Vol. 21: 57–65, 2014
doi: 10.3354/ab00571

AQUATIC BIOLOGY
Aquat Biol

Published online June 18

Effect of temperature and dissolved oxygen on swimming performance in crucian carp

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ABSTRACT: Changing environmental conditions may affect the swimming performance of fish by affecting energy sources through changes in temperature and concentration of dissolved oxygen (DO). It has become increasingly important to investigate the effect of temperature and DO on the swimming performance of fish species as hypoxia in aquatic environments worldwide is increasing due to the effects of anthropogenic global warming. To test how different swimming modes respond to thermal and DO changes, 3 measures of swimming performance were tested: critical swimming speed (U_{crit}), constant acceleration speed (U_{cat}), and maximum speed during a fast-start (U_{fast}). The changes in these 3 aspects of swimming performance in juvenile crucian carp *Carassius carassius* were quantified at 2 different temperatures (10 and 20°C) and 3 different DO concentrations (2.5, 5, and 9 mg l^{-1}). U_{cat} was ca. 110 to 156% of U_{crit}, whereas U_{fast} was ca. 394 to 472% of U_{crit}, depending on the experimental conditions. Temperature had a significant effect on all 3 measures of swimming performance, whereas DO had significant effects only on U_{cat} and U_{crit} (U_{crit} but not U_{cat} decreased in the 2.5 mg l^{-1} DO group). The active metabolic rate ($MO_{2active}$) under the different experimental conditions suggested that the decrease in U_{crit} at a lower temperature and DO level could be partially explained by a decrease in oxygen uptake capacity. These results indicate that all 3 swimming measurements should be used when addressing how temperature affects swimming performance.

KEY WORDS: Aerobic and anaerobic locomotion · Constant acceleration speed · Critical swimming speed · Crucian carp · Environmental condition · Fast-start swimming performance · Swimming performance

INTRODUCTION

Swimming is an important physiological activity and a survival-determining function for fish because it plays a role in food capture, predator avoidance and reproductive behavior. Swimming performance in fish can be classified as either steady or unsteady (Webb 1984). Steady swimming describes constant-speed locomotion in a straight line and is commonly employed in nature during competition for limited resources, such as searching for food, obtaining mates or seeking favorable abiotic conditions (Plaut 2001, Domenici 2003, Blake 2004). Since Brett (1964), the most common method of measuring the steady swimming capability of fish has involved determining the critical swimming speed (U_{crit}, i.e. speed at which a fish can no longer maintain position or the maximum sustainable swimming speed) (Beamish 1966, Hammer 1995, Kolok 1999). Although fish rely on anaerobic metabolism to different degrees while reaching U_{crit} (Nelson et al. 1996), U_{crit} is highly correlated with active metabolic rate ($MO_{2active}$, i.e. the maximum oxygen uptake capacity during the U_{crit} test) and is widely accepted as an indicator for aerobic swimming performance. Thus, U_{crit} is most likely limited by oxygen delivery, metabolite supply and/or

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the buildup of waste products (Reidy et al. 2000, Richards et al. 2002). The constant acceleration speed (U_{cat}; duration of minutes) and fast-start swimming (U_{fast}; duration of seconds) have been viewed as forms of unsteady swimming, which are highly important in evading predatory strikes (Webb 1986, Katzir & Camhi 1993, Walker et al. 2005). The U_{fast} test, which is completed in seconds, is powered by intracellular stores of adenosine triphosphate (ATP) and creatine phosphate (PCr) and is most likely limited by neuromuscular morphology and physiology (Reidy et al. 2000). The U_{cat} test in fish generally involves the use of 3 endogenous fuels stored within the white muscle: glycogen, ATP and PCr. In the early stages of acceleration swimming, energy is largely derived from the breakdown of PCr and ATP (Dobson & Hochachka 1987, Marras et al. 2010), whereas glycogenolysis provides the majority of the ATP required to sustain muscular exertion at later stages (Dobson & Hochachka 1987, Wood 1991). Thus, U_{cat} may be more closely related to anaerobic metabolic capacity in fish. Nevertheless, the energy sources used and the limiting factors of performance vary profoundly among the 3 measures of swimming performance.

