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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 (El-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.

Table 1
The body mass and body length of Chinese bream in experiments investigating specific dynamic action (SDA), thermal tolerance, critical swimming speed (U_{crit}) and the fast-start escape response (means $\pm$ S.E., $p < 0.05$).

		Constant temperature			Diel fluctuating temperature		Significance
		15 °C	20 °C	25 °C	15 °C	25 °C	
SDA	N	8	8	8	8	8	
	Body mass (g)	7.85 ± 0.15	8.26 ± 0.13	8.47 ± 0.06	7.77 ± 0.42	8.11 ± 0.23	F = 1.532 $p = 0.214$
	Body length (cm)	7.61 ± 0.06	7.61 ± 0.04	7.74 ± 0.07	7.55 ± 0.15	7.65 ± 0.06	F = 0.651 $p = 0.630$
Thermal tolerance	N	16	16	16	16		
	Body mass (g)	5.79 ± 0.29	5.70 ± 0.26	6.23 ± 0.38	6.35 ± 0.36		F = 0.968 $p = 0.414$
	Body length (cm)	6.95 ± 0.1	6.83 ± 0.09	7.08 ± 0.14	7.09 ± 0.13		F = 1.107 $p = 0.353$
U_{crit}	N	10	9	9	9	8	
	Body mass (g)	6.98 ± 0.3	7.62 ± 0.58	8.69 ± 0.4	7.78 ± 0.21	7.53 ± 0.41	F = 2.560 $p = 0.053$
	Body length (cm)	7.35 ± 0.1	7.34 ± 0.16	7.78 ± 0.15	7.66 ± 0.05	7.44 ± 0.14	F = 2.404 $p = 0.066$
Fast-start	N	8	10	9	8	8	
	Body mass (g)	6.31 ± 0.52	8.12 ± 0.35	8.56 ± 0.45	7.01 ± 0.26	7.31 ± 0.33	F = 5.120 $p = 0.002$
	Body length (cm)	7.04 ± 0.21	7.68 ± 0.09	7.77 ± 0.16	7.31 ± 0.15	7.46 ± 0.14	F = 3.841 $p = 0.010$

2.3. Effects of constant and diel-fluctuating temperature on swimming performance

2.3.1. The effects of constant and diel-fluctuating temperature on U_{crit} and swimming O_2

After 30 d of temperature acclimation, the U_{crit} of individual fish in the constant-temperature groups was measured at the corresponding temperature, and the temperature of the diel-fluctuating temperature group was measured at both the 15 and 25 °C conditions with a Brett-type swim-tunnel respirometer (see details in Li et al., 2010; Pang et al., 2010). In brief, fish were individually transferred into the swim tunnel and allowed to acclimate for 1 h at a water speed of 7 cm s^{-1} (i.e., the speed at which a fish travels approximately one body length), allowing full water exchange (Fu et al., 2013a,b). After 1 h, the water speed was increased to 50% U_{crit}; i.e., to either 35 (15 and 20 °C test temperature) or 42 (25 °C test temperature) cm s^{-1} over a 2 min period (a pilot experiment found that the U_{crit} was about 70 cm s^{-1} in both 15 and 20 °C while the U_{crit} was about 80 cm s^{-1} in 25 °C), after which the water speed was increased by 7 cm s^{-1} increments every 20 min until the fish reached exhaustion (Jain et al., 1997; Jain and Farrell, 2003). Fatigue was defined as the time at which the fish failed to move off of the rear honeycomb screen of the swimming chamber for 20 s (Lee et al., 2003). U_{crit} was calculated for each fish using Brett's equation (Brett, 1964):

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

where V is the highest speed at which the fish swam for the full time period (cm s^{-1}), ΔV is the velocity increment (7 cm s^{-1}), T is the prescribed period of swimming at that speed (20 min) and t is the duration for which the fish swam at the final speed (min).

During the measurement of U_{crit}, the dissolved oxygen level (DO, mg L^{-1}) was recorded once every 2 min. The MO_2 (mg kg^{-1} h^{-1}) of an individual fish during swimming was calculated from the depletion of oxygen according to the following equation:

$$\dot{M}O_2 = 60slopeVOL/m \tag{2}$$

where $slope$ (mg L^{-1} min^{-1}) is the decrease in the water DO per minute, VOL is the total volume of the respirometer (3.5 L) minus the volume of the fish and m is the body mass (kg) of the fish. The slope was obtained from the linear regression of water DO (mg L^{-1}) on

time (min). The maximum observed MO_2 during the U_{crit} test was defined as the active MO_2 ($MO_{2active}$).

