



Integrating Water Flow, Locomotor Performance and Respiration of Chinese Sturgeon during Multiple Fatigue-Recovery Cycles

Lu Cai¹, Lei Chen², David Johnson^{3,4}, Yong Gao², Prashant Mandal³, Min Fang^{1,3}, Zhiying Tu^{1,3}, Yingping Huang^{1,3*}

1 Collaborative Innovation Center for Geo-Hazards and Eco-Environment in Three Gorges Area, Hubei Province, Yichang, PR China, **2** Institute of Chinese Sturgeon Research, China Three Gorges Project Corporation, Yichang, PR China, **3** Engineering Research Center of Eco-environment in Three Gorges Reservoir Region, Ministry of Education, China Three Gorges University, Yichang, PR China, **4** School of Natural Sciences and Mathematics, Ferrum College, Ferrum, Virginia, United States of America

Abstract

The objective of this study is to provide information on metabolic changes occurring in Chinese sturgeon (an ecologically important endangered fish) subjected to repeated cycles of fatigue and recovery and the effect on swimming capability. Fatigue-recovery cycles likely occur when fish are moving through the fishways of large dams and the results of this investigation are important for fishway design and conservation of wild Chinese sturgeon populations. A series of four stepped velocity tests were carried out successively in a Steffensen-type swimming respirometer and the effects of repeated fatigue-recovery on swimming capability and metabolism were measured. Significant results include: (1) critical swimming speed decreased from 4.34 bl/s to 2.98 bl/s; (2) active oxygen consumption (i.e. the difference between total oxygen consumption and routine oxygen consumption) decreased from 1175 mgO₂/kg to 341 mgO₂/kg and was the primary reason for the decrease in U_{crit} ; (3) excess post-exercise oxygen consumption decreased from 36 mgO₂/kg to 22 mgO₂/kg; (4) with repeated step tests, white muscle (anaerobic metabolism) began contributing to propulsion at lower swimming speeds. Therefore, Chinese sturgeon conserve energy by swimming efficiently and have high fatigue recovery capability. These results contribute to our understanding of the physiology of the Chinese sturgeon and support the conservation efforts of wild populations of this important species.

Citation: Cai L, Chen L, Johnson D, Gao Y, Mandal P, et al. (2014) Integrating Water Flow, Locomotor Performance and Respiration of Chinese Sturgeon during Multiple Fatigue-Recovery Cycles. PLoS ONE 9(4): e94345. doi:10.1371/journal.pone.0094345

Editor: Josep V. Planas, Universitat de Barcelona, Spain

Received: December 16, 2013; **Accepted:** March 12, 2014; **Published:** April 8, 2014

Copyright: © 2014 Cai et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This work was supported by Major Science and Technology Program for Water Pollution Control and Treatment in the National Twelfth Five-Year Plan of China (Grant number: 2012ZX07104-002-04) and the National Nature Science Foundation of China (Grant number: 50979049, 51309140). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: yingpinghuang@126.com

Introduction

Water flow is commonly believed to be of an important environmental factor to fish. Natural selection favors locomotor and respiration strategies appropriate for an existing flow [1]. Chinese sturgeon (*Acipenser sinensis*, Gray 1834) has been listed as Class I Endangered Species by the Chinese Government [2] and is also listed as Critically Endangered (CR) in the IUCN Red List of Threatened Species (version 2013.1). The species is anadromous and currently occurs only in the middle and lower reaches of the Yangtze River and near-shore in the Yellow and East China Seas [3]. Although captive breeding of Chinese sturgeon is now feasible [4,5], wild populations have declined significantly because of dam construction, overfishing and pollution [6–10]. Chinese sturgeon once migrated further than any other sturgeon, over 3,200 km in the Yangtze River. Restoration of the wild sturgeon populations is difficult due to long maturation time, infrequent spawning and low productivity [11–12]. Although the species has a life span of 50–60 years, the species breeds only three or four times and the hatchling survival rate is estimated at <1%.

Dam construction has blocked spawning migration [13] and the sturgeon populations have declined dramatically [10].

Augmenting wild populations by release of captive breed sturgeon is a great achievement for species conservation but not sufficient. Building fishways that allow migration is another important part of the effort to maintain wild populations [14,15]. Data on swimming capability and the physiological response to exercise and fatigue provide important design criteria for fishways [16–19].

Publications on Chinese sturgeon have been more frequent in recent years [20] but have focused on biochemistry and habitat assessment. Research on swimming capability and excess post-exercise oxygen consumption, for one repetition, has been reported (e.g., [21–24]). However, fish typically undergo multiple fatigue-recovery cycles while moving through fishways of large dams [25] and data on the effects of repeated fatigue-recovery is necessary for the design of effective fishways. In this study, the effect of repeated fatigue-recovery cycles on swimming capability and metabolism were investigated using a stepped velocity test in a Steffensen-type swimming respirometer. The study documents the change in respiration and swimming capability of fish undergoing repeated fatigue-recovery cycles. These results contribute to our understanding of the physiology of the Chinese sturgeon and

support the conservation efforts of wild populations of this important species.