Because of the temporal and spatial patchiness of fish environments, variations in temperature and dissolved oxygen (DO) are environmentally relevant physiological challenges that can dictate a species' ecological distribution and Darwinian fitness. Thus, how the swimming performance of fish is affected by variations in temperature and DO may be critical for their survival in the field (Perry et al. 2005, Mandic et al. 2009). Changes in temperature and levels of DO have diverse effects on oxygen availability and metabolite flux, as well as intracellular stores of ATP and PCr, and endogenous fuels stored within the white muscle, which are limiting factors of U_{crit}, U_{fast} and U_{cat}, respectively. Thus, environmental changes may affect different swimming performances in various physiological manners. The response of different swimming modes may be critical for survival in the field. In recent years, hypoxia in aquatic environments worldwide has increased due to the effects of anthropogenic global warming (Diaz & Rosenberg 2008, Pörtner & Farrell 2008, Roze et al. 2013). Therefore, it has become increasingly important to investigate the effect of temperature and DO on the swimming performance of fish species. Theoretically, a temperature decrease may have a universal negative effect on all 3 measures of swimming performance due to changes in the biochemical reaction rate. A decrease in DO may result in a more depressed aerobic swimming performance (i.e. U_{crit}) than the other 2 swimming performances. A depressed U_{crit} under lower temperatures and DO concentrations has been widely documented (Pang et al. 2011, Zhao et al. 2012); however, little work has been performed on U_{fast} and U_{cat} (Lefrançois et al. 2005, Lefrançois & Domenici 2006, Wang et al. 2012). Furthermore, no study has investigated the effects of different environmental changes on the different swimming capacities within a single fish species. Thus, the main objective of this study was to investigate the responses of 3 different swimming performance parameters to a suite of environmental stressors.

To achieve our goal, we selected crucian carp *Carassius carassius* as the experimental animal because it is widely distributed in varied aquatic environments and is highly adaptive to variations in diverse environments. Temperature and DO were selected as the environmental factors to be modified because they are the most frequently encountered and environmentally relevant physiological challenges (Randall & Brauner 1991, Claireaux et al. 2000). The low temperature (10°C) selected in this study simulated the environment of the crucian carp in winter, whereas the hypoxic level simulated the extreme hypoxia situation in summer according to data on local water bodies in Chongqing, China. We also measured $MO_{2active}$ as indicated by the oxygen consumption rate (MO_2) during the U_{crit} test to investigate the role of oxygen uptake capacity and swimming efficiency on the possible change of U_{crit} among different experimental conditions.

MATERIALS AND METHODS

Animals and maintenance

Juvenile crucian carp *Carassius carassius* (n = 200) were purchased from the Fisheries Hatchery of Hechuan Aquaculture School (Hechuan, Chongqing City, China) and were acclimated for 1 mo in a recirculating water tank system (350 l) before the experiment. All experiments were conducted according to the Guidelines on the Humane Treatment of Laboratory Animals established by the Ministry of Science and Technology of the People's Republic of China. During the acclimation, the temperature of the dechlorinated tap water was maintained at 20°C (±0.5°C), and DO was maintained at near saturation (approximately 9 mg l^{-1}). Fish were fed to satiation once daily on a commercial diet (Tongwei aquatic feed; dietary composition: 41.2 ± 0.9% protein; 8.5 ±

0.5% lipid; 25.7 ± 1.2% carbohydrate and 12.3 ± 0.4% ash). The photoperiod was established as 12:12 h light:dark to simulate the natural light cycle. Fish were fasted for 24 h before any measurement. After the acclimation period, healthy fish of similar size were selected as the experimental fish.

Experimental design

The fish were divided into 4 groups with 24 individuals within each group (5.96 to 11.95 g, 5.96 to 7.71 cm; see details in Table 1). Fish in the control group were transferred to a rearing tank with identical conditions to those of the acclimation period, i.e. 20°C and 9 mg O_2 l^{-1}. To investigate the effect of temperature on the swimming performance of crucian carp, 24 fish were transferred to an identical rearing tank under similar conditions to the control treatment, however, the temperature was decreased by 1°C d^{-1} until 10°C was reached (Pang et al. 2011, 2013, 2014). The fish were maintained at the experimental temperature by the thermo-regulated water reservoir for another 4 wk before experimental measurements were taken. To investigate the effect of DO on swimming performance, the other 2 groups of fish were maintained at 20°C, however DO levels were kept at 2 hypoxic levels: 5.0 mg O_2 l^{-1} (11.20 kPa) and 2.5 mg O_2 l^{-1} (5.60 kPa) which were maintained by water supplied from a 350 l reservoir tank covered with translucent plastic and the with water bubbled with nitrogen to achieve the target DO levels. DO was monitored by DO probes (HQ30, Hach Company). Each group was exercised using 3 different measures of swimming performance, i.e. U_{fast}, U_{cat} and U_{crit}. MO_2 was also measured during the U_{crit} test (see 'Measurement of U_{crit} and swimming MO_2' below for more details).

