



Effect of temperature on hypoxia tolerance and its underlying biochemical mechanism in two juvenile cyprinids exhibiting distinct hypoxia sensitivities



Wei He, Zhen-Dong Cao, Shi-Jian Fu*

Laboratory of Evolutionary Physiology and Behavior, Chongqing Key Laboratory of Animal Biology, Chongqing Normal University, Chongqing 401331, China

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ABSTRACT

It is increasingly important to investigate the effect of temperature on hypoxia tolerance in fish species, as worldwide hypoxia worsens with increases in global warming. We selected the hypoxia-tolerant crucian carp (*Carassius carassius*) and the hypoxia-sensitive Chinese bream (*Parabramis pekinensis*) as model fish and investigated their hypoxia tolerance based on the critical oxygen tension of the routine metabolic rate ($MO_{2\text{rout}}$) (P_{crit}), aquatic surface respiration (ASR_{crit}) and loss of equilibrium (LOE_{crit}) after two weeks of acclimation at either 10, 20 or 30 °C. We also measured the tissue substrate (glycogen and glucose of muscle and liver) and lactate levels of both normoxia- and hypoxia-treated fish (post- LOE). Crucian carp exhibited significantly lower P_{crit} and LOE_{crit} but not ASR_{crit} . Crucian carp possessed higher hypoxia tolerance, partially due to a higher tissue glycogen reserve, which provides cellular fuel under severe hypoxia, as well as higher lactate tolerance and clearance ability than Chinese bream. The hypoxia tolerance was maintained in crucian carp but was decreased in Chinese bream as the temperature increased. The difference between the two species is based on the greater recruitment of tissue glycogen, resulting in an increased level of cellular fuel during hypoxia in crucian carp than in Chinese bream. In addition, crucian carp possessed the greater liver lactate clearance capacity, and the smaller increase in the $MO_{2\text{rout}}$ at higher temperatures compared to Chinese bream. Furthermore, substrate shortage and decreased lactate tolerance at high temperatures in Chinese bream might also contribute to the difference in hypoxia tolerance between the two species.

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1. Introduction

Environmental hypoxia is a common abiotic challenge caused by temperature fluctuations, low photosynthetic activity and low or stagnant water flow that many aquatic organisms experience in their habitat (Karim et al., 2003; Diaz and Breitburg, 2009; Martínez et al., 2011). At any sufficiently low level of dissolved oxygen would negatively impact the behavior and/or physiology of fish. In general, fish respond to hypoxia via a set of physiological, behavioral, biochemical and molecular responses that serve to either enhance oxygen uptake in the oxygen-depleted environment or limit the potentially devastating consequences of oxygen limitation in the tissue. First, fish may down-regulate metabolism to decrease the oxygen demand during hypoxia exposure. The critical oxygen tension (P_{crit}) for routine oxygen consumption rate ($MO_{2\text{rout}}$) is the minimum oxygen level required to sustain the routine oxygen consumption rate. P_{crit} is thought to reflect the ability of an organism to extract oxygen from the environment to maintain $MO_{2\text{rout}}$ as oxygen tension decreases; a lower P_{crit} is associated

with higher hypoxia tolerance. Consequently, P_{crit} has been employed routinely as an important measure of hypoxia tolerance in aquatic organisms, including fish species (Pörtner and Grieshaber, 1993; Chapman et al., 2002; Nilsson and Östlund-Nilsson, 2008; Mandic et al., 2009). In addition to the downregulation of metabolism, aquatic surface respiration (ASR) is one of the most common responses to hypoxia (Graham, 1990; Diaz and Rosenberg, 1995; Soares et al., 2006; Urbina et al., 2011), whereby fish breathe water from surface film, which allows them to access the more highly oxygenated water at the water–air interface (Shingles et al., 2005; Sloman et al., 2006). ASR is hypothesized to be triggered by environmental oxygen tensions at which respiratory mechanisms fail to compensate for environmental hypoxia (Takasusuki et al., 1998). If the oxygen tension decreases further, fish may exhibit loss of equilibrium (LOE). The oxygen tension threshold for LOE (LOE_{crit}), which represents the oxygen tension at which the fish can no longer maintain body balance due to systemic disorganization, is considered as an ecological index of lethality (Coutant, 1969; Paladino et al., 1980; Chapman et al., 1995; Currie et al., 2004). Therefore, P_{crit} , the critical oxygen tension for ASR (ASR_{crit}), and LOE_{crit} are three potentially useful hypoxia tolerance indicators for fish (Chapman et al., 2002; Barnes et al., 2011; Mandic et al., 2013).

* Corresponding author.

E-mail address: shijianfu9@hotmail.com (S.-J. Fu).

In recent years, hypoxia in aquatic environments worldwide has been further aggravated due to the effects of anthropogenic global warming (Diaz and Rosenberg, 2008; Roze et al., 2013) because temperature plays a fundamental role in regulating metabolic processes and the elevation of temperature increases the respiration rates of organisms while diminishing oxygen solubility (Guderley, 2004; Sørensen et al., 2014). As a result, the combination of increased temperature and reduced oxygen availability is currently impacting upon several freshwater and marine fish populations (Ficke et al., 2007; Rabalais et al., 2009). Therefore, it has become increasingly important to investigate the effect of temperature on hypoxia tolerance in fish species and to understand the mechanisms that fish use to persist and survive under hypoxic conditions at various temperatures. In general, it has been demonstrated that the P_{crit} is significantly increased, indicating reduced hypoxia tolerance, as temperature increases in fish species, such as barramundi (*Lates calcarifer*) and coral-dwelling gobies (*Gobiodon histrio* and *Gobiodon erythrosipilus*) (Collins et al., 2013; Sørensen et al., 2014). However, few reported studies have attempted to elucidate the effect of temperature on the hypoxia tolerance of fish species using all three of the aforementioned parameters. Therefore, the first aim of this study was to investigate the effect of temperature on hypoxia tolerance in fish species based on P_{crit} , ASR_{crit} and LOE_{crit} to reveal the connections between the physiology and the behavior of experimental fish by analyzing and comparing these parameters. To perform our investigation, we selected two eurythermic cyprinids with closely phylogenetical relationship from the Three Gorges Reservoir, China, i.e. crucian carp (*Carassius carassius*), a hypoxia-tolerant cyprinid, and Chinese bream (*Parabramis pekinensis*), a hypoxia-sensitive cyprinid according to a recently published study (Dhillon et al., 2013; Fu et al., 2014) as experimental models. The water temperature in this region increased in recent years after construction of Three Gorges Dam under the background of global warming. Thus, the sensitivities of hypoxia tolerance to temperature among different fish species might result in profound effect on their thriving in future in thermal changing environment.

