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Effect of repeated exercise fatigue on the swimming performance of juvenile rock carp (*Procypris rabaudi*, Tchang)

Ying-ping Huang[1,2] | **Ali Haris Malik**[1] | **Zhi-ying Tu**[2] | **David Johnson**[2,3] | **Wei-Ming Li**[2] | **Xi Yuan**[1,2]

[1]College of Hydraulic & Environmental Engineering, China Three Gorges University, Hubei Yichang, China

[2]Engineering Research Center of Eco-Environment in Three Gorges Reservoir Region, Ministry of Education, China Three Gorges University, Yichang, China

[3]School of Natural Sciences and Mathematics, Ferrum College, Ferrum, VA, USA

Correspondence

Xi Yuan, College of Hydraulic & Environmental Engineering, China Three Gorges University, Hubei Yichang, China.
Email: cd123yx@163.com

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Abstract

The swimming performance of juvenile rock carp (*Procypris rabaudi*, Tchang) subjected to repeated fatigue exercise was studied using a flume-type respirometer at 20°C. The critical swimming speed (U_{crit}) and oxygen consumption rate (MO_2) of juvenile rock carp were measured during two successive stepped velocity tests, following a 60 min rest interval. U_{crit} of rock carp was giving a recovery ratio (R_r) of 92.64%, and exertion exercise decreases U_{crit}. When MO_2 was plotted as a linear function of U, the slope for trial 1 was 1.06 and 1.50 for trial 2, indicating a decreasing in swimming efficiency. The maximum metabolic rate (MMR) increased from 17.06 ± 1.14 mmol O_2/(kg·hr) to 19.14 ± 1.23 mmol O_2/(kg·hr), and the exercise post oxygen consumption rate (EPOC) increased from 9.00 to 9.65 mmol O_2/kg. Repeated fatiguing exercise increased both the aerobic and anaerobic cost of reaching U_{crit}, but anaerobic metabolism accounted for a larger proportion in the trial 2. The data investigation on the swimming performance and the physiological response to fatigue provide important design criteria for fishways.

KEYWORDS

critical swimming speed, excess post-exercise oxygen consumption (EPOC), oxygen consumption, *Procypris rabaudi*, repeat fatiguing exercise

1 | INTRODUCTION

Repeat swimming performance testing is a useful, non-invasive and ecologically relevant tool for monitoring the fitness of fish (Jain et al., 1998; Jain & Farrell, 2000; Kieffer & May, 2020; Nelson et al., 2015). Critical swimming speed (U_{crit}) is a useful measure of swimming performance because it conveys important information regarding ability to forage, escape predation, and maintain position (Brett, 1964; Ward et al., 2003; Starrs et al., 2011; Penny & Kieffer, 2019). U_{crit} is determined by forcing a fish to swim against a laminar flow in a swim tunnel, as water velocity is stepped increased at regular intervals until the fish is exhausted (Brett, 1964; Hvas & Oppedal, 2019; Plaut, 2001). Repeated fatigue-recovery cycles is typical for fish moving through fishways, and the information obtained by repeated stepped-velocity testing provides information important for designing effective fishways (Yagci, 2010).

The metabolic rate, measured as oxygen consumption rate (MO_2), is widely used to determine physiological response to energy demanding processes (Christensen et al., 2018; Clark et al., 2013; Lefevre et al., 2017). Changes in MO_2, at a given level of exertion, is an indicator of physiological stress in fish, and repeated fatigue exercise has been reported to alter MO_2 (Lee et al., 2003; Pang et al., 2015). Excess post-exercise oxygen consumption (EPOC) is the oxygen deficit produced by anaerobic metabolism during exhaustive exercise, used to estimate the anaerobic metabolic capacity of fish (Lee et al., 2003; Macnutt et al., 2006; Zhang et al., 2018). The activity producing exhaustion, exercise intensity and duration, nutritional status, body mass, and exercise training all affect recovery time and the magnitude of EPOC for a given fish species (Fu et al., 2007; Lee et al., 2003; Zhao et al., 2012). The stepped-velocity test is often used to determine U_{crit} and the associated metabolic cost, but information is limited on the effect of repeated U_{crit} trials on metabolic expenditure, swimming performance and recovery time. Insight gained from measuring metabolic parameters during repeated stepped velocity tests helps resource managers optimize fishway design and supports efforts to conserve wild fish populations.

