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The effects of constant and diel-fluctuating temperature acclimation on the thermal tolerance, swimming capacity, specific dynamic action and growth performance of juvenile Chinese bream

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ABSTRACT

We investigated the effects of constant and diel-fluctuating temperature acclimation on the thermal tolerance, swimming capacity, specific dynamic action (SDA) and growth performance of juvenile Chinese bream (*Parabramis pekinensis*). The critical thermal maxima (CT_{max}), critical thermal minima (CT_{min}), lethal thermal maxima (LT_{max}), lethal thermal minima (LT_{min}), critical swimming speed (U_{crit}) and fast-start escape response after 30 d acclimation to three constant temperatures (15, 20 and 25 °C) and one diel-fluctuating temperature (20 ± 5 °C) were measured. In addition, feeding rate (*FR*), feeding efficiency (*FE*) and specific growth rate (*SGR*) were measured. The diel-fluctuating temperature group showed lower CT_{min} than the 20 °C group but a similar CT_{max}, indicating a wider thermal scope. SDA linearly increased with the temperature. Temperature variation between 20 and 25 °C had little effect on either swimming or growth performance. However, fish in the 15 °C group exhibited much poorer swimming and growth performance than those in the 20 °C group. U_{crit} decreased slightly under low acclimation temperature due to the pronounced improvement in swimming efficiency under cold temperature. Fish in the diel-fluctuating temperature group fed more but exhibited similar *SGR* compared to 20 °C group, possibly due in part to an increase in energy expenditure to cope with the temperature fluctuation. The narrower thermal scope and lower CT_{max} of Chinese bream together with the conservation of CT_{max} with temperature acclimation, suggests that local water temperature elevations may have more profound effects on Chinese bream than on other fish species in the Three Gorges Reservoir.

1. Introduction

Oscillations in the earth's climate produce associated fluctuations in the temperature regimes of many aquatic and terrestrial ecosystems (Pörtner et al., 2001). In many taxa, temperature has a profound effect on several fitness-determining traits such as growth (Green and Fisher, 2004), metabolism (Pang et al., 2010), and locomotive performance (Jain and Farrell, 2003). Therefore, the predicted warming of the atmosphere will directly or indirectly affect aquatic animal populations at all life stages (Pörtner et al., 2001). There is a large body of literature describing the responses of fish to continuous temperature variation (Beitinger et al., 2000; Das et al., 2005; Pang et al., 2010). Several studies have addressed the physiological responses of aquatic organisms to the frequent, diel-cycling temperature changes that occur during their life histories (Hokanson et al., 1997; Dickerson and Vinyard, 1999; Tian and Dong, 2005; Dong et al., 2006).

Thermal tolerance varies widely among different fish species, and it is assumed to be the most important factor determining species distributions (Fry, 1947). Accordingly, population dynamics may vary considerably among fish species within a particular habitat due to species differences in thermal tolerance under temperature changes (Pörtner, 2002). The thermal biology of fishes has been studied for over 100 years (Heath, 1884; Vernon, 1899; Currie et al., 1998; Pörtner, 2002). Studies have found that the temperature tolerance of fish is dependent upon the acclimation temperature (Das et al., 2005) and that high physiological plasticity in thermal tolerance may greatly facilitate the adaptation of fish to new environments (Nilsson and Sollid, 2006; Yang et al., 2013). Thermal tolerance indicators have traditionally been established from laboratory studies that involve heating or cooling test fish at a prescribed rate from a series of acclimation temperatures until they lose either their body equilibrium (critical thermal method, CTM) or their gill movement (lethal thermal method, LTM) (Currie et al., 1998; Widmer et al., 2006). Thus, the critical thermal maximum (CT_{max}), critical thermal minimum (CT_{min}), lethal thermal maximum (LT_{max}), lethal thermal minimum (LT_{min}), and thermal tolerance scope (difference between CT_{max} and CT_{min}) are the frequently used indicators of thermal biology (Das et al., 2005; Wang et al., 2008). Thermal

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tolerance is most often defined in relation to constant temperature conditions. However, fluctuating temperature cycles are often observed in natural environments and may vary between 5 and 20 °C per day (Heath, 1967; Brett, 1971; Houston and Schrapp, 1994). Tolerance to diel temperature cycles may be particularly relevant for natural fluvial habitats (Heath, 1967; Brett, 1971; Houston and Schrapp, 1994). Thus, the primary aim of the present study was to investigate the thermal tolerance of Chinese bream (*Parabramis pekinensis*), a common species in the Three Gorges Reservoir, under both constant temperatures (15, 20, and 25 °C) and diel-fluctuating temperature acclimation conditions (20 ± 5 °C).

Swimming performance is a survival-determining trait in fish because it is involved in food capture, predator avoidance and reproductive behavior (Pang et al., 2011). Swimming performance can be classified as either steady or unsteady (Webb, 1984). Steady swimming describes linear, constant-speed locomotion, and it is commonly employed in nature during competition for limited resources, such as food, mates and favorable abiotic conditions (Plaut, 2001; Blake, 2004). The critical swimming speed (i.e., the speed at which a fish can no longer maintain its position in the water column or its maximum sustainable swimming speed, U_{crit}) is widely used to evaluate steady swimming performance (Plaut, 2001; Yan et al., 2012; Fu et al., 2013a, b). In contrast, fast-start performance (i.e., brief, sudden accelerations of fish during predator–prey encounters) is usually used to evaluate unsteady swimming performance (Domenici and Blake, 1997; Yan et al., 2012). The thermal plasticity of swimming performance is likely important to fish species. Therefore, the second aim of the present study was to investigate the steady and unsteady swimming performances of juvenile Chinese bream under both constant and diel-fluctuating temperature conditions.

