Swimming performance

At first, a single fish ($n = 6$) was placed in the open tank and allowed to acclimate for 12 h. Fish behaviour was monitored with the CCD recorder, and we obtained 10 min records at 09:00, 12:00, 15:00 and 18:00 h. Then a stepped velocity test (Brett 1964, Cai et al. 2013) began, and the fish ($n = 14$) was placed in the swim chamber (respirometer) and allowed to acclimate to a low current velocity (~0.10 m s⁻¹) for 120 min. The velocity was subsequently raised in 0.5 body length (BL) increments every 30 min until the fish was exhausted. Each 30 min interval included 5 min for stabilization, 20 min of DO measurement and 5 min of flushing with aerated water. The test fish was exhausted when it did not resume swimming after being brought back to the front of the swimming channel 3 times using a small net. U_{crit} was calculated as described by Brett (1964):

$$U_{crit} = U_1 + U_2 (T_1/T_2) \quad (1)$$

where U_1 is the highest speed attained, U_2 is the speed increment (0.5 BL s^{-1}), T_1 is the time elapsed at fatigue speed, and T_2 is the interval time (30 min). The absolute values (m s^{-1}) were converted to relative swimming speed in body lengths per second (BL s^{-1}).

After the speed test, one group (total $n = 8$) was left in the swimming chamber and used in the respiration study. The velocity was reset to 0.5 BL s^{-1} and the DO in the respirometer was recorded every 10 min for 60 min. The remaining fish (total $n = 6$) were immediately removed from the swimming chamber using a knotless net, and placed in the open tank where the behavior of the exhausted fish was monitored by the CCD camera. Fish were recorded for 5 min every 10 min for 60 min, and these videos were used to analyze the swimming behavior (TBF, TBA and U) with SwisTrack.

Oxygen consumption

Oxygen consumption rate (MO_2 ; $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) was measured by recording oxygen concentration over time as the sturgeon swam at a designated speed for 30 min. The steps were repeated during the acclimation period and periods of elevated swimming speed. MO_2 was calculated from the slope of the decline in DO in the swimming chamber during each measurement period. The swimming chamber DO decreased $0.20\text{--}0.45 \text{ mg l}^{-1}$ each 10 min, depending on the size and swimming speed of the fish. The respirometer was then flushed with aerated water from an external tank for 5 min to keep DO levels above 75% (Tierney 2011).

MO_2 was determined from the slope of the linear regression of DO versus time over the 20 min measuring period using the formula:

$$\text{MO}_2 = V[d(\text{DO})/dt]M^{-1} \quad (2)$$

where V is the respirometer volume (l), $d(\text{DO})/dt$ is the slope ($\text{mg O}_2 \text{ h}^{-1}$), i.e. the linear regression of the decrease in DO with time, and M is the fish mass (kg). Background DO without fish was measured repeatedly and found to be negligible (the oxygen consumption rate of ammonia contamination or bacterial oxidation in the system was $<1\%$ of the oxygen consumption rate of the test fish, and therefore of negligible impact) (Cai et al. 2014a).

During the swimming period, variation of MO_2 with U was obtained by fitting the data to the function:

$$\text{MO}_2 = a + bU^c \quad (3)$$

where a , b and c are constants, and c is the speed exponent. The standard metabolic rate (SMR) was esti-

mated from the equation above with U set to zero. Following the low current velocity in the swimming chamber, MO_2 was measured over a period of 30 min (MO_2 routine, or RMR). The maximum metabolic rate (MMR) is the maximum value of MO_2 during the U_{crit} test (Norin & Clark 2016). The metabolic scope (MS) was calculated as MMR divided by SMR (Steinhausen et al. 2005). EPOC ($\text{mg O}_2 \text{ kg}^{-1}$) is oxygen consumption following exhaustive exercise, and is equal to the oxygen required during the post-exercise return to RMR (the area under the MO_2 curve and above the RMR during the recovery period) (Lee et al. 2003).

TBF and TBA

The fish were filmed at 25 frames per second with a CCD camera mounted at a height of 0.5 m above the respirometer. The film was played back in slow motion to determine TBF and TBA. Video recordings were analyzed to obtain TBF and TBA at the various swimming speeds. TBF was determined by counting the number of complete tail beat cycles per minute at a constant water flow velocity. TBA was determined by measuring the maximum distance that the tip of the tail moved from one lateral extent to the other. TBA (BL) is calculated as the maximum distance divided by body length.

Statistics

Statistical analysis was carried out using SPSS and Origin software packages. The effects of swimming speed on MO_2 , TBF and TBA were analyzed using repeated-measures ANOVA. The level of significance was determined by multiple comparisons (least significant difference). Raw data of TBF and TBA obtained in the open tank were used to plot the linear function. The data are given as means \pm SE, with $p < 0.05$ being considered statistically significant.