Materials and Methods

Ethics Statement

This study was conducted in strict accordance with the laws governing animal experimentation in China. The protocol was approved by the China Three Gorges University. All efforts were made to minimize suffering.

Test fish

Juvenile sturgeon were obtained from the institute of Chinese sturgeon research, China Three Gorges Project Corporation, in Yichang, China (30°56' N; 111°15' E) and were of the second filial generation of cultured Chinese sturgeon. The sturgeon (body length: 10.89±0.11 cm and body weight 8.38±0.27 g, mean ± S.E.) were maintained in cylindrical tanks (80 cm in diameter and 90 cm deep). They were fed to satiation each morning at 8:00 am with Tubificidae. Water temperature varied from 19.3°C to 20.8°C and dissolved oxygen (*DO*) maintained above 7.0 mg/L. Ammonia-N and nitrite-N were lower than 0.050 mg/L and 0.007 mg/L, respectively. Forty eight hours prior to the experiment, feeding was interrupted to prevent the elevated oxygen consumption rate associated with digestion [26].

Respirometer

The sturgeon were tested in a sealed 14 L Steffensen-type swimming respirometer submerged in a 55.7 L tank (84.0 cm long ×39.9 cm wide ×17.0 cm deep) to maintain temperature. A schematic diagram of the respirometer was included in an earlier publication [27]. Respirometer components include a motor with speed controller and propeller and a rectangular swimming chamber (4.5 L, 35.5 cm long ×11.0 cm wide ×11.5 cm deep) with a Lucite multi-aperture rectifier at the entrance to maintain laminar flow and a wire grid at the exit. Normal respirometer operating assumptions were made: (1) swimming speed (*U*) is equal to water flow speed as measured with an acoustic Doppler velocity meter (Nortek AS, Oslo, Norway), and (2) oxygen consumption can be calculated from the change in dissolved oxygen, as measured by an oxygen electrode (Hach HQ30d, Loveland, USA).

Protocol for stepped velocity test

Ten sturgeons were tested and the body length (bl), fork length, total length and body mass of each sturgeon were measured. Before testing, fish were acclimated overnight in the respirometer at a very low flow speed (0.3~0.5 bl/s) and then allowed to swim at 0.5 bl/s from 7:00–8:00 am the next morning [12,28]. When testing began, flow speed was increased by 0.5 bl/s every 20 min and dissolved oxygen was measured at 5 min intervals. When the sturgeon was exhausted (swimming ceased and the fish rested against the wire grid for 20 s), flow speed was adjusted to 0.5 bl/s during the 30 min recovery period [27]. This comprises a single stepped velocity test and each sturgeon tested was subjected to four tests in succession to simulate a repeated cycle of fatigue and recovery.

Data collection and analyses

All experimental data was expressed as mean ± S.E. and was analyzed and fitted using Origin (Version 8.1). The level of significance was determined using ANOVA Fisher LSD. Fit to mathematical models was evaluated following the Akaike information criterion *AIC* [29,30] using the model correcting for finite sample size and frequently applied in behavioral ecology [31];

$$AICc = n \log(RSS/n) + 2k + 2k(k+1)/(n-k-1) \quad (1)$$

where *RSS* is the residual sum of squares from the fitted model, *n* is sample size, and *k* is the total number of parameters. Its use helps prevent overfitting and offers a relative estimate of the information lost by a given model. The value of *AICc* is inversely related to the goodness of fit of a given model.

Based on data from the stepped velocity test, the critical swimming speed (*U_{crit}*) of the test fish is calculated as described by Brett [32]. Oxygen consumption rate (*MO₂*) is calculated using Equation 2;

$$MO_2 = (d(DO)/dt - d(DO)'/dt) \times V/m \quad (2)$$

where *V*(L) is the volume of the respirometer, *m* (kg) is the mass of the sturgeon, *d(DO)/dt* (mgO₂/(L×h)), which is the slope of the linear regression of *DO* decreasing over time (*R*²>0.99), is the rate of change in dissolved oxygen in the respirometer during the step test and *d(DO)'/dt* (mgO₂/(L×h)) is the rate of change in dissolved oxygen in the control (respirometer with no fish). Routine oxygen consumption rate (*MO_{2, routine}*) of each sturgeon is the *MO₂* at 0.5 bl/s (Cai et al., 2013b). Maximum oxygen consumption rate (*MO_{2, max}*) of each sturgeon is the maximum value of *MO₂* during the stepped velocity test. The aerobic scope (*AS*) is the difference between *MO_{2, max}* and *MO_{2, routine}* and is related to the energy potentially available for swimming [33,34].