Rock carp (*Procypris rabaudi*, Tchang) are endemic to the upper reaches of the Yangtze River, and wild populations are declining due to pollution, overfishing, and migration barriers (Wang et al., 2015). The information needed to support conservation of this species is not yet sufficient, particularly for metabolism and swimming behavior. The objectives of this study were to: (a) Assess the swimming performance of juvenile rock carp, and define the relationship between oxygen consumption rate (MO_2) and swimming speed (U). (b) Determine the short-term effects of swimming to fatigue on swimming performance and EPOC.

Highlights

1. A single cycle of a stepped velocity swim test decreased swimming efficiency of juvenile rock carp (*Procypris rabaudi*, Tchang).
2. In the second trial, anaerobic metabolism contributed more to U_{crit}.

2 | MATERIALS AND METHODS

2.1 | Test fish

Juvenile rock carp (standard length, 9.75 ± 0.13 cm; mass, 19.56 ± 0.94 g) were obtained from a fish hatchery in Yichang City Hubei Province. The fish ($N = 20$) were maintained in a 0.4 m^3 (0.50 × 0.80 × 1.00 m) aquarium with dechlorinated water at 20°C, dissolved oxygen (DO) >6.50 mg/L, ammonia-N <0.050 mg/L, and nitrite-N <0.007 mg/L. During the two weeks acclimation period, fish was fed once daily at 9:00, with commercial fish food and uneaten food and feces were cleared after 2 hr. After the acclimation period, 20 test fish were randomly transferred to four holding tanks (0.40 × 0.60 × 0.35 m). Fish were fasted for 48 hr before testing.

2.2 | Experimental device

Swimming tests were carried out in a flume-type swimming respirometer, with a swim chamber of dimensions 65 × 10 × 10 cm, and a maximum flow velocity of 1.36 m/s. A honeycomb (1 cm cell diameter) placed upstream of the chamber helps to maintain laminar flow, and a grid at the end of the chamber prevents fish from being swept away. Flow velocity was measured with a three-dimensional acoustic Doppler velocity meter (Nortek AS). The respirometer was flushed with a submersible pump to maintain the dissolved oxygen (DO) level. During the experiment, the respirometer was sealed, and the DO in the respirometer was monitored with an oxygen electrode (HACH HQ30d).

2.3 | Test protocol

Juvenile rock carp ($n = 10$) were subjected to two successive stepped velocity tests, each followed by a 60 min recovery period. Before testing, a single fish was adapt to the apparatus for 2 hr at a flow rate of 1.0 BL/s (body length per second). After adaptation, the velocity was increased in increments of 1.0 BL/s each 30 min until the fish was exhausted (failure to move away from the swimming chamber screen for 20 s, Lee et al., 2003). The water velocity was then reduced to 1.0 BL/s for a 60 min recovery period (referred as trial 1). After the recovery period, the test fish was subjected to the second test, again followed by a 60 min recovery period (trial 2).

2.4 | Determination of U_{CRIT}

The critical swimming speed (U_{crit}, BL/s) was calculated using the flow velocity at fatigue, velocity increment and time step (Equation 1, Brett, 1964):

$$U_{crit} = U_I + (T_I/T_{II})U_{II}, \tag{1}$$

where U_I (BL/s) is the highest water velocity at which the fish swam for the full time interval, U_{II} is the water velocity increment; T_{II} is the step time interval and T_I is the time elapsed during the interval of fatigue ($U_{II} = 1$ BL/s, $T_{II} = 30$ min).