RESULTS

The relationship between MO_2 and U in juvenile Siberian sturgeon *Acipenser baerii* is shown in Fig. 1. SMR was $149.24 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ and MMR was $385.04 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$. MMR was 2.58-fold higher than SMR. EPOC at 60 min was $65.20 \text{ mg O}_2 \text{ kg}^{-1}$.

Prior to the test, a single fish, while swimming freely in the open tank, displayed no significant variation in speed ($1.90 \pm 0.12 \text{ BL s}^{-1}$, or $0.35 \pm 0.01 \text{ m s}^{-1}$; Fig. 2).

Mean U_{crit} was $2.28 \pm 0.09 \text{ BL s}^{-1}$, or 0.51 m s^{-1} . The test fish stopped swimming when the water velocity in the respirometer was increased from 0.45 to 0.56 m s^{-1} . After the 60 min recovery period, the recovery U ($1.42 \pm 0.05 \text{ BL s}^{-1}$, or $0.27 \pm 0.01 \text{ m s}^{-1}$) of the test fish in the open tanks had not returned to the average speed observed prior to testing.

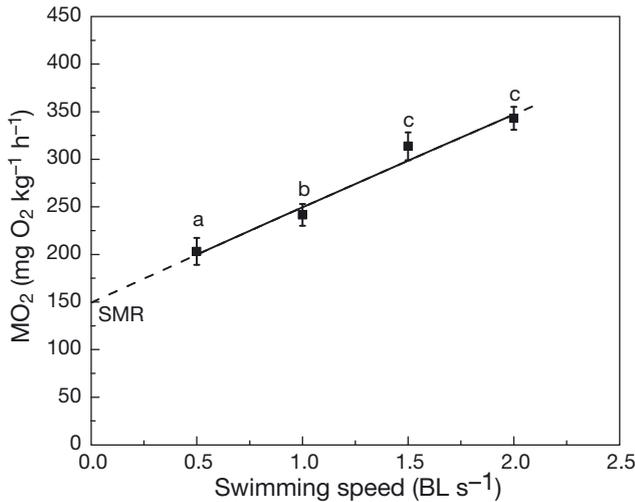


Fig. 1. Oxygen consumption rate (MO_2) versus swimming speed in *Acipenser baerii*. MO_2 was expressed as a power function of swimming speed (U) by the equation $\text{MO}_2 = 149.24 + 101.76U^{0.97}$ ($R^2 = 0.93$, $p < 0.001$). SMR: standard metabolic rate. Different lowercase letters denote a significant difference in variations of swimming speed ($p < 0.05$)

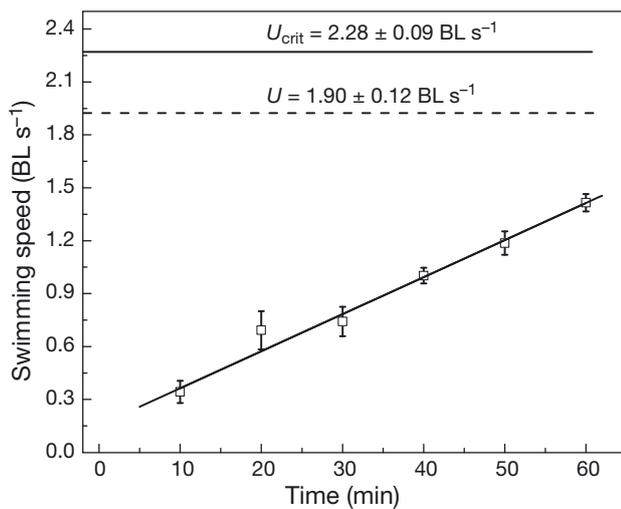


Fig. 2. Recovery from fatigue in *Acipenser baerii* measured over 60 min after the stepped velocity test. Mean (\pm SE) swimming speed (U) prior to the test was $1.90 \pm 0.12 \text{ BL s}^{-1}$ ($0.35 \pm 0.01 \text{ m s}^{-1}$; horizontal dashed line). Horizontal solid line is U_{crit} ($2.28 \pm 0.09 \text{ BL s}^{-1}$, or $0.51 \pm 0.05 \text{ m s}^{-1}$; horizontal solid line). Following fatigue, fish transferred to an open tank swam very slowly at first and then increased their speed but did not completely recover

The results indicate that TBF can be used to estimate U . U plotted against TBF gave a significant linear correlation in both the respirometer and the open tank (Fig. 3). TBF increased significantly with U ($p < 0.05$). At the same U , the TBF was lower in the open tank than in the respirometer, although the difference was not significant. The relationship between TBA (BL) and U is displayed in Fig. 4, and the TBA observed in the respirometer and open tank are different.