During the swimming period, variation of *MO₂* with *U* was obtained by fitting the data to Equation 3 [35,36]:

$$MO_2 = a + bU^c \quad (3)$$

where *a*, *b* and *c* are constants. Active oxygen consumption (*AOC*) is the difference between aerobic oxygen consumption and routine oxygen consumption during the period and was obtained by computing the area under the *MO₂* curve during the period. During the recovery period, variation of *MO₂* over time (*t*) was obtained by fitting the data to Equations 4 and 5 [37,38]:

$$MO_2 = a + be^{ct} \quad (4)$$

$$MO_2 = e^{a+bt+ct^2} \quad (5)$$

where *a*, *b* and *c* are constants. Excess post-exercise oxygen consumption (*EPOC*) is the difference between aerobic oxygen consumption and routine oxygen consumption during recovery from exhaustion and was obtained by computing the area under the *MO₂* curve during the period. Assuming that *EPOC* is the oxygen consumed to recover from anaerobic metabolism, total oxygen consumption was obtained by adding *EPOC* to aerobic oxygen consumption [32]. Total oxygen consumption was calculated by the iterative method of Lee et al. [37] until *EPOC* and the area between the *MO₂* curve and the broken line (representing anaerobic metabolism) differed <0.5%. The broken line was then used to estimate *U* at the onset of anaerobic respiration (*U_a*).

Results

The U_{crit} of test sturgeon decreased with successive recoveries from fatigue (Fig. 1), yielding values of 4.34 ± 0.18 , 3.77 ± 0.20 , 3.27 ± 0.22 , 2.98 ± 0.26 bl/s, respectively, over four cycles. The relationship between the U_{crit} and the test number (N) was linear and the decrease was significant:

$$U_{crit} = 4.76 - 0.47N (F = 118, P = 0.00836, R^2 = 0.975)$$

The ΔU_{crit} ($U_{crit, N+1} - U_{crit, N}$) values were 0.57, 0.50, 0.29 bl/s and the recovery ratios ($U_{crit, N+1} / U_{crit, N}$) were 86.9%, 86.7% and 91.1%.

Metabolic parameters were displayed in Table 1. Differences in $MO_{2, routine}$ among the four tests were not significant. And differences in $MO_{2, max}$ were also not significant; values for $MO_{2, routine}$ were similar but $MO_{2, max}$ and AS decreased with test number.

As shown in Fig. 2, U_{crit} varied exponentially with AS :

$$U_{crit} = 2.78448 + 0.00114 \times e^{0.0224AS} (F = 1882, P = 0.00163, R^2 = 0.998)$$

Data for the variation of MO_2 with U was fitted to Equation 3 and the results are shown in Table 2. The speed coefficient (c), a measure of swimming efficiency, increased during tests 2 and 3 and then decreased in test 4.

Figure 3 illustrates the results of further analysis of the physiological changes that occurred during the four stepped velocity tests. The decreases in $EPOC$ indicates that anaerobic capacity decreases with successive cycles of fatigue and recovery; the decrease in the last test was significant larger than in the second and third tests. The onset of anaerobic metabolism occurred at lower swimming speeds (absolute U_a , 1.82, 1.79, 1.64, 1.57 bl/s, respectively, for tests 1~4). However, because the decrease in U_{crit} was more pronounced, relative U_a increased with successive testing (41.94%, 47.48%, 50.15% and 52.68%).

During the recovery period, MO_2 decreased rapidly over time; the relationship fitted to Equations 4 and 5 is shown in Table 3.

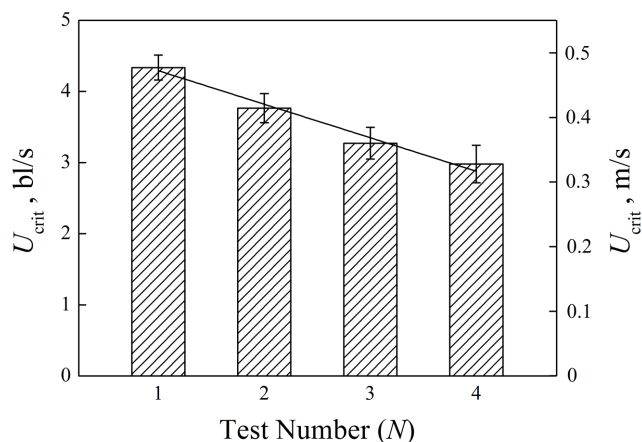


Figure 1. Variation of critical swimming speed (U_{crit} , mean ± S.E.) over four cycles of fatigue-recovery.
doi:10.1371/journal.pone.0094345.g001

Table 1. Respiratory metabolic parameters*.

Test	$MO_{2, routine}$ mgO ₂ /(kg × h)	$MO_{2, max}$ mgO ₂ /(kg × h)	Mean AS mgO ₂ /(kg × h)	AOC mgO ₂ /kg	EPOC mgO ₂ /kg
1	266.60 ± 30.94	598.80 ± 40.55	332.20	1,175.48	35.70
2	231.51 ± 33.10	532.51 ± 35.06	301.00	625.67	31.51
3	241.40 ± 20.70	512.65 ± 26.07	271.25	458.38	29.99
4	263.81 ± 22.50	492.37 ± 68.45	228.56	341.34	21.57

*Routine oxygen consumption rate ($MO_{2, routine}$, mean ± S.E.) is the oxygen consumption rate (MO_2) at 0.3–0.5 BL/s; maximum oxygen consumption rate ($MO_{2, max}$, mean ± S.E.) is the maximum value of MO_2 during the stepped velocity test; the aerobic scope (AS) is the difference between $MO_{2, max}$ and $MO_{2, routine}$; active oxygen consumption (AOC) is the difference between aerobic oxygen consumption and routine oxygen consumption during swimming period; excess post-exercise oxygen consumption (EPOC) is the difference between aerobic oxygen consumption and routine oxygen consumption during recovery from exhaustion. Differences in $MO_{2, routine}$ and $MO_{2, max}$ not significant among successive tests: $MO_{2, routine}$, $F = 0.392$, $P = 0.759$; $MO_{2, max}$, $F = 1.050$, $P = 0.390$.