The recovery ratio (R_r) was calculated using Equation 2:

$$R_r = \left(U_{crit\ 2}/U_{crit\ 1}\right) \times 100\%, \tag{2}$$

where subscripts 1 and 2 indicate the U_{crit} of trial 1 and trial 2.

2.5 | Determination of oxygen consumption

The oxygen consumption rate [MO_2 mmol O_2/(kg·hr)] for each swimming speed was determined by recording the decrease in DO in the sealed respirometer for over the 30 min step. MO_2 was calculated using Equation 3 with the slope of the regression line obtained by plotting DO against time (Fitzgibbon et al., 2007):

$$MO_2 = V \times d\,(DO)\,/(dt) \times M^{-1}, \tag{3}$$

where V is the respirometer volume (12 L), d(DO)/(dt) is the slope, and M is the fish mass (kg). Background respiration (no fish in respirometer) was subtracted from total oxygen consumption to obtain the corrected oxygen consumption.

The relationship between MO_2 mmol O_2/(kg·hr) and U (BL/s) was been fitted to linear, exponential, and power functions (Herskin & Steffensen, 1998; Macnutt et al., 2006; Steinhausen et al., 2005). For the data generated in this study was best fit by a linear function using Akaike Information Criterion (AIC), and Equation 4 was used to express MO_2 as a function of U relationship:

$$MO_2 = a + bU, \tag{4}$$

where a, the intercept, is the standard metabolic rate (SMR; i.e., MO_2 at $U = 0$), and b, the slope, is the speed coefficient. Following acclimation, the routine MO_2 (RMR) was determined over a period of 30 min ($U = 1$ BL/s). The maximum metabolic rate (MMR) was maximum oxygen consumption measured during the stepped velocity test. The difference between MMR and SMR is the metabolic scope (MS) (Claireaux & Chabot, 2016).

At fatigue, the flow speed was decreased to 1·BL/s during the 60 min recovery period, and EPOC (mmol O_2/kg) was calculated based on MO_2 measurements during the recovery period. Variation of MO_2 over time (t, min) was obtained by fitting data to Equations 5 (where a and b are fitting constants):

$$MO_2 = ae^{bt}. \tag{5}$$

2.6 | Data Analysis

The oxygen consumption (MO_2) was tested using two-way analysis of variance (ANOVA) (Fisher least significant difference [LSD]) with swimming speed as factors. The U_{crit}, RMR, and MS were compared between trails using one-way ANOVA (Fisher LSD). All statistics were performed using SPSS software with $p = .05$. The results were graphed and presented as mean ± *SE*. Fit to the MO_2-U models was evaluated using the Akaike information criterion AIC (Cai et al., 2014).

3 | RESULTS

The mean value of U_{crit1} was 9.11 ± 0.23 BL/s and, after the 60 min recovery period, U_{crit2} was 8.44 ± 0.29 BL/s (Table 1). The recovery ratio (R_r) was 92.64 ± 1.51% and the decrease in U_{crit} was significant ($F = 4.83$; $p < .01$).

Data on the variation of MO_2 mmol O_2/(kg·hr) with U (BL/s) for the two trials were fitted to Equation 4 (Figure 1) and the results are given in Table 2. Energy expenditure increased with swimming speed. The SMR for trial 2 was lower than for trial 1, and the MMR and MS for trial 2 were significant higher than for trial 1 ($p < .05$) (Table 1). The speed coefficient (b), inversely related to swimming efficiency, increased from 1.06 ± 0.06 in trial 1 to 1.50 ± 0.06 in trial 2. During the recovery period, the variation of MO_2 with t was fitted to an exponential function (Figure 2). EPOC was 9.00 mmol O_2/kg in trial 1, and increased to 9.65 mmol O_2/kg in trial 2.