Experimental facility and measurements

Measurement of U_{fast}

U_{fast} was measured with a device developed by the Laboratory of Evolutionary Physiology and Behavior, Chongqing Normal University (see Yan et al. 2012 for details). The device included a high-speed camera (A504K, Basler; 500 frames s^{-1}) and an LED matrix light source and sink (engraved with 1 cm^{-1} grid lines on the bottom). The fish were anesthetized with neutralized tricaine methane sulfonate (MS-222, 50 mg l^{-1}) and dorsally marked at the center of the mass position with titanium oxide. The duration of the entire process was less than 30 s, and fish were allowed to recover for 4 h following the procedure. Fish from each group were then gently herded toward the acclimation zone of the U_{fast} experimental system and allowed to rest for another 1 h in all experimental groups (Yan et al. 2013). The depth of the water in the tank was 10 cm. DO was maintained at saturation, except in the 2 hypoxic groups (the DO levels were allowed a variation of ±0.1 mg l^{-1}). Water temperature in the swimming chamber was maintained at either 10 (for the low temperature group only) or 20 ± 0.1°C. An individual fish was then introduced into the filming zone through an alleyway. Escape responses were elicited by an electrical impulse

Table 1. Experimental conditions and body sizes of crucian carp in different treatment groups. U_{crit}: critical swimming speed; U_{cat}: constant acceleration speed; U_{fast}: macximum speed during a fast-start

Treatment	Rearing condition Temperature (°C)	Rearing condition DO (mg l^{-1})	Testing condition Temperature (°C)	Testing condition DO (mg l^{-1})	Measured variables	Body mass (mean ± SE, g)	Body length (mean ± SE, cm)
Control	20	9 (saturated)	20	9 (saturated)	U_{crit}	8.58 ± 0.52	6.85 ± 0.13
					U_{cat}	9.08 ± 0.28	6.80 ± 0.06
					U_{fast}	8.63 ± 0.19	6.68 ± 0.04
Low temperature group	10	11 (saturated)	10	11 (saturated)	U_{crit}	8.97 ± 0.28	6.85 ± 0.06
					U_{cat}	9.17 ± 0.23	6.85 ± 0.10
					U_{fast}	9.30 ± 0.39	6.81 ± 0.11
Moderate DO group	20	9 (saturated)	20	5	U_{crit}	9.10 ± 0.44	6.76 ± 0.11
					U_{cat}	9.26 ± 0.21	6.86 ± 0.05
					U_{fast}	7.99 ± 0.25	6.78 ± 0.10
Low DO group	20	9 (saturated)	20	2.5	U_{crit}	8.89 ± 0.44	6.99 ± 0.06
					U_{cat}	8.96 ± 0.34	7.21 ± 0.44
					U_{fast}	8.77 ± 0.29	6.90 ± 0.06

(0.75 V cm^{-1}; 50 ms) administered when the fish maintained a position at the center of the filming zone. The high-speed camera was used to record the entire escape process (time span: 3 s). The resulting images were analyzed using image processing software (ACDsee 10, ACD Systems International) and digitized by TpsUnil and TpsDig software (http://life.bio.sunysb.edu/morph) to define the track of the centroid of the locomotion performed by the fish during its escape response. The maximum linear velocity (i.e. U_{fast}) was calculated based on the centroid locomotion track.

Measurement of U_{cat}

A Brett-type swim tunnel respirometer (3.5 l; Fig. 1) was used to measure fish U_{cat}. Individual fish were transferred into the swim tunnel and allowed to recover for 4 h at a water velocity of 6 cm s^{-1} in all experimental groups (approximately 1 body length [BL] s^{-1}) (Fu et al. 2013, Yan et al. 2013). The flow of aerated water through the respirometer was maintained continuously during this recovery period. DO and temperature were maintained as previously described in the U_{fast} test. The water velocity in the swim tunnel was then steadily increased at a rate of 0.1667 cm s^{-2} (i.e. 10 cm s^{-1} min^{-1}; Marras et al. 2010). The water was accelerated at this rate until the fish were exhausted. Exhaustion was defined as the failure of the fish to move away from the rear honeycomb screen of the swimming chamber for at least 20 s; the water velocity at which the fish were exhausted was used as the U_{cat} value (Reidy et al. 2000, Marras et al. 2010). The U_{cat} measurement process usually lasted for several minutes and showed a negligible effect on DO.