2.3.2. Effects of constant and diel-fluctuating temperature on fast-start escape response

The fast-start instrument was developed by the Laboratory of Evolutionary Physiology and Behavior, Chongqing Normal University (see Yan et al., 2012, for details). The device includes a high-speed camera (BASLER company, Germany, A504K, 500 frames s-1) and a light-emitting diode (LED) matrix light source and sink (engraved with 1 × 1 cm grid lines on the bottom). First, fish from each group were individually marked with a small white plastic ball (diameter: 1 mm) on their dorsal surface at the center-of-mass (CM) position (Yan et al., 2013). Then, individual fish were gently herded toward the acclimation zone of the fast-start experimental system and allowed to rest for 1 h. The water in the tank was 10 cm deep. Then, each individual fish was introduced into the filming zone through the alleyway. Measurements were taken of individuals in the constant-temperature groups at each corresponding temperature, and the temperature of individuals in the diel-fluctuating temperature group was measured at both 15 and 25 °C. Escape responses were elicited by an electrical impulse (30 V; 50 ms) administered when the fish was stably positioned at the center of the filming zone. The high-speed camera recorded the entire time course of the experimental escape process (time span: 3 s). Each trial was initiated (at 0 ms) upon the illumination of the LED (synchronized with the electrical stimulus). The coordinates of the CM were measured with an E-Ruler. Based on the centroid locomotion track and the time interval of each adjacent track, the following parameters were calculated using a basis kinematics approach. Parameter response latency (R) was defined as the time elapsed between the initiation of the stimulus (LED light) and the onset of the escape behavior. Maximum linear velocity (V_{max}) was calculated from the maximum distance traveled by the center of mass in 2 ms (two consecutive video frames). Maximum linear acceleration (A_{max}) was calculated from the change in v_{max} (Yan et al., 2013).

2.4. Effects of constant and diel-fluctuating temperature on growth performance

Fish were individually raised in 120 independent compartments (length × wide × high = 15 × 5 × 12 cm) immersed in indoor aquaculture systems at the different treatment temperatures for 30 d. The fish

were fed to satiation twice daily (at 9:00 AM and 19:00 PM) with dry commercial floating pellets with similar size ((3.76 ± 0.03) mg per pellet) (Tongwei Group, Chengdu, China; composition: $41.2 \pm 0.9\%$ protein; $8.5 \pm 0.5\%$ lipid; $25.7 \pm 1.2\%$ carbohydrate and $12.3 \pm 0.4\%$ ash). Uneaten food and feces were removed 1 h after feeding using a siphon, and food consumption was calculated by the number of pellets and the average weight of pellets. After the 30 d treatment period and a subsequent 24 h of fasting, the body mass and length of each experimental fish were measured to mg and mm, respectively. The following growth performance parameters were calculated:

$$\text{Feeding rate}(FR, \%) = 100 \times F_c/[(W_t + W_0)/2]/t, \tag{3}$$

$$\text{Feed efficiency}(FE) = (W_t - W_0)/F_c, \tag{4}$$

$$\text{Specific growth rate}(SGR, \%) = 100 \times (Ln(W_t) - Ln(W_0))/t, \tag{5}$$

where F_c represents the total amount of food consumed by the fish (g), W_0 is the initial mass (g) of the experimental fish, W_t is the final mass (g) of the fish and t is the experimental period (d).

2.5. Effects of constant and diel-fluctuating temperature on SDA

The $\dot{M}O_2$ of individual fish was measured using a continuous-flow respirometer (Fu et al., 2005). After 24 h of fasting, 8 temperature-acclimated fish from each constant-temperature group and 16 fish from the diel-fluctuating temperature group were placed in the respirometer chamber for 24 h acclimation (the diel-fluctuating temperature group was measured at both 15 and 25 °C). $\dot{M}O_2$ was measured three times at 1 h intervals, and the average value was taken as the resting $\dot{M}O_2$ ($\dot{M}O_{2rest}$). Individual fish from each group was fed a meal-sized compound feed (pellet feed diluted to a ratio of 1:1.5 with water), comprising approximately 1.5% of their body mass (Li et al., 2013). A gavage protocol was performed because the fish did not voluntarily eat in the respirometer chamber. A pilot experiment had shown that the gavage protocol had no significant effect on the $\dot{M}O_2$ of juvenile Chinese bream. Fish were gently removed from the respirometer chamber and anesthetized with tricaine methane sulfonate (MS-222, 80 mg L^{-1}) for approximately 2–3 min in a small container until they lost their normal reflexes. The tip of a syringe (1 mL) attached by a plastic cannula was then inserted into the proximal intestine (Chinese bream possess no stomach), and the chyme was gently introduced for about 1 min (Li et al., 2013). The fish were subsequently returned to the respirometer chamber. $\dot{M}O_2$ was measured at 1 h intervals for 12 h. The following formula was used to calculate the $\dot{M}O_2$ (mg kg^{-1} h^{-1}) of individual fish:

$$MO_2 = \Delta O_2 \times v/m \tag{6}$$

where ΔO_2 is the difference in DO (mg L^{-1}) between the experiment chamber and the control chamber (chamber without fish), v is the water flow rate in the experiment chamber (L h^{-1}) and m is the body mass of the fish (kg). DO was measured at the outlet of the chamber using an oximeter. The flow rate of water through the respirometer chamber was measured by collecting the water outflow from each tube. We quantified the following three parameters as described by Jobling (1981) and Secor (2009): (1) peak MO_2 (MO_{2peak}), the observed maximum O_2 uptake rate during SDA; (2) duration, calculated as the time elapsed between feeding and the return of MO_2 to within the standard error of MO_{2rest} of a given fish; and (3) SDA magnitude, calculated as the total energy expenditure above MO_{2rest} during the duration of SDA (the MO_2 was converted to energy using a conversion factor of 13.56 J·mg O$_2^{-1}$ (Elliott and Davies, 1975)).

2.6. Data analysis

All values are presented as mean $\pm$ S.E., and $p < 0.05$ was used as the level of statistical significance. The effects of temperature on all variables were tested by one-way analysis of variance (ANOVA). The effects of swimming speed and acclimation treatment on swimming MO_2, and the effects of postfeeding time and acclimation treatment on feeding MO_2 were evaluated by two-way repeat measurement of ANOVA. The ANOVA were followed by Duncan's multiple-comparison test where appropriate to identify differences between treatment groups.

3. Results

3.1. Thermal tolerance

There was no significant difference detected in either body mass or body length among the different treatment groups (Table 1). CT_{max} showed significant differences among all the treatment groups ($p < 0.05$). CT_{max} decreased significantly with decreasing temperature in the constant-temperature groups, whereas the value of CT_{max} in the diel-fluctuating temperature group was between those of the 25 and 20 °C temperature groups (Fig. 1). Similar to CT_{max}, CT_{min} decreased with a decreasing temperature in the three constant-temperature groups. However, the diel-fluctuating temperature group showed no significant difference in CT_{min} from the 20 °C group. The thermal tolerance scopes were 30.18, 28.55, and 28.66 °C in the 15, 20, and 25 °C constant-temperature groups, respectively, and 30.57 °C in the diel-fluctuating temperature group. LT_{max} differed significantly among all four treatment groups ($p < 0.05$). LT_{max} decreased with a decreasing temperature in the constant-temperature groups, whereas the mean value of LT_{max} of diel-fluctuating temperature group was between those of the 25 and 20 °C groups. Chinese bream showed no sign of LT_{min} (i.e., no loss of gill movements) when acclimated at 15 °C; therefore, 0 °C was assigned as the value of LT_{min} for that group. LT_{min} decreased significantly with a decreasing acclimation temperature, and significant differences were observed among all groups. Furthermore, the LT_{min} value of the diel-fluctuating temperature group was between those of the 15 and 20 °C groups ($p < 0.05$). No fish survived over the next 24 h after LT_{max} testing in any of the four experiment groups. However, all fish in the 15, 20 °C and diel-fluctuating temperature groups, and 6 out of 8 in the 25 °C group, survived the following 24 h after LT_{min} testing.

3.2. Swimming performance

3.2.1. Effect of temperature on U_{crit} and O_{2max}

The U_{crit} of 25 °C group was significantly higher than those of the 20 and 15 °C groups (Fig. 2A). U_{crit} was highest in the diel-fluctuating group measured at 25 °C (but not significantly different from the 25 °C group) and lowest in the diel-fluctuating temperature group at 15 °C (but not significantly different from the 15 °C group). $MO_{2active}$ in the 20 and 25 °C groups was significantly higher than in the 15 °C group ($p < 0.05$). $MO_{2active}$ was significantly higher in the diel-fluctuating temperature group at 25 °C than in all of the other groups and was lowest in the diel-fluctuating temperature group at 15 °C (but not significantly different from the 15 °C group) (Fig. 2B).