doi:10.1371/journal.pone.0094345.t001

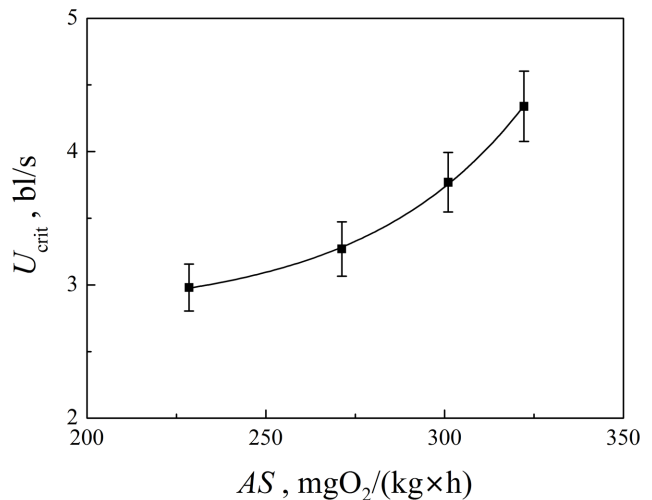


Figure 2. Variation of critical swimming speed (U_{crit} , mean ± S.E.) with aerobic scope (AS). The AS is the difference between maximum oxygen consumption rate and routine oxygen consumption rate.
doi:10.1371/journal.pone.0094345.g002

Table 2. Relationship between oxygen consumption rate and swimming speed*.

Test	Equation	F	P	R ²
1	$MO_2 = 241.8 + 60.9U^{1.20}$	1.6×10^6	<0.00001	0.964
2	$MO_2 = 232.7 + 30.5U^{1.70}$	0.8×10^6	<0.00001	0.959
3	$MO_2 = 233.7 + 32.3U^{1.71}$	6.3×10^6	<0.00001	0.997
4	$MO_2 = 247.1 + 50.0U^{1.42}$	8.1×10^6	<0.00001	0.993

*Oxygen consumption rate, MO_2 , mgO₂/(kg × h); swimming speed, U , bl/s.
doi:10.1371/journal.pone.0094345.t002