Measurement of U_{crit} and swimming MO_2

U_{crit} and MO_2 were measured using a Brett-type swim tunnel respirometer (Fig. 1). A fish was introduced into the water tunnel and left in the water at a low water velocity (6 cm s^{-1}) for 4 h before the experiments began (Yan et al. 2012, 2013). DO and temperature were maintained as previously described. After the recovery period, the water velocity was increased by 6 cm s^{-1} every 20 min until the fish became exhausted, i.e. until the fish failed to move away from the rear honeycomb screen of the swimming chamber for a time span of 20 s (Lee et al. 2003 a,b, Yan et al. 2013). The swim tunnel was opened for 2 min for water exchange during the speed shift period (i.e. once every 20 min). DO values in the water were recorded at 2 min intervals. DO concentration ranged from 5.1 to 4.8 mg l^{-1} and 2.6 to 2.3 mg l^{-1} for 2 hypoxic swimming conditions, whereas it never dropped below 95% saturation for the normoxic swimming condition. The fish were removed after

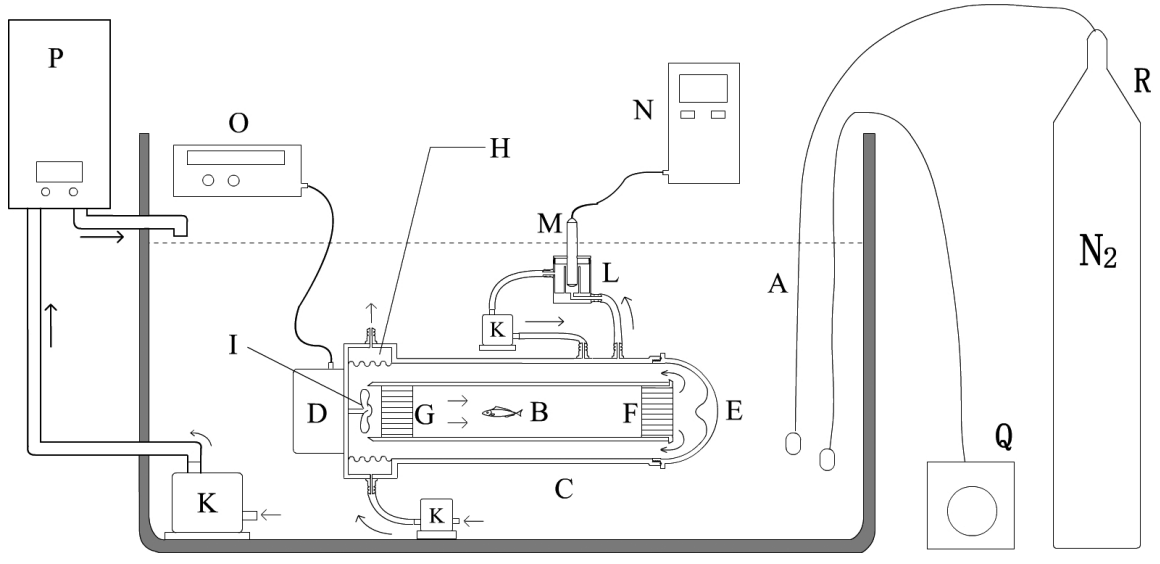

Fig. 1. Structure of the fish swim tunnel respirometer: (A) reservoir tank; (B) swim tube; (C) swim chamber; (D) frequency variable motor; (E) sealing cover; (F and G) honeycomb duct; (H) heat exchanger; (I) propeller; (K) pump; (L) sampling bottle; (M) oxygen probe; (N) oxygen meter; (O) variable frequency power supply; (P) water-processing and temperature-controlling system; (Q) air pump; (R) N_2 bottle

exhaustion, and background MO_2 was measured. U_{crit} was calculated for each fish using Brett's equation (Brett 1964):

$$U_{crit} = V + (t / T)\,\Delta V \quad (1)$$

where V is the highest speed at which the fish swam during the full length of the experiment (cm s^{-1}), t is the time that the fish swam at the final speed (min), T is the prescribed period of swimming per speed (20 min), and ΔV is the velocity increment (6 cm s^{-1}). The MO_2 (mg kg^{-1} h^{-1}) of each fish during swimming was calculated from the depletion of oxygen according to the following equation:

$$MO_2 = (S_t \times 60 - S_0) \times V / (m / 1000) \quad (2)$$

where S_t and S_0 (mg l^{-1} min^{-1}) represent the decrease in the water's DO per minute with and without fish, respectively. These values were obtained from the linear regressions between time (min) and DO (mg l^{-1}), where V is the volume of the respirometer and m is the body mass (g) of the fish. The maximum MO_2 during the U_{crit} test was defined as the active MO_2 ($MO_{2active}$).

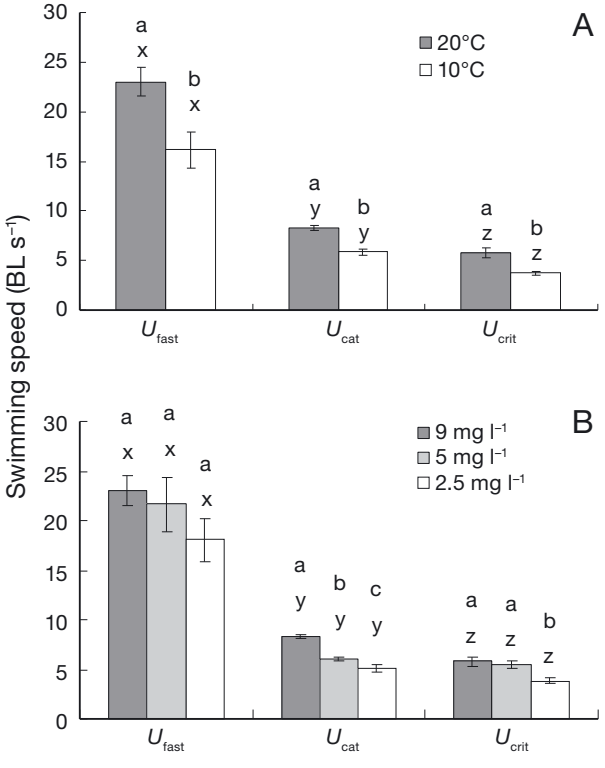

Fig. 2. Effect of (A) temperature and (B) dissolved oxygen on U_{fast}, U_{cat} and U_{crit} levels in juvenile crucian carp. Data are mean ± SE. Letters (a, b and c) above bars indicate a significant difference among the different treatment groups within U_{fast}, U_{cat} or U_{crit}; letters (x, y and z) indicate a significant difference among U_{fast}, U_{cat} and U_{crit} within each treatment group

Data analysis

All 3 absolute swimming speeds (cm s^{-1}) were converted to relative swimming speeds (BL s^{-1}) by dividing by the body length of individual fish. All values are presented as the means ± SE; $p < 0.05$ was used as the level of statistical significance. The effect of the experimental treatment (temperature and DO) and the measuring method (U_{fast}, U_{cat} and U_{crit}) on swimming performance was determined using a 2-way ANCOVA, using body length as a covariate. Following the ANCOVA, the difference between the values of different variables within each treatment group and the difference between the values of each variable within either DO group were determined by a Duncan multiple-comparison test, whereas the difference in each variable between the 2 temperature groups was determined by a *t*-test. The effects of swimming speed and experimental treatment on swimming MO_2 were determined using a 1-way ANCOVA (i.e. we performed a regression for each treatment group and compared their coefficients).

RESULTS

Effect of temperature and DO on swimming performance

There was a significant difference between U_{fast}, U_{cat} and U_{crit} within each temperature group ($p < 0.001$) (Fig. 2A, Table 2). When measured at 20°C, U_{crit} was 5.77 BL s^{-1}, whereas U_{fast} and U_{cat} were 399 and 144 % that of U_{crit}, respectively. U_{crit} decreased more significantly (35 %) compared to U_{fast} (35 vs. 29 %) and U_{cat} (29 %) ($p < 0.001$) as the temperature decreased from 20 to 10°C. Thus, the difference between U_{crit} and the other 2 measures of swimming performance increased at a lower temperature (interaction effect, $p = 0.033$).

