



## The thermal acclimation rate varied among physiological functions and temperature regimes in a common cyprinid fish



Kang-Kang Fu, Cheng Fu, Ying-Lian Qin, Yang Bai, Shi-Jian Fu\*

Laboratory of Evolutionary Physiology and Behavior, Chongqing Normal University, Chongqing 400047, China

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### ABSTRACT

The acclimation rate of physiological functions that bear fitness costs under a changing environment is key to making predictions for fish, yet this has seldom been investigated. This study aimed to test whether there were different responses when different physiological functions reached steady states and to determine possible relationships with metabolic constraints during temperature changes in fish. Qingbo (*Spinibarbus sinensis*), a common cyprinid in southern China, was first pre-acclimated at either high (25 °C) or low (15 °C) temperature for eight weeks and assumed to be at thermal equilibrium. Then, the temperature was reversed, that is, the temperature was decreased from 25 °C to 15 °C in one group, defined as the cooling group, whereas the temperature of the other group was increased from 15 °C to 25 °C, defined as the warming group. The thermal tolerance, swimming performance and feeding metabolism were measured before temperature reversal as well as 1, 2, 4 and 8 weeks. The growth performance was also measured after the temperature reversal. Typical thermal compensation was suggested by a stronger heat tolerance, faster swimming speed and higher postprandial metabolic response in those acclimated at 25 °C than in those acclimated at 15 °C before temperature reversal. Cold tolerance suggested by the critical minimal temperature (CT<sub>min</sub>) of the cooling group reached a thermal steady state within one week, whereas the adjustment of heat tolerance to the temperature increase indicated by the critical maximum temperature (CT<sub>max</sub>) was much slower, reaching a steady state two weeks after the temperature reversal. The high flexibility of the standard metabolic rate as well as the postprandial metabolism and relatively lower feeding metabolism demonstrated that there were negligible effects at the aerobic scope for other physiological functions during digestion in qingbo, even during the temperature acclimation period. However, there was a slower adjustment of the swimming performance with the temperature decrease, which parallels the change of metabolic capacity. Furthermore, both the cooling and warming treatments had negative effects on growth performance, with the former mainly occurring through extra energy expenditure, whereas the latter mainly occurred through decreased feeding. It suggested that the slow adjustment of heat tolerance after the temperature increase compared to that of cold tolerance might be a challenge for cyprinids distributed in southern China. Furthermore, the decreased metabolic scope and hence swimming performance after the temperature decrease might have a fitness cost in qingbo and possibly other cyprinids in China.

### 1. Introduction

The environmental conditions of aquatic habitats are currently changing due to anthropogenic climate change, and among them, the change in environmental temperature is predicted to affect the distribution and abundance of aquatic ectotherms due to increasing constraints on organismal physiology (Pörtner and Farrell, 2008; Verhille et al., 2016). Thus, the compensation of physiology to thermal change might be crucial for survival in the future, and physiological studies can help predict the effects of climate change on fish species (Somero, 2010). It has been suggested that organisms that show high

physiological flexibility might be favored and hence be able to survive in a thermal fluctuation condition or habitat undergoing thermal changes (Sandblom et al., 2014). Flexibility includes not only the range over which physiological performance can change due to environmental changes but also the acclimation rate, that is, how fast physiology can adjust to the new thermal condition, and acclimation rate might be more crucial than the former when organisms undergo frequent thermal fluctuation; however, little is known about this concept in fish species.

The maintenance of different physiological functions might not be equal in ecological relevance in life history, at least during short periods

\* Corresponding author.

E-mail address: [shijianfu9@cqnu.edu.cn](mailto:shijianfu9@cqnu.edu.cn) (S.-J. Fu).

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**Table 1**

The effect of thermal treatment and acclimation period on the measured variables based on the results of two-way analysis of covariance (ANCOVA).

Variables		Covariate effect <sup>a</sup>	Group effect	Period effect	Interaction effect
Thermal tolerance	CT <sub>max</sub>	$F_{1,79} = 1.001$ $P = 0.320$	$F_{1,79} = 122.3$ $P < 0.001$	$F_{4,79} = 12.62$ $P < 0.001$	$F_{4,79} = 212.5$ $P < 0.001$
	CT <sub>min</sub>	$F_{1,79} = 0.662$ $P = 0.418$	$F_{1,79} = 391.1$ $P < 0.001$	$F_{4,79} = 10.33$ $P < 0.001$	$F_{4,79} = 261.5$ $P < 0.001$
SDA	SMR	$F_{1,77} = 0.632$ $P = 0.429$	$F_{1,77} = 33.02$ $P < 0.001$	$F_{4,77} = 0.607$ $P = 0.659$	$F_{4,77} = 17.46$ $P < 0.001$
	PMR	$F_{1,77} = 0.144$ $P = 0.706$	$F_{1,77} = 80.66$ $P < 0.001$	$F_{4,77} = 1.930$ $P = 0.114$	$F_{4,77} = 54.92$ $P < 0.001$
	PMS	$F_{1,77} = 0.610$ $P = 0.437$	$F_{1,77} = 27.62$ $P < 0.001$	$F_{4,77} = 1.501$ $P = 0.210$	$F_{4,77} = 22.37$ $P < 0.001$
	Ucrit	$F_{1,109} = 1.632$ $P = 0.204$	$F_{1,109} = 333.8$ $P < 0.001$	$F_{4,109} = 12.15$ $P < 0.001$	$F_{4,109} = 108.9$ $P < 0.001$
Swimming performance	MMR	$F_{1,109} = 0.187$ $P = 0.666$	$F_{1,109} = 229.4$ $P < 0.001$	$F_{4,109} = 13.33$ $P < 0.001$	$F_{4,109} = 77.02$ $P < 0.001$
	AMS	$F_{1,109} = 1.046$ $P = 0.309$	$F_{1,109} = 55.67$ $P < 0.001$	$F_{4,109} = 3.779$ $P = 0.006$	$F_{4,109} = 15.48$ $P < 0.001$