TABLE 1 Metabolic rate and critical swimming speeds (U_{crit}, BL/s, BL, body length) for the two trials of juvenile rock carp *Procypris rabaudi*; SMR mmol O_2/(kg·hr) is standard metabolic rate (estimated by $U = 0$), MMR mmol O_2/(kg·hr) is the maximum metabolic rate, and MS mmol O_2/(kg·hr) is the metabolic scope (MMR–SMR)

	Trial 1	Trial 2
SMR	8.42 ± 0.16	8.00 ± 0.15
MMR	17.06 ± 1.14[a]	19.14 ± 1.23[b]
MS	8.64 ± 1.14[a]	11.14 ± 1.23[b]
EPOC	9.00 ± 0.45	9.65 ± 0.48
U_{crit}	9.11 ± 0.23[a]	8.44 ± 0.29[b]

Note: Excess post-exercise oxygen consumption (EPOC, mmol O_2/kg) during the 60 min recovery period ($U = 1$ BL/s). a and b, values without a common superscript are significantly different, $p < .05$.

4 | DISCUSSION

The present study is the first to investigate repeat swim testing and metabolic capacities (SMR, MMR and MS) of juvenile rock carp. The U_{crit} of juvenile rock carp is higher than U_{crit} of juvenile largemouth bronze gudgeon *Coreius guichenoti* (Tu et al., 2012), and bighead carp *Aristichthys nobilis* (Yuan et al., 2014) that were 6 BL/s-7 BL/s at 20°C. The body of rock carp of similar body weight is longer and thinner than the two cyprinids, and a slender morphology produces less drag at a given counter current velocity (Boily & Magnan, 2002). When the stepped-velocity test was repeated after the 60-min recovery period, the recovery ratio was 92.65%, comparable to that of sockeye salmon *Oncorhynchus nerka* (about 85%) after the same rest period (Lee et al., 2003). Other researches on the repeated swimming trials found a lower recovery ratio (Christensen et al., 2018; Jain et al., 1998; McKenzie et al., 2007). U_{crit} is a valuable reference for setting design criteria of fishways (Cai et al., 2018), and based on repeated stepped- velocity tests, the slot velocities of upstream fishways should be lower than in downstream fishways.

The estimated SMR was 8.42 mmol O_2/(kg·hr) in trial 1, and 8.00 mmol O_2/(kg·hr) in trial 2. The metabolic scope (MMR-SMR) was 8.64 mmol O_2/(kg·hr), in trial 1, and 11.14 mmol O_2/(kg·hr) in trial 2. SMR accounted for 49.36% MO_2 in trial 1 and decreased to 41.80% in trial 2. The relatively low energy cost of propulsion implies that rock carp are strong in ascending barriers (Ohlberger et al., 2007). MS is an integrated measure of cardiorespiratory and red muscle capacity, and is particularly relevant for the rock carp, a potamodromous riverine fish that migrates considerable distances (Marras et al., 2010). Animals remain within the bounds of the MS for most of their daily activities and it is useful for comparison environmental effects within a species and for interspecific comparisons of performance (Nelson, 2016). The MS of rock carp is higher than that of *Coreius guichenoti* (6.76 ± 0.74 mmol O_2/(kg·hr), at 20°C) (Tu et al., 2012), and lower than other cyprinids such as the carp *Cyprinus carpio* (22.81 ± 0.91 mmol O_2/(kg·hr), at 15°C) and the roach *Rutilus rutilus* (23.15 ± 2.86 mmol O_2/(kg·hr), at 15°C) (Tudorache