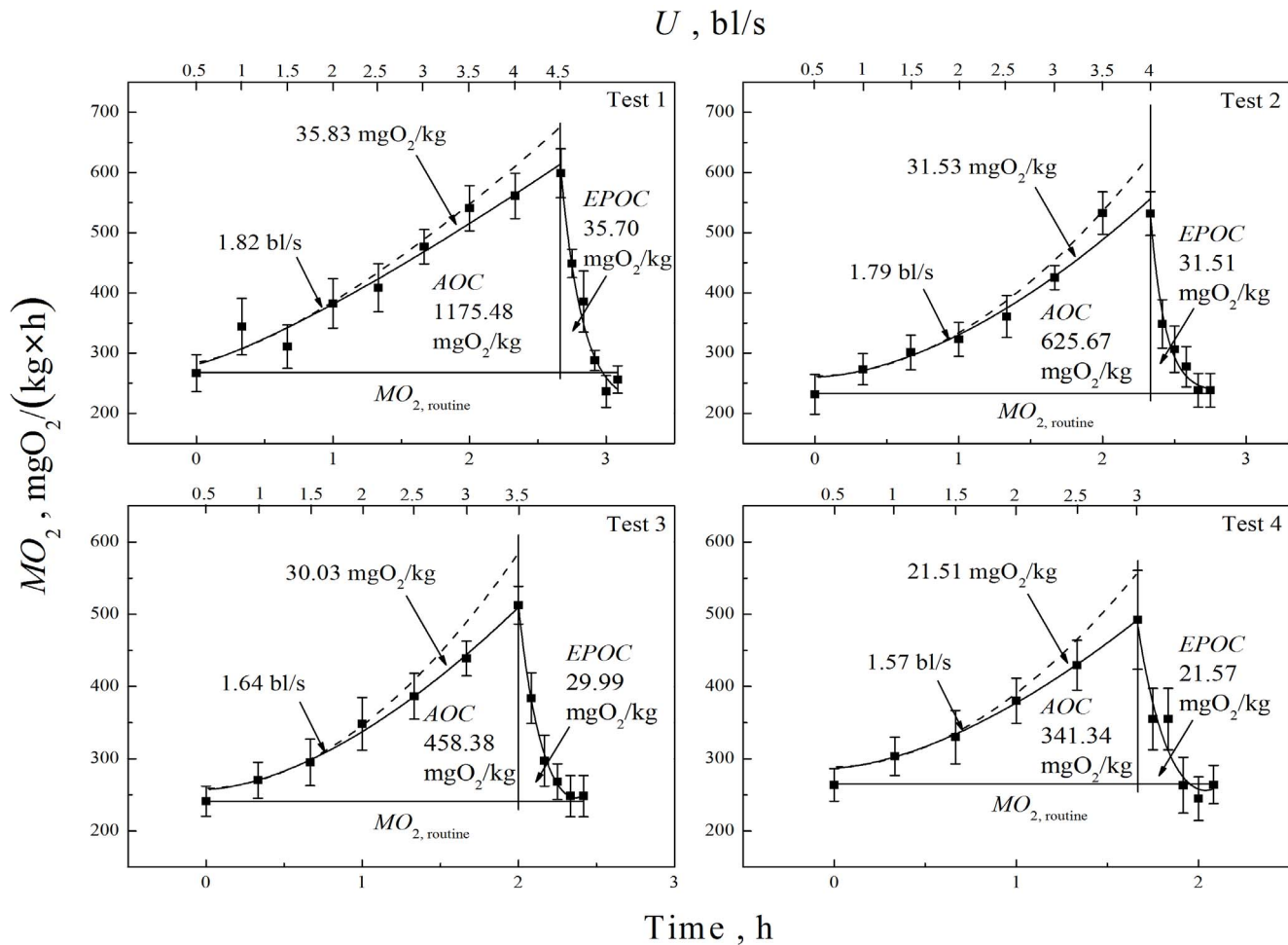


Figure 3. Variation of oxygen consumption rate (MO_2 , mean \pm S.E.) over time. Active oxygen consumption (AOC) is the difference between aerobic oxygen consumption and routine oxygen consumption during swimming period; excess post-exercise oxygen consumption (EPOC) is the difference between aerobic oxygen consumption and routine oxygen consumption during recovery from exhaustion.
doi:10.1371/journal.pone.0094345.g003

Discussion

Critical swimming speed, U_{crit}

Juvenile sturgeon, such as shortnose sturgeon *Acipenser brevirostrum* [39] and Amur sturgeon (*Acipenser schrenckii*) [27], generally display U_{crit} levels of 2 bl/s~3 bl/s. However, the U_{crit} of Chinese sturgeon was found to be above that range, indicating that Chinese sturgeon have better swimming capability. In addition, there was a linear decrease ($R^2 = 0.975$) in U_{crit} of the Chinese sturgeon with repeated fatigue-recovery cycles (Fig. 1). However, the difference

in U_{crit} declined with repeated testing ($A_{U_{crit}}$ 0.57, 0.50, 0.29 bl/s) and the recovery ratio increased from 86.9% to 91.1%. A better fit could have been obtained using a higher order equation but would have resulted in overfitting according to AIC analysis. The recovery ratio for Chinese sturgeon is comparable to sockeye salmon (*Oncorhynchus nerka*), with a recovery ratio of approximately 85% after a resting time of 1 hour [40]. Because exertion decreases U_{crit} , the slot velocities of upstream fishways should be lower than those in downstream fishways.

Table 3. Variation of oxygen consumption rate over time during the recovery period*.

Test	Equation	F	P	R^2
1	$MO_2 = 211.6 + 8.8 \times 10^9 e^{-6.35t}$	0.5×10^6	<0.00001	0.968
2	$MO_2 = 235.0 + 1.6 \times 10^{12} e^{-9.61t}$	1.1×10^6	<0.00001	0.979
3	$MO_2 = e^{36.1 - 25.9t + 5.5t^2}$	8.5×10^6	<0.00001	0.998
4	$MO_2 = e^{24.8 - 18.9t + 4.6t^2}$	0.4×10^6	<0.00001	0.837

*Oxygen consumption rate, MO_2 , mgO₂/(kg×h); time, t, h.
doi:10.1371/journal.pone.0094345.t003

$MO_{2, \text{ routine}}$ and $MO_{2, \text{ max}}$

Differences in $MO_{2, \text{ routine}}$ over the four test cycles were small and erratic (Table 1), indicating little, if any, influence of fatigue on the routine metabolic rate. While differences in $MO_{2, \text{ max}}$ were not significant, the changes were more pronounced and decreased with each test cycle. This leads to a decrease in AS and is consistent with the observed decrease in the U_{crit} . The relationship between AS and U_{crit} is shown in Fig. 2, indicating an exponential increase in U_{crit} with AS .

Speed exponent, c

The exponent c (Equation 3) is inversely related to swimming efficiency [34,38]. In the first test, c was 1.20, similar to those of the white sturgeon, lake sturgeon and Amur sturgeon [27,41]; not surprising as the four *Acipenser* species are closely related [42]. In the three successive tests, the values of c did not change consistently ($c = 1.70, 1.71, 1.42$, respectively, for Tests 2, 3, and 4). There are numerous reports on the effect of fish morphology on swimming efficiency [43,44]. In this investigation morphology was consistent among the tests and results indicate that repeated fatigue-recovery cycles affect physiological function. It has been reported that different fish use different swimming strategies [45,46], but it remains unclear as to whether the sturgeon are adjusting swimming strategy in response to repeated fatigue-recovery cycles. Swimming efficiency was highest in Test 1, lower in Tests 2 and 3, with some recovery displayed in Test 4.