<sup>a</sup> The body mass is used as the covariate for all of the tested variables except Ucrit, for which the body length is used as the covariate.

of physiological challenges, such as temperature change situations. For example, the maintenance of protein function and cardiac mitochondrial output, which are closely related to fish mortality under temperature fluctuations, should be more important than the maintenance of swimming performance, whereas withholding digestive performance and body weight might be less important (Eliason et al., 2011; Iftikar et al., 2015). Moreover, the heat tolerance capacity is more ecologically relevant under temperature increases, while the cold tolerance capacity is more relevant under temperature decreases. Thus, an investigation of the acclimation rate among different physiological functions and (or) under different thermal regimes is very important. However, little is known about these differences in fish species. Among all physiological functions, it has been suggested that the critical thermal limits (critical thermal maxima, CT<sub>max</sub> and critical thermal minima, CT<sub>min</sub>) are assumed to be the most important factors for determining the distribution of a species (Sears et al., 2011). As temperatures change, the thermal limit can be approached and exceeded for a length of time, compromising the survival of individual fish (Bear et al., 2007; Underwood et al., 2012; Whitney et al., 2016). Therefore, knowledge of the plasticity of critical thermal limits is important in understanding how a species may respond biologically to different thermal regimes (Whitney et al., 2016; Xia et al., 2017). Recently, it has been suggested that increasing constraints on the metabolic scope (MS) available for performance and fitness are predicted to affect the distribution and abundance of aquatic ectotherms (Pörtner and Farrell, 2008; Pörtner, 2010; Ejbye-Ernst et al., 2016; Motyka et al., 2017; Sandblom et al., 2016). The MS is defined as the difference between the maximal metabolic rate (MMR) and standard metabolic rate (SMR). Thus, an investigation of the potential MS for different physiological functions, such as the aerobic swimming performance and digestion, as well as the growth performance, that undergo temperature changes might yield interesting findings.

Because of global warming, the effects of temperature increases have drawn a great deal of attention from scientists. However, the water temperature decreases much faster than the temperature increases in the field due to the physical traits of water, and this situation becomes more severe when considering the El Niño phenomenon. Furthermore, the drain water from dams is also a physiological challenge for fish species that live downstream of dams in some of Chinese rivers or adjacent small water bodies. Physiological adjustments to decreases in water temperature also deserve more attention. Thus, the present study aimed to test whether there were different responses when different physiological functions reached steady states and to determine possible relationships with metabolic constraints during temperature changes.

To achieve our goal, qingbo (*Spinibarbus sinensis*), a native warm

water cyprinid fish species that is mainly distributed in the Yangtze River of southern China was selected as the experimental model. We first acclimated fish at low (15 °C) and high (25 °C) temperatures for eight weeks (the eight-week period is assumed to be long enough to fully thermally acclimate most physiological functions) to reach thermal equilibrium. The temperatures applied in this study, i.e., 15 and 25 °C, are similar to the seasonal temperature fluctuations in the Three Gorges Reservoir of China, where the fish were caught (Pang et al., 2014). Then, we reversed the water temperature and reared the fish at each reversed temperature for eight weeks and defined a either warming or cooling group. The thermal tolerance limits (CT<sub>max</sub> and CT<sub>min</sub>); aerobic swimming performance, as suggested by the critical swimming speed (Ucrit); digestion function, as suggested by the post-prandial metabolic response (or specific dynamic action, SDA); as well as the SMR, the maximum metabolic rate during either swimming (MMR) or digestion (PMR), were measured before and after the temperature change (0, 1, 2, 4 and 8 weeks). Meanwhile, we also measured the growth performance (feeding rate, food efficiency and weight gain) of fish after the temperature reversal.

## 2. Materials and methods

### 2.1. Experimental animals and acclimation

This study was approved by Animal Care and Use Committee of Key Laboratory of Animal Biology of Chongqing (Permit Number: Zhao-20140916-01) and performed in strict accordance with the recommendations in the Guide for the Care and Use of Animal at the Key Laboratory of Animal Biology of Chongqing, China. Juvenile qingbo (*Spinibarbus sinensis*) (see Table 1, Table 2 and Supplementary Table 1 for the body size and sample size) were purchased from local fishermen and maintained in 20 ± 1 °C (the field temperature when the fish were purchased from fishermen) de-chlorinated, fully aerated tap water tanks with water re-circulated through biological filters for 2 weeks before the experiment. Throughout the experimental period, the photoperiod was maintained at 12 L:12 D, and the dissolved oxygen level was kept above 90% saturated dissolved oxygen. The fish were fed once daily (at 9:00 am) to satiety with commercial feed (Tongwei, China, dietary composition: 41.2 ± 0.9% protein; 8.5 ± 0.5% lipid; 25.7 ± 1.2% carbohydrate and 12.3 ± 0.4% ash). Uneaten food and feces were removed with a siphon 30 min after feeding. The food intake was calculated by the the food consumption from the number and mean weight of the pellets (5.05 ± 0.03 mg; a screen mesh was used to acquire pellets of the same size).

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