Table 2. The effect of body length (covariate), treatment (temperature and DO), and method (U_{fast}, U_{cat} and U_{crit}) on swimming speed of crucian carp, based on a 2-way ANCOVA. *$p < 0.05$

	Temperature			DO		
	df	*F*	p	df	*F*	p
Covariate	1	0.155	0.696	1	1.510	0.224
Treatment (T)	1	21.81	<0.001*	2	4.058	0.022*
Method (M)	2	127.0	<0.001*	2	135.7	<0.001*
T × M	2	3.717	0.033*	2	0.592	0.669

There was a significant difference among U_{fast}, U_{cat} and U_{crit} within each DO group ($p < 0.001$) (Fig. 2B, Table 2). U_{fast} showed no significant variation among the different DO groups. However, compared to the normoxic group (9 mg l^{-1}), U_{cat} showed a significant decrease ($p < 0.05$) of 27 and 39% in the 5 and 2.5 mg l^{-1} groups, respectively. U_{crit} showed no significant change as DO decreased from normoxic to 5 mg l^{-1}; however, it showed a significant decrease (34%) when measured at 2.5 mg l^{-1} compared to the normoxic group ($p < 0.05$). Thus, hypoxic conditions had a more significant effect on U_{cat} and U_{crit} than U_{fast}, and the difference between U_{fast} and the other 2 measures of swimming performance was increased when measured in hypoxia. Furthermore, the difference between U_{cat} and U_{crit} decreased from 44% in the control (normoxic) group to 10% in the 5 mg l^{-1} group.

Effect of temperature and DO on metabolic rate at different swimming speeds

$MO_{2active}$ significantly decreased (48%) as temperature decreased from 20 to 10°C (Fig. 3A). $MO_{2active}$ showed no significant change in moderate hypoxia (5 mg l^{-1}); however, $MO_{2active}$ decreased significantly (39%) when measured in the lowest hypoxic condition (2.5 mg l^{-1}) (Fig. 3B).

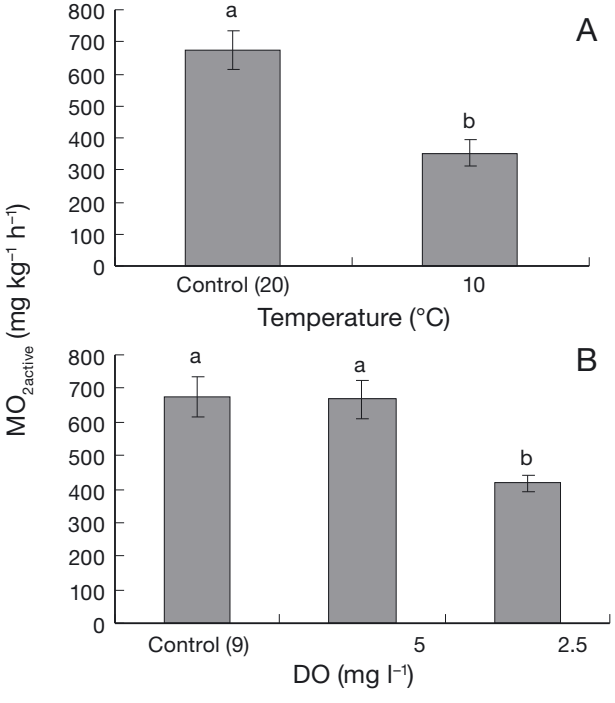

Fig. 3. Effect of (A) temperature and (B) dissolved oxygen (DO) on $MO_{2active}$ levels in juvenile crucian carp. Letters above bars indicate significant differences in $MO_{2active}$ among the different treatment groups

MO_2 increased significantly with swimming speed in both temperature groups ($p < 0.001$) (Fig. 4A). There was no significant difference in slopes of the MO_2 speed curves between the 2 temperature groups (Fig. 4A, Table 3); however, the high temperature group showed a significantly higher MO_2 compared to the low temperature group ($p < 0.05$) (Fig. 4A).

MO_2 increased significantly with an increase in swimming speed for all 3 experimental groups ($p < 0.001$) (Fig. 4B). There were no significant differences between the MO_2 speed curves of the 2 hypoxic and control groups (Fig. 4B, Table 3).