DISCUSSION

Oxygen consumption and swimming performance

Aerobic metabolic expenditure for swimming is typically quantified by measuring the MO_2 , as swimming speed increases incrementally at regular time intervals. The model assumes that energy expenditure increases with swimming speed (Ohlberger et al. 2007, Clark et al. 2013). In previous studies (Lee et al. 2003, Cai et al. 2013, 2014b), MO_2 and U were expressed in a power equation, linear equation or exponential function. Considering the present results, the speed exponent is very close to 1, and thus it can be expressed in a linear equation as $\text{MO}_2 =$

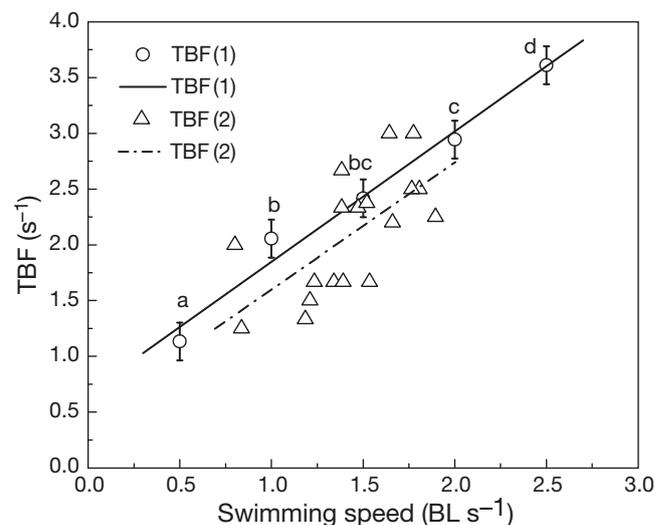


Fig. 3. Tail beat frequency (TBF) versus swimming speed in *Acipenser baerii* in the respirometer and open tank. Open circles: TBF in the respirometer (before fatigue); open triangles: TBF in the open tank (after fatigue); solid line: linear correlation between TBF and swimming speed (U) in the respirometer, $\text{TBF}(1) = 1.28U + 0.43$ ($R^2 = 0.97$, $p < 0.01$); dot-dashed line: linear correlation between TBF and swimming speed in the open tank, $\text{TBF}(2) = 1.14U + 0.46$ ($R^2 = 0.40$, $p < 0.01$). Different lowercase letters denote a significant difference in variations of swimming speed ($p < 0.05$)

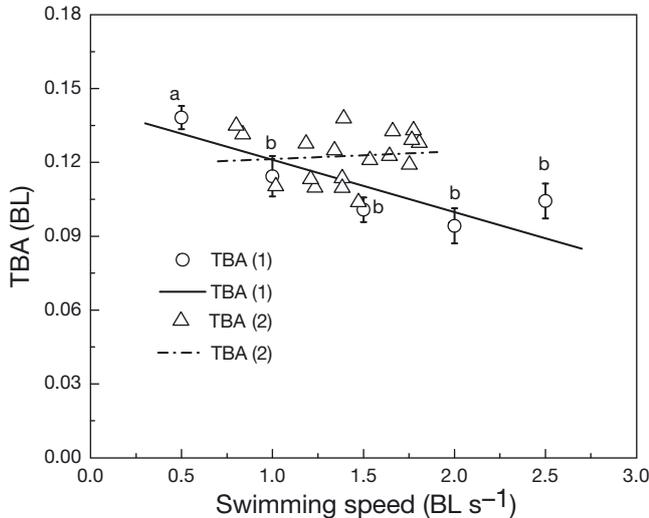


Fig. 4. Tail beat amplitude (TBA[BL]) versus swimming speed in *Acipenser baerii* in the respirometer and open tank. Open circles: TBA in the respirometer (before fatigue); open triangles: TBA in the open tank (after fatigue); solid line: linear correlation between TBA, and swimming speed in the respirometer, $TBA(1) = -0.02U + 0.15$ ($R^2 = 0.64$, $p = 0.06$); dot-dashed line: linear correlation between TBA and swimming speed in the open tank, $TBA(2) = 0.003U + 0.13$ ($R^2 = 0.39$, $p = 0.79$). Different lowercase letters denote a significant difference in variations of swimming speed ($p < 0.05$)