Excess post-exercise oxygen consumption, EPOC

During fatigue recovery the variation of oxygen consumption rate with time is usually described by Equation 4 [27,37]. The data fit for Test 1 and Test 2 was good (Table 3) but data for Test 3 and Test 4 could not be fit to Equation 4 because the fit did not converge. After fitting the data to several other functions Equation 5 was selected, based on fit and *AIC* analysis, to estimate the onset of anaerobic respiration and its contribution to U_{crit} .

Information on *EPOC* is helpful for establishing design criteria for the resting pools of fishways [27,47]. The *EPOC* is inversely related to the recovery capability from exhaustion [37]. The *EPOC* in the first test was 35.7 mgO₂/kg, much lower than for salmon but similar to Amur sturgeon [27,37], indicating high recovery capability for Chinese sturgeon. Although *EPOC* decreased with repeated recovery from fatigue, it does not necessarily follow that the recovery capability increased because U_{crit} and AS also decreased and *AOC* decreased by 70% from Test 1 to Test 4 (Table 1).

The *EPOC* is directly related to anaerobic respiration [37] and the decrease in *EPOC* indicates that repeated recovery from fatigue

lowers capacity for anaerobic metabolism. With each fatigue-recovery cycle anaerobic respiration begins at a lower swimming speed but contributes less to achieving U_{crit} . However, it can be seen in Fig. 3 and Table 1 that oxygen consumption is primarily from aerobic respiration and the decrease in aerobic respiration is the primary cause for the decrease in U_{crit} . It was reported that salmon pass fishways using primarily aerobic respiration [25], consistent with our results.

Swimming speed at onset of anaerobic respiration, U_a

Aerobic metabolism with red muscle fiber provides propulsion in general, but white muscle fiber contributes to achieving high speeds [36,48,49]. It was reported that anaerobic swimming in cyprinids begins to augment propulsion when swimming speed reaches 30~50% U_{crit} [50]. However, aerobic power is different in different fish species [37,50,51]. In this study, the relative U_a was between 41.94% and 52.68% U_{crit} (absolute U_a , 1.82, 1.79, 1.64, 1.57 bl/s, respectively, for tests 1~4) similar to the higher range of cyprinids. So, with repeated step tests, white muscle (anaerobic metabolism) began contributing to propulsion at lower absolute swimming speeds.

Conclusions

Repeated cycles of fatigue and recovery affect the swimming capability of Chinese sturgeon; U_{crit} , *AOC* and absolute U_a decrease with decreasing swimming capacity. These results contribute to our understanding of the physiology of the Chinese sturgeon and support the conservation efforts of wild populations of this important species.

Acknowledgments

We thank Miss Tian Suyi, Mr. Guo Baifu and Mr. Yuan Tao who also contributed to the work providing assistance with writing and aquaculture operations. This work was supported by Major Science and Technology Program for Water Pollution Control and Treatment in the National Twelfth Five-Year Plan of China (Grant number: 2012ZX07104-002-04) and the National Nature Science Foundation of China (Grant number: 50979049, 51309140).

Author Contributions

Conceived and designed the experiments: L. Cai. Performed the experiments: L. Cai. Analyzed the data: L. Cai DJ. Contributed reagents/materials/analysis tools: L. Chen YG. Wrote the paper: L. Cai. Contributed substantially to revisions: YH DJ PM MF ZT.

References

- Langerhans RB (2009) Predictability of phenotypic differentiation across flow regimes in fishes. *Integr Comp Biol* 48: 750–768. doi:10.1093/icb/ict092.
- Wei Q, Ke F, Zhang J, Zhuang P, Luo J, et al. (1997) Biology, fisheries, and conservation of sturgeons and paddlefish in China. *Environ Biol Fish* 48: 421–255. doi:10.1023/A:1007395612241.
- Wei Q, He J, Yang D, Zheng W, Li L (2004) Status of sturgeon aquaculture and sturgeon trade in China: a review based on two recent nationwide surveys. *J Appl Ichthyol* 20: 321–332. doi:10.1111/j.1439-0426.2004.00593.x.
- Guo B, Chang J, Xiao H, Zhu B, Wan J, et al. (2011) The reproductive biology of first filial generation of *Acipenser sinensis* growing up in the freshwater environment. *Acta Hydrob Sinica* 35: 940–945. doi:10.3724/SP.J.1035.2011.00940.
- Wei Q, Li L, Du H, Zhang X, Xiong W, et al. (2013) Research on technology for controlled propagation of cultured Chinese sturgeon (*Acipenser sinensis*). *J Fish Sci China* 20: 1–11. doi:10.3724/SP.J.1118.2013.00001.
- Xie P (2003) Three-Gorges Dam: risk to ancient fish. *Science* 302: 1149–1151.
- Xie S, Li Z, Liu J, Xie S, Wang H, et al. (2007) Fisheries of the Yangtze River show immediate impacts of the Three Gorges Dam. *Fisheries* 32: 343–344.
- Hu J, Zhang Z, Wei Q, Zhen H, Zhao Y, et al. (2009) Malformations of the endangered Chinese sturgeon *Acipenser sinensis*, and its causal agent. *P Natl Acad Sci USA* 106: 9339–9344. doi:10.1073/pnas.090106.
- Turvey ST, Barrett LA, Hao Y, Zhang L, Zhang X, et al. (2010) Rapidly shifting baselines in Yangtze fishing communities and local memory of extinct species. *Conserv Biol* 24: 778–797. doi:10.1111/j.1365-2761.2004.00590.x.
- Wang C, Kynard B, Wei Q, Du H, Zhang H (2013) Spatial distribution and habit suitability indices for non-spawning and spawning adult Chinese sturgeons below Gezhouba Dam, Yangtze River: Effects of river alterations. *J Appl Ichthyol* 29: 31–40. doi:10.1111/jai.12094.
- Pikitch KE, Doukakis P, Lauck L, Chakrabarty P, Erickson LD (2005) Status, trends and management of sturgeon and paddlefish fisheries. *Fish Fish* 6: 233–265. doi:10.1111/j.1467-2979.2005.00190.x.
- He X, Lu S, Liao M, Zhu X, Zhuang M, et al. (2013) Effects of age and size on critical swimming speed of juvenile Chinese sturgeon *Acipenser sinensis* at seasonal temperatures. *J Fish Biol* 82: 1047–1056. doi:10.1111/j.1095-8649.2012.12015.x.