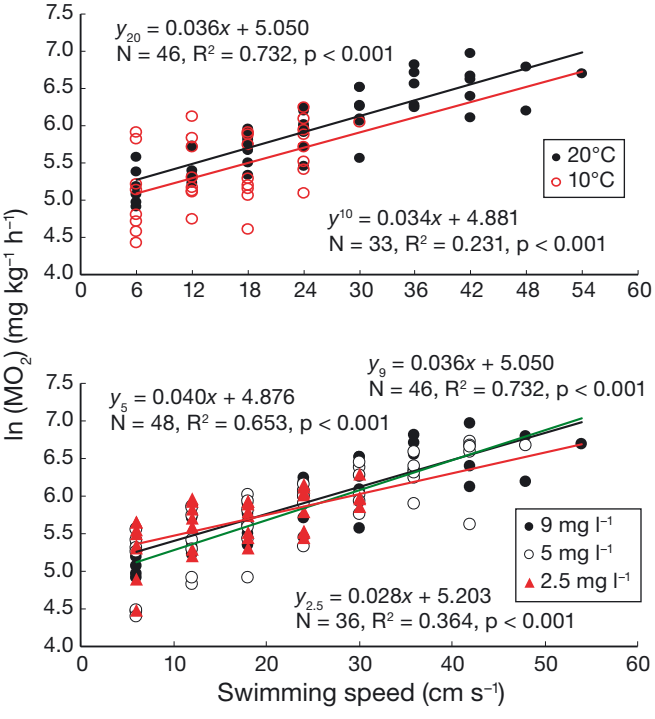

Fig. 4. MO_2 swimming speed curves of juvenile crucian carp at different (A) temperatures and (B) DO concentrations

Table 3. Differences in MO_2 swimming speed curves between the control and treatments using 1-way ANCOVA. See Fig. 4 for the regression equation and the intercept and slope coefficient value of each group

	df	Intercept		Slope	
		F	p	*F*	p
Temperature	1,78	45.62	<0.001	0.039	0.844
DO	2,126	1.203	0.303	1.353	0.262

DISCUSSION

Swimming performance is a survival-determining function, and different aspects of swimming performance are influenced by variation in an individual's environment, including temperature and DO. These environmental variables may influence swimming performance through a variety of underlying physiological processes (Arnold 1983, Garland & Losos 1994, Feder et al. 2010). The results from this study suggest that U_{fast} was the most conservative variable among the 3 swimming performance measurements and was only sensitive to thermal variation. Furthermore, U_{cat} was more sensitive to change in DO than U_{crit}.

Effect of temperature on swimming performance

In this study, U_{fast}, U_{cat} and U_{crit} decreased by 28 to 38% as temperature decreased from 20 to 10°C. These results are consistent with most published studies of fish species (Hammer 1995, Claireaux et al. 2000, Lee et al. 2003b, Fangue et al. 2008, Zeng et al. 2009, Yan et al. 2012). The reduction in swimming performance with decreasing temperature could stem from changes in both the external and internal environment of the fish. The external factor is mainly increased water viscosity, and hence, increased drag force when swimming at low temperatures, which may show similar negative effects on all 3 swimming modes (Temple & Johnston 1997). The internal factor is mainly the reduced metabolic power and skeletal muscle contractility (both aerobic and anaerobic) (Randall & Brauner 1991, Day & Butler 2005), which are consequences of a reduction in the mitochondrial function of muscle tissues (Guderley 2004), decreased biochemical reaction rates (Franklin 1998), lower contents of some energy substrates (PCr and ATP) in the bodies of fish living in cold water (Kieffer et al. 1994, Kieffer 2000), and/or the reduction of cardio-respiratory functions at low temperatures (Claireaux et al. 2000, Joaquim et al. 2004). The muscle contractility decided by ATP and PCr may have a crucial effect on U_{fast}, whereas the muscle contractility decided by the biochemical reaction rates in either red or white muscles may show alternative effects on either U_{crit} or U_{cat}. Furthermore, cardio-respiratory performance may mainly affect U_{crit} (the transportation of oxygen and metabolites) rather than U_{cat} or U_{fast}, which may be the reason why U_{crit} was more sensitive to temperature change in crucian carp in this study. However, the effect of temperature on different swimming modes is dependent on fish species and temperature ranges. A previous study on 6 cyprinids observed that U_{crit} increased by 7 to ~37%, whereas U_{fast} increased by 26 to ~103% as temperature increased from 15 to 25°C, with U_{crit} generally being much less sensitive to thermal change than U_{fast} (Yan et al. 2012); results that are not consistent with the results of this study. Furthermore, Yan et al. (2012) also suggested that thermal sensitivity of U_{crit} and U_{fast} was negatively correlated.