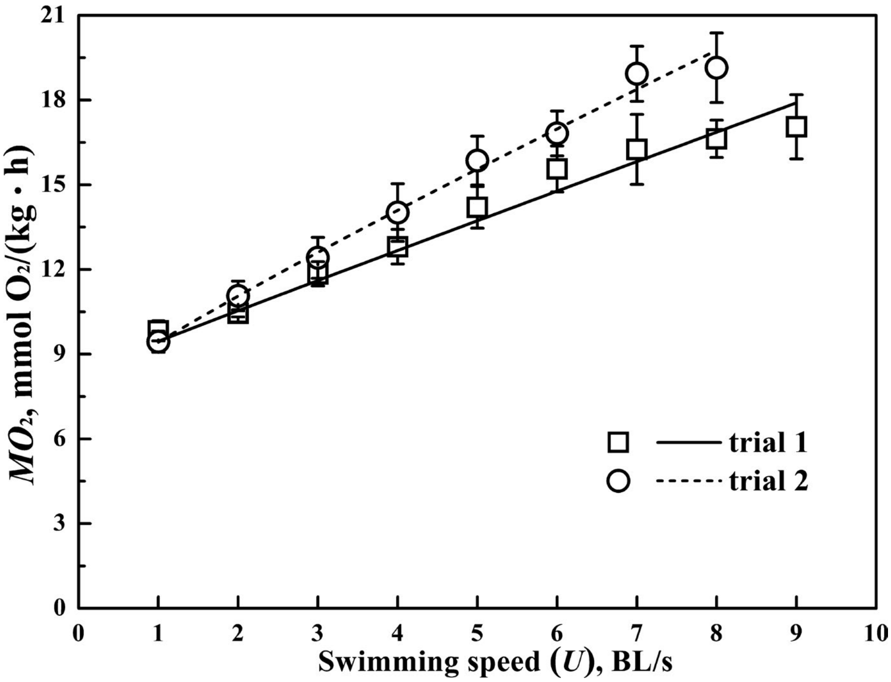

FIGURE 1 Mean (±*SE*) oxygen consumption rate [MO_2, mmol O_2/(kg·hr)] for juvenile rock carp *Procypris rabaudi* as a linear function of swimming speed (*U*, BL/s) in trial 1 and trial 2

TABLE 2 Oxygen consumption [MO_2, mmol O_2/(kg·hr)] expressed as a linear function of swimming speed (*U*, BL/s) for juvenile rock carp *Procypris rabaudi*, $MO_2 = a + b \times U$, where *a* and *b* are constants (mean ± *SE*)

	a	*b*	R^2
Trial 1	8.42 ± 0.16	1.06 ± 0.06	.98
Trial 2	8.00 ± 0.15	1.50 ± 0.04	.99

et al., 2008). In this case, the swim chamber could restrict burst-coast motion as test fish approached U_{crit} (Tudorache et al., 2007), resulting in a low estimate for MS of rock carp.

The power values *c*, of *U* in the MO_2 power function $MO_2 = a + bU^c$, is inversely related to swimming efficiency and values range from 1.1 to 3.0 for 30 fish species (Videler & Nolet, 1990). Interestingly, for the data generated in this study on rock carp, the power value was 1, indicating that MO_2 is a linear function of *U* and that the swimming efficiency of juvenile rock carp is high. The constant slope implies that the COT (MO_2/*U*) for rock carp does not increase with swimming speed. The value for *U* in trial 1 was 1.06 and increased to 1.50 in trial 2, indicating an increase in the cost of transport and a decrease in swimming efficiency. It has been reported that muscle enzyme activity increases with training (Bagatto et al., 2001; Farrell et al., 1990), reducing the O_2