$151.19 + 98.03U$ ($R^2=0.96$, $p < 0.05$), whereas the swimming speed index obtained by the power equation can be used for comparison with other species. Therefore, in this paper we simultaneously used 2 ways to express the relationship between MO_2 and U , but the model fit shown in Fig. 1 used the power equation. The speed exponent, obtained from the power equation, is 1.31 for juvenile *Acipenser schrenckii*, 1.20 for *A. sinensis* (Cai et al. 2013, 2014a) and 0.96 for *A. baerii*. The range for several cyprinid species is 1.1 to 3.0 (Videler & Nolet 1990). The value of the speed exponent is inversely related to swimming efficiency (Tu et al. 2012, Cai et al. 2014b). For sturgeons, including *A. baerii*, the speed exponent is low, indicating a high swimming efficiency. It has been suggested that low MS indicates a low aerobic capacity and activity (Steinhausen et al. 2005), with juvenile *A. schrenckii* achieving a metabolic scope of 2.12 at 20°C (Cai et al. 2013), in comparison to 1.71 at 18°C and 1.45 at 26°C for juvenile paddlefish (*Polyodon spathula*) (Aboagye & Allen 2014). The present results showed that a 2.58-fold increase in metabolic rate could be achieved by *A. baerii*. The relatively low MMR resulted in a low MS, in accordance with the low U_{crit} and high swimming efficiency achieved by juvenile sturgeon.

EPOC is used as an indicator of anaerobic capacity and includes the oxygen required to restore tissue and cellular oxygen and high-energy phosphates (Scott 1998), metabolic imbalances in lactate and glycogen (Arthur et al. 1992, Meyer-Rochow et al. 1994), and the necessary ionic and osmotic balance (Byrne et al. 1972). It has been suggested that EPOC is lower and recovery more rapid in active fish due to higher cardio-respiratory capacity and the ability to extract oxygen from the environment and distribute it to the tissues more rapidly (Hancock & Gleeson 2008). However, the cost of such a high-capacity cardio-respiratory system is a high expenditure of maintenance energy, as suggested by the higher pre-exercise MO_2 in fasting carps (Cai et al. 2014b). In the present study, EPOC, measured over a 60 min recovery period, was $65.20 \text{ mg O}_2 \text{ kg}^{-1}$ for *A. baerii*, a relatively low value, indicating a high recovery capability, so that resting pools for fishways can be less extensive.

Previous work has suggested that transgenic-induced changes in morphology have contributed to differences in MO_2 . For example, differences in white and red muscle distributions, related to the volume fraction of mitochondria and aerobic capacities, have been reported in the sturgeon *A. stellatus* (Kryvi et al. 1980), and changes were demonstrated in red and white muscle of actively swimming, riverine versus more stationary lacustrine *Retropinna retropinna* individuals (Meyer-Rochow & Ingram 1993). Furthermore, it appears that sequential exercise improves the rate of recovery sufficiently to induce a 'training effect'. According to Milligan et al. (2000), test fish recover from handling stress more quickly if the swimming chamber or tunnel water velocity is adjusted to 0.5 BL s^{-1} , rather than no flow. For this reason, fatigue recovery in the present study was carried out at a water velocity of 0.5 BL s^{-1} .

TBF and TBA

Field estimates of swimming speeds are important in the context of behaviors such as foraging, migration or predator-prey interactions. TBF is often used as an indicator of swimming behavior and has been shown to correlate positively with swimming speed (Ohlberger et al. 2007). Based on the significant correlation between TBF and U , the present investigation has quantified the relationship for *A. baerii*. The constraining effect of the swimming chamber clearly affects TBA more than TBF, and that seems reasonable as the chamber produces a wall effect that would constrain the amplitude more than the frequency.

In the present study, it was also observed that *A. baerii* modify their swimming behavior by station-holding (i.e. modifying the angle of the pectoral fins against the bottom of the swim tunnel to generate negative lift [Liao 2007] or substrate skimming [Kieffer et al. 2009]). It has also been suggested that consistent swimming performance results in high TBF variability in U_{crit} determinations in the respirometer, because of the initiation of swimming at high speeds to specifically avoid station-holding behavior (Deslauriers & Kieffer 2012). It was therefore expected that TBF would be negatively correlated with station-holding at any given velocity. Webb (1993) studied *the swim tunnel wall effects in steelhead trout Oncorhynchus mykiss*; TBF and TBA decreased with spacing between solid walls, and fish did less work when swimming near a wall. However, U_{crit} was lower for fish swimming between walls. Swimming and resting on the bottom in their natural habitat allowed the fish to remain concealed between rocks and in crevices, protecting them from predators and reducing the energy required to swim against the current.

CONCLUSIONS

This study provides information on MO_2 , U_{crit} , TBF and TBA of *Acipenser baerii* at ca. 24°C tested by step-wise velocity increments in a flume-type respirometer. *A. baerii* swimming performance is low, but swimming efficiency is high, whereas the energy cost of transport is low, associated with the fish's long-distance migratory habit. Station-holding behaviors frequently limit the swim speeds considerably. Therefore, station-holding behavior should be considered in future studies on migrating risk assessments.

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