Effect of DO on swimming performance

Changes in DO showed no significant effect on $U_{fast,}$ which was consistent with previous studies on European sea bass *Dicentrarchus labrax* and golden grey mullet *Liza aurata* (Lefrançois et al. 2005, Lefrançois & Domenici 2006). The absence of a DO effect on U_{fast} is easily understood because the fast-start movement occurs within seconds and is mainly limited by ATP and PCr in muscle tissues, and thus may be largely independent of DO levels. However, it is notable to observe that U_{cat} was more sensitive to DO change than U_{crit}, as the former showed a significant decrease at a moderate DO level (5 mg l^{-1}), whereas the latter did not. This result is surprising because U_{crit} is more likely to be aerobic swimming, whereas U_{cat} is more likely to be anaerobic swimming. The reason may be because the limitation of U_{crit} in some fish species was caused by the mobilization, transportation and utilization of energy fuels rather than the oxygen availability. This result has been clearly demonstrated in species such as dark-barbel catfish *Pelteobagrus vachelli* (Fu et al. 2009), common carp *Cyprinus carpio* (Zhang et al. 2010) and crucian carp (Zhang et al. 2012) (a so-called additive metabolic mode compared to a locomotion priority mode in species whose swimming activity can occupy all of their cardio-respiratory capacity; Fu et al. 2011). For these types of species, a moderate DO decrease may not affect U_{crit}. Previous studies on mulloway *Argyrosomus japonicus* and darkbarbel catfish (Pang et al. 2012) observed that U_{crit} showed no change with a moderate DO decrease. In the present study, $MO_{2active}$ showed no decrease at a moderate DO level in crucian carp, which also supported that U_{crit} was not limited by the respiratory capacity in normoxia. Furthermore, U_{cat} is comprised of 2 components: an entirely aerobic component of steady swimming supported by aerobic 'red muscle' fibers instead of a component at the top end of the performance range (Peake 2008). Although U_{cat} relies more on anaerobic metabolism than U_{crit}, U_{cat} is dictated by

both aerobic and anaerobic swimming, and the aerobic components of U_{cat} depend more on oxygen availability than the transportation and utilization of substrates because of its shorter duration compared to U_{crit}. Thus, small changes in DO will decrease U_{cat}. Further investigation into the effect of DO changes on U_{cat} and U_{crit} among fish with different metabolic modes (additive vs. priority mode) is necessary.

Differences between U_{crit}, U_{cat} and U_{fast}

At 20°C and normoxic DO levels, U_{crit} was 5.77 BL s^{-1}, whereas U_{cat} was 144% that of U_{crit}. These results are consistent with the ranges of previously published studies. For example, U_{cat} was 30% higher than U_{crit} in largemouth bass *Micropterus salmoides*, 20 to ~60% higher in rainbow trout *Oncorhynchus mykiss* and 77% higher in Atlantic cod *Gadus morhua* (Farlinger & Beamish 1977, Farrell 2008, Reidy et al. 2000). However, because U_{cat} was more sensitive to DO, the difference between U_{cat} and U_{crit} decreased at a moderate DO level. U_{fast} was 399% that of U_{crit} in the control group, which is similar to, or slightly higher than, that of other cyprinids (Yan et al. 2012).

Concluding remarks

In conclusion, the results of this study suggest that temperature change has a universal effect on all measures of swimming performance, likely due to its effects on multiple physiological and biochemical functions in fish. However, the thermal sensitivity of different swimming modes differs among fish species. The inner physiological and biochemical mechanisms and their ecological relevance require further investigation. Our results suggest that all 3 swimming measurements should be used when studying how temperature affects swimming performance. U_{cat} was more sensitive to changes in DO than U_{crit}, which was unanticipated. It may be because the aerobic swimming components of U_{cat} depend more on oxygen availability than the transportation of energy. Among the 3 measures of swimming performance, U_{fast} was the most conservative variable. The difference between U_{fast} and the remaining variables was typically increased when the environmental conditions deviated from optimal conditions (i.e. when the fish were under stress). This study indicates that variations in temperature and DO variations may have a significant effect on swimming performance and the outcome of routine physiological activities in the field.

Acknowledgements. This study was funded by the National Science Foundation of China (NSFC 31172096) and the Key Project of the Natural Science Foundation of CQ (cstc2013 jjB20003).

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Editorial responsibility: Roderick Finn, Bergen, Norway

Submitted: February 24, 2014; Accepted: April 21, 2014
Proofs received from author(s): June 13, 2014