Under hypoxic conditions, two biochemical strategies are widely used in fish species, i.e., decreasing energy turnover and increasing the energetic efficiency of ATP-producing pathways, including suppressing aerobic metabolic ATP production, enhancing glycolytic capacity and alternative pathways that display improved energetic efficiency (Seibel, 2011). These changes are associated with the mobilization, transportation and utilization of substrates (primarily glycogen and glucose from liver and muscle) and the transportation and clearance of metabolites (primarily lactate) (Mandic et al., 2013). However, the extent and location of the metabolites used depend on the duration and severity of hypoxia, as well as the pathway, tissue and species involved (Martínez et al., 2011). Crucian carp is considered as the champion of hypoxia tolerance (Nilsson and Renshaw, 2004; Dhillon et al., 2013). Its impressive anoxia-tolerant is associated with its large muscle and liver glycogen stores and its high lactate tolerance (Lutz and Nilsson, 1997; Nilsson and Renshaw, 2004). However, compared to crucian carp, Chinese bream (*P. pekinensis*) is much more sensitive to hypoxia (Fu et al., 2014). Furthermore, the adaptive responses of crucian carp to hypoxia, such as morphological changes in the gills that reduce the water–blood diffusion distance (Sollid et al., 2003) during hypoxia (or high temperature) and the ability to convert lactate to ethanol and CO_2 to avoid self-lactate poisoning (Van Waarde, 1991), are absent from Chinese bream (Fu et al., 2014). The biochemical responses to hypoxia at different temperatures may also differ between these two fish species. Thus, the second aim of this study was to investigate the underlying biochemical mechanism of the potentially different hypoxia tolerance responses at varying temperatures between the two fish species.

In order to investigate the difference of the hypoxia tolerance and its underlying biochemical mechanism with the increase of temperature between the two cyprinids, we selected the temperature range (10 to 30 °C) based on the annual variation of local water bodies in Chongqing, China. Then, we measured the decrease in oxygen

tension based on the MO_{2rout} , ASR and LOE of fish after two weeks of acclimation at 10, 20 or 30 °C. We also measured the tissue substrate levels and the lactate content immediately after LOE in each thermal acclimation group.

2. Material and methods

2.1. Fish

All juvenile crucian carp (*C. carassius*) and Chinese bream (*P. pekinensis*) were obtained from a local farmer. The fish were transported to Chongqing Normal University and maintained in an indoor re-circulating rearing system for one week. During this period, the temperature of the dechlorinated fresh water was maintained at 20 ± 2 °C. The photoperiod was 12L:12D, and the oxygen concentration was maintained above 7 mg L^{-1} . One tenth of the water was replaced daily. Throughout the experimental period, the fish were fed daily (10:00 AM) to satiation using commercial food. All of the experiments were performed 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.

2.2. Temperature acclimation

After one week of holding, 72 healthy fish from each species were randomly selected and assigned to three temperature (10, 20 and 30 °C) treatment groups (24 for each group). The average body mass of the crucian carp and the Chinese bream were 7.32 ± 0.20 and 5.90 ± 0.25 g, respectively. The water temperature was gradually increased or decreased to the target temperature by two-centigrade steps each day. Then, the experimental fish were housed at the target temperature for another two weeks before any measurements. The rearing conditions in the tanks were identical to those of the acclimation period.

2.3. Measurement of hypoxia indicators

2.3.1. Determination of MO_2 and P_{crit}

MO_2 and P_{crit} for each fish (eight in each group) were determined using closed respirometry (Zhang et al., 2010). Each fish was placed in the respirometer chamber overnight (8–12 h) to habituate to the apparatus and reduce the effect of handling stress. During this time, the respirometer was submerged in a thermal-controlled water bath (target temperature ± 0.5 °C). Each respirometer chamber remained open, allowing air-saturated water to flow into the respirometer using an attached circulating water pump. Then, the respirometer was sealed, and the decrease in oxygen concentration was continuously recorded every 2 min using an oxygen probe (HQ30, Hach Company, Loveland, Colorado, USA). The measurements were stopped when the oxygen concentration displayed no further decrease. Then, the fish was removed from the chamber to measure its body mass.

The following formula was used to calculate the MO_2 ($\text{mg kg}^{-1} \text{ h}^{-1}$) of each fish:

$$MO_2 = ([O_2]_k - [O_2]_{k+1})V / (t \times m) \quad (1)$$

where $[O_2]_k$ refers to the oxygen concentration (mg L^{-1}) at the sampling time point k, $[O_2]_{k+1}$ represents the concentration at the following time point (these values were calculated according to the O_2 solubility coefficient in water at the corresponding temperature and pressure), V (L) represents the total volume of the respirometer minus the volume of the fish, t (h) corresponds to the interval between the time points k and k + 1, and m (kg) represents the body mass of the fish.

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