13. Barthem RB, Ribeiro M, Petrere M (1991) Life strategies of some long-distance migratory catfish in relation to hydroelectric dams in the Amazon Basin. *Biol Conserv* 56: 339–345.
14. Cheong ST, Kavvas LM, Anderson KE (2006) Evaluation of adult white sturgeon swimming capabilities and applications to fishway design. *Environ Biol Fish* 77: 197–208. doi:10.1007/s10641-006-9071-y.
15. Rodriguez TT, Agudo PJ, Mosquera PL, Gonzalez PE (2006) Evaluating vertical-slot fishway design in terms of fish swimming capabilities. *Ecol Eng* 27: 37–48. doi:10.1016/j.ecoleng.2005.09.015.
16. Cooke SJ, Hinch SG, Farrell AP, Patterson DA, Miller-Saunders K, et al. (2008) Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental Biology: an interdisciplinary case study on adult Fraser river sockeye salmon. *Fisheries* 33: 321–339. doi:10.1577/1548-8446-33.7.321.
17. Yagci O (2010) Hydraulic aspects of pool-weir fishways as ecologically friendly water structure. *Ecol Eng* 36: 36–46. doi:10.1016/j.ecoleng.2009.09.007.
18. Van Leeuwen TE, Rosenfeld JS, Richards JG (2011) Adaptive trade-offs in juvenile salmonids metabolism associated with habitat partitioning between coho salmon and steelhead trout in coastal streams. *J Anim Ecol* 80: 1012–1023. doi:10.1111/j.1365-2656.2011.01841.x.
19. Fu SJ, Cao ZD, Yan GJ, Fu C, Pang X (2013) Integrating environmental variation, predation pressure, phenotypic plasticity and locomotor performance. *Oecologia* 173: 343–354. doi:10.1007/s00442-013-2626-7.
20. Jaric I, Gessner J (2012) Analysis of publications on sturgeon research between 1996 and 2010. *Scientometrics* 90: 715–735. doi:10.1007/s11192-011-0583-7.
21. Farrell AP, Gamperl AK, Birtwell IK (1998) Prolonged swimming, recovery and repeat swimming performance of mature Sockeye Salmon *Oncorhynchus nerka* exposed to moderate hypoxia and pentachlorophenol. *J Exp Biol* 201: 2183–2193.
22. Jain KE, Farrell AP (2003) Influence of seasonal temperature on the repeat swimming performance of rainbow trout *Oncorhynchus mykiss*. *J Exp Biol* 206: 3569–3579. doi:10.1242/jeb.00588.
23. Macnutt JM, Hinch SG, Farrell AP, Stopp S (2004) The effect of temperature and acclimation period on repeat swimming performance in cutthroat trout. *J Fish Biol* 65: 342–353. doi:10.1111/j.0022-1112.2004.00453.x
24. Tiemey KB, Farrell AP (2004) The relationships between fish health, metabolic rate, swimming performance and recovery in return-run sockeye salmon, *Oncorhynchus nerka* (Walbaum). *J Fish Dis* 27: 663–671. doi:10.1111/j.1365-2761.2004.00590.x.
25. Pon LB, Hinch SG, Cooke SJ, Patterson DA, Farrell AP (2009) Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon (*Oncorhynchus nerka*) in the Seton River, British Columbia. *J Fish Biol* 74: 1323–1336. doi:10.1111/j.1095-8649.2009.02213.x.
26. Herrmann JP, Enders EC (2000) Effect of body size on the standard metabolism of horse mackerel. *J Fish Biol* 57: 746–760. doi:10.1111/j.1095-8649.2000.tb00272.x.
27. Cai L, Taupier R, Johnson D, Tu Z, Liu G, et al. (2013) Swimming capability and swimming behavior of juvenile *Acipenser schrenckii*. *J Exp Zool Part A* 319: 149–155. doi:10.1002/jez.1780.
28. Pang X, Yuan XZ, Cao ZD, Fu SJ (2013) The effects of temperature and exercise training on swimming performance in juvenile qingbo (*Spinibabus sinensis*). *J Comp Physiol B* 183: 99–108. doi:10.1007/s00360-012-0690-7.
29. Akaike H (1987) Factor analysis and AIC. *Psychometrika* 52: 317–332. doi:10.1007/BF02294359.
30. Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika* 76: 297–307. doi:10.1093/biomet/76.2.297.
31. Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observation, and comparisons. *Behav Ecol Sociobiol* 65: 23–35. doi:10.1007/s00265-010-1029-6.
32. Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. *J Fish Res Board Can* 21: 1183–1226. doi:10.1139/f64-103.
33. Killen SS, Marras S, Steffensen JF, McKenzie DJ (2012) Aerobic capacity influences the spatial position of individuals within fish schools. *Proc R Soc Lond B* 279: 357–364. doi:10.1098/rspb.2011.1006.
34. Tu Z, Li L, Yuan X, Huang Y, Johnson D (2012) Aerobic swimming performance of juvenile Largemouth bronze gudgeon (*Coreius guichenoti*) in the Yangtze River. *J Exp Zool Part A* 317: 294–302. doi:10.1002/jez.1723.
35. Behrens JW, Prabel K, Steffensen JF (2006) Swimming energetics of the Barents Sea capelin (*Mallotus villosus*) during the spawning migration period. *J Exp Mar Biol Ecol* 331: 208–216. doi:10.1016/j.jembe.2005.10.012.
36. Tu Z, Yuan X, Han J, Shi X, Huang Y, et al. (2011) Aerobic swimming performance of juvenile Schizothorax chongi (Pisces, Cyprinidae) in the Yalong River, southwestern China. *Hydrobiologia* 675: 119–127. doi:10.1007/s10750-011-0809-y.
37. Lee CG, Farrell AP, Lotto A, Hinch SG, Healey MC (2003) Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. *J Exp Biol* 206: 3253–3260. doi:10.1242/jeb.00548.
38. Cai L, Liu G, Taupier R, Fang M, Johnson D, et al. (2013) Effect of temperature on swimming performance of juvenile *Schizothorax prenanti*. *Fish Physiol Biochem*. doi:10.1007/s10695-013-9860-0.
39. Deslauriers D, Kieffer JD (2012) Swimming performance and behaviour of young-of-the-year shortnose sturgeon (*Acipenser brevirostrum*) under fixed and increased velocity swimming tests. *Can J Zool* 90: 345–351. doi:10.1139/z2012-004
40. Jain KE, Birtwell IK, Farrell AP (1998) Repeat swimming performance of mature sockeye salmon following a brief recovery period: a proposed measure of fish health and water quality. *Can J Zool* 76: 1488–1496.
41. Peake S (2005) Swimming and respiration. Sturgeons and Paddlefish of North America 27: 147–166. doi:10.1007/1-4020-2833-4_8.
42. Billard R, Lecointre G (2000) Biology and conservation of sturgeon and paddlefish. *Rev Fish Biol Fisher* 10: 355–392. doi:10.1023/A:1012231526151.
43. Pettersson LB, Hedenstrom A (2000) Energetics, cost reduction and functional consequences of fish morphology. *Proc R Soc Lond B* 267: 759–764. doi:10.1098/rspb.2000.1068.
44. Ohlberger J, Staaks G, Holker F (2006) Swimming efficiency and the influence of morphology on swimming costs in fishes. *J Comp Physiol B* 176: 17–25. doi:10.1007/s00360-005-0024-0.
45. 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: 421–432. doi:10.1242/jeb.01380.
46. Castro-Santos T, Sanz-Ronda FJ, Ruiz-Legazpi J (2013) Breaking the speed limit - comparative sprinting performance of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Can J Fish Aquat Sci* 70: 280–293. doi:10.1139/cjfas-2012-0186.
47. Webber JD, Chun SN, Maccoll TR, Mirise LT, Kawabata A, et al. (2007) Upstream swimming performance of adult White Sturgeon: effects of partial baffles and a ramp. *T Am Fish Soc* 136: 402–408. doi:10.1577/T06-064.1.
48. Rome LC, Funke RP, Alexander RM (1990) The influence of temperature on muscle velocity and sustained performance in swimming carp. *J Exp Biol* 154: 163–178.
49. Marras S, Killen SS, Domenici P, Claireaux G, McKenzie DJ (2013) Relationships among traits of aerobic and anaerobic swimming performance in individual European Sea bass *Dicentrarchus labrax*. *PLOS ONE* 8: e72815. doi:10.1371/journal.pone.0072815.
50. Jones DR (1982) Anaerobic exercise in teleost fish. *Can J Zool* 60: 1131–1134. doi:10.1139/z82-157.
51. Svendsen JC, Tudorache C, Jordan AD, Steffensen JF, Aarestrup K, et al. (2010) Partition of aerobic and anaerobic swimming costs related to gait transitions in labriform swimmer. *J Exp Biol* 213: 2177–2183. doi:10.1242/jeb.041368.