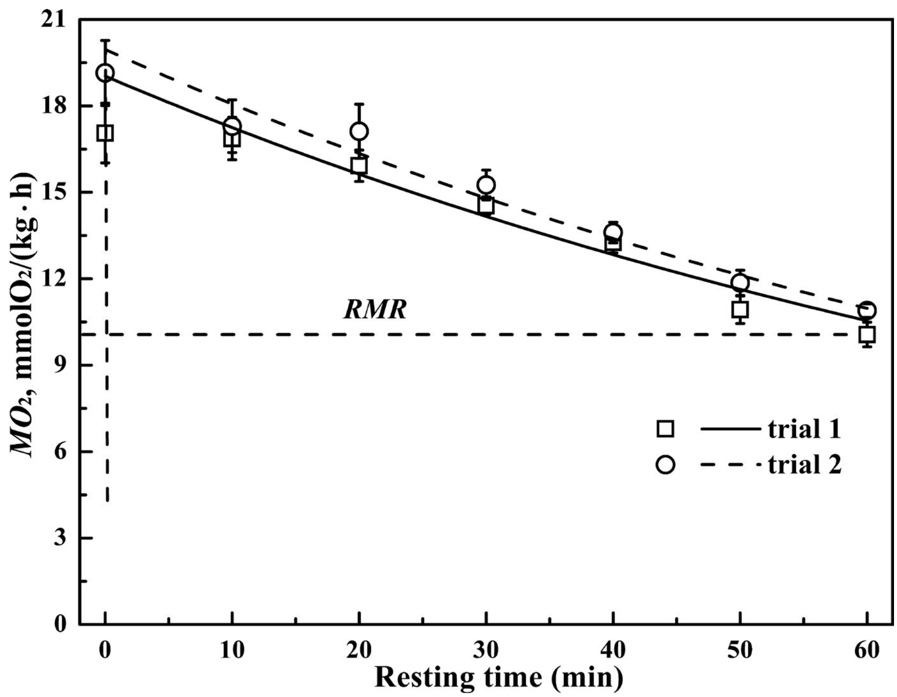

FIGURE 2 Variation of oxygen consumption rate [MO_2, mmol O_2/(kg·hr)] over time (a 60 min recovery period) for juvenile rock carp *Procypris rabaudi*. Excess post-exercise oxygen consumption (EPOC, mmol O_2/kg) is the area bound by the vertical and horizontal broken lines (RMR) on the MO_2 recovery curve [$MO_2 = a + b \times e^{(c \times t)}$]

required for muscle to do a given amount of work (Farrell et al., 1998). The decrease in rock carp swimming efficiency reported here is inconsistent with an earlier study in which a single trial of a stepped velocity test was sufficient to increase the swimming efficiency of Chinese sturgeon *Acipenser sinensis* (Yuan et al., 2017). However, the U_{crit} of juvenile rock carp is about twice of the Chinese sturgeon (body length 8.50–11.00 cm). Thus, it appears that fatigue-recovery cycles have a positive 'training effect' in species with naturally low swimming efficiency.

Information on EPOC is directly related to anaerobic metabolism and helpful for establishing design criteria for the resting pools of fishways (Webber et al., 2007). The EPOC is lower and recovery more rapid in species able to extract oxygen from the environment and distribute it to the tissues more rapidly (Hancock & Gleeson, 2008). The EPOC of juvenile rock carp increased from 9.00 mmol O_2/kg in trial 1 to 9.65 mmol O_2/kg in trial 2, indicating that repeated recovery from temporarily lowers aerobic capacity. It reported an exponential increase in the EPOC with increasing exercise intensity (Laforgia et al., 2006), with repeated tests, white muscle (anaerobic metabolism) contributing to more to achieving U_{crit}. However, more research is needed on the physiological response of rock carp to multiply fatigue-recovery cycles during migration.

5 | CONCLUSIONS

This is the first report on the effects of repeated exercise fatigue on the swimming performance and metabolism of rock carp. Juvenile rock carp have a relatively high U_{crit} (9.11 ± 0.23 BL/s), and a relatively short recovery period (R_r = 92.64% after 60 min). But a single cycle of the stepped-velocity swim test decreasing swimming efficiency, increased EPOC and decreased the U_{crit}. Thus, the slot velocities of upstream fishways should be lower than those in downstream fishways. The findings from this study contribute to fish science and provide information important for developing design criteria for fishways.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL APPROVAL

"All applicable international, national, and/or institutional guidelines for the Care and use of animals were followed by the authors."

DATA AVAILABILITY STATEMENT

All data, models, and code generated or used during the study appear in the submitted article.

ORCID

Xi Yuan https://orcid.org/0000-0001-7138-1638

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