Temperature is widely recognized as important in the growth performance of fish (Brander, 1994; Brown et al., 2004). Generally, a species' feeding rate, diet conversion efficiency, and, consequently, growth rate will be impaired when rearing temperatures exceed the optimum (EI-Sayed and Kawanna, 2008). Thus, data on the optimal temperatures for growth performance in fish species are important for effective aquaculture operations. In the late 20th century, researchers observed greater growth under thermal cycles than under constant temperature held at the mean of those cycles, leading to the hypothesis that thermal cycles allow higher rates of food intake and consumption than constant temperature conditions (Diana, 1984). The effects of different temperature regimes (constant vs. diel-fluctuating temperature) on feeding and growth rates are species-specific (Pörtner et al., 2001; Dong et al., 2006). Digestion is an important physiological activity in animals. The increase in the oxygen consumption rate (MO_2) during digestion above routine MO_2 values is commonly referred to as the specific dynamic action (SDA) (Jobling, 1981). Temperature has been found to exert profound effects on the digestive process and, hence, SDA (Luo and Xie, 2008; Pang et al., 2011). Investigating the effects of temperature on SDA may improve our understanding of the mechanisms of growth performance change under different temperature conditions. The third aim of this study was to investigate the effects of constant and diel-fluctuating temperature acclimation on SDA and growth performance in juvenile Chinese bream.

We selected a eurythermic fish species, Chinese bream, as our experimental model. Chinese bream is a frequent or even dominate fish species in the Three Gorge Reservoir. The water temperature in the Three Gorge Reservoir showed large seasonal change that varied from 12 to 15 °C in winter and from 22 to 25 °C in summer in the recent years (Sun et al., 2010). Furthermore, the average water temperature increased by about 2 °C in winter but showed no change in summer after construction of Three Gorges Dam (Yu et al., 2007). A recent study showed that the physiology of Chinese bream is more sensitive to temperature than that of other cyprinids (He et al., 2014). To investigate the effect of acclimation temperature on thermal tolerance in Chinese bream, we measured CT_{max}, CT_{min}, LT_{max} and LT_{min}; i.e., we calculated the thermal tolerance scope after 30 d acclimation under three constant temperatures and one diel-fluctuating temperature condition. To investigate the effects of acclimation temperature on swimming performance, we measured U_{crit} and MO_2 at different swimming speeds and measured the fast-start escape response under each acclimation temperature (the swimming performance of the diel-fluctuating temperature group was measured at both 15 and 25 °C). To investigate the effect of temperature on growth performance in Chinese bream, we measured the specific growth rate (*SGR*), feeding rate (*FE*) and feed efficiency (*FR*) over a 30 d growth experiment.

2. Materials and methods

2.1. Experimental animals and housing conditions

Experimental juvenile Chinese bream (*P. pekinensis*; 4–9 g, N = 200) were obtained from the Fisheries Hatchery of the Hechuan Aquaculture School (Hechuan, Chongqing City, China). The fish were maintained in dechlorinated, 20 ± 0.5 °C, fully aerated tap-water tanks for 2 weeks at Chongqing Normal University before the start of the experiment. During this period and throughout the experimental period, the lights were continuously on (Tandler and Beamish, 1980; Blaikie and Kerr, 1996). Two weeks later, 120 fish were selected and then randomly divided into four temperature treatment groups of 30 individuals (three constant temperature groups: 15, 20 and 25 °C; one diel-fluctuating temperature group: 25 °C from 8:30 h–20:30 h and 15 °C from 20:30 h–8:30 h). The switch period between the two temperatures was about 4 h. The temperature manipulation was achieved by heaters (Xilong Company, Guangdong, China, XL-999) and chillers (Risheng Group, Guangdong, China, C-1000A) automatically. The oxygen level was maintained above 90% saturation. The ammonia-N ranged from 0.005 to 0.025 mg L^{-1}, and the pH ranged from 6.8 to 7.3 during the experiment. One-tenth of the water in each tank was replaced daily with fresh water. The fish were fed to satiation twice daily at 9:00 h and 19:00 h with a commercial diet. Uneaten food and feces were removed 1 h after feeding using a siphon. 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.

2.2. Effects of constant and diel-fluctuating temperature on thermal tolerance

To investigate the effects of constant and diel-fluctuating temperature on thermal tolerance in Chinese bream, 16 temperature-acclimated fish from each group were randomly selected after 24 h of fasting (see body size in Table 1). The thermal tolerance of experimental fish was measured as described previously (Wang et al., 2008). In brief, eight fish were introduced into a tank for 1 h of acclimation for either a maximum- or minimum-temperature value test. The temperature of each experimental treatment group was the same as the acclimation temperature except that the temperature of diel-fluctuating temperature group was 20 °C. Then, the thermal tolerance under a rate of temperature change of 0.3 °C min^{-1} was evaluated. Either a water chiller or heater and a voltage regulator were used to achieve the experimental rate of temperature change (Dong et al., 2006). The dissolved oxygen content of the experiment was maintained above 90% saturation, and a digital thermometer was used for temperature recording. The values of CT_{max} or CT_{min} were recorded as the temperatures at which the fish showed a loss of body equilibrium, whereas the values of LT_{max} or LT_{min} were recorded as the temperatures at which gill movements ceased (Wang et al., 2008). After these temperatures were recorded, the experimental fish were transferred back to their housing tank for 24 h recovery, and the survival rates after thermal tolerance testing were calculated for each temperature group.