MO_2 increased significantly with swimming speed in all groups ($p < 0.05$) (Fig. 3). Within the three constant-temperature groups, there was no significant difference in MO_2 between the 20 and 25 °C groups at all swimming speeds, whereas the MO_2 of the 15 °C group was significantly lower than those of the 20 and 25 °C groups at all swimming speeds. When measured at 25 °C, fish in the diel-fluctuating temperature group showed significantly higher MO_2 values than did those in the 25 °C group, except for those swimming

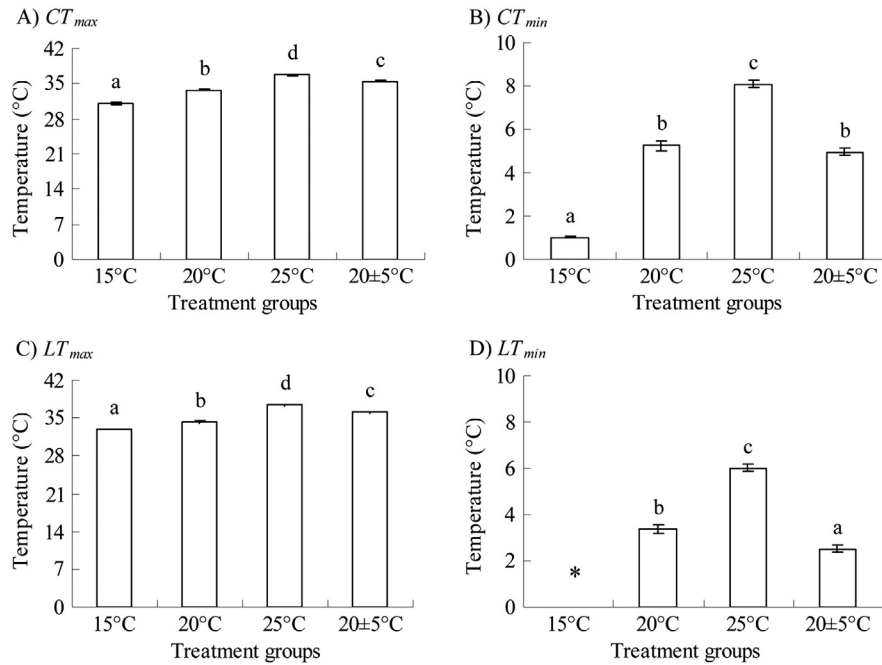**Fig. 1.** The critical thermal maximum (CT_{max}) (panel A), critical thermal minimum (CT_{min}) (panel B), lethal thermal maximum (LT_{max}) (panel C) and lethal thermal minimum (CT_{min}) (panel D) of Chinese bream under different temperature treatments (means $\pm$ S.E., N = 8). * indicates that gill movements persisted when the temperature decreased to near 0.8 °C. The (20 $\pm$ 5 °C) means the diel fluctuating temperature group (a, b, c, d indicate significant differences among groups, $p < 0.05$).

at 63 and 70 cm s^{-1}. However, when measured at 15 °C, fish in the diel-fluctuating temperature group showed no significant difference in MO_2 from those of the 15 °C group, except for those swimming at 35 cm s^{-1}.
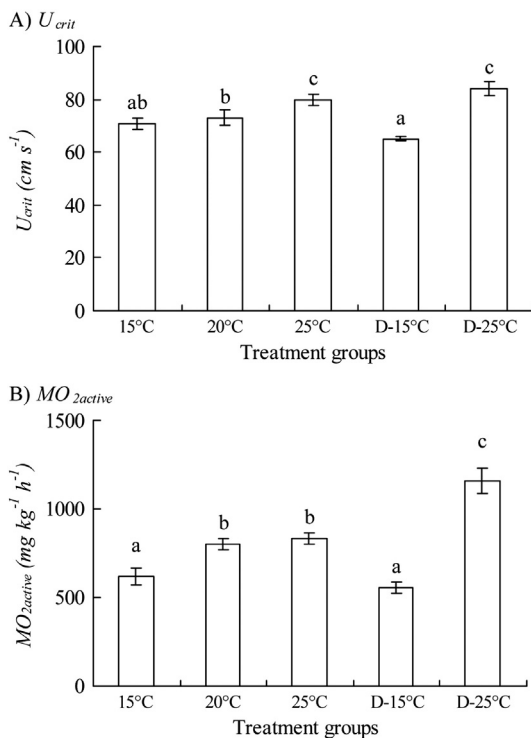

Fig. 2. The critical swimming speed (U_{crit}) (panel A) and the maximum observed MO_2O_2 during the U_{crit} test ($MO_{2active}$) (panel B) of Chinese bream acclimated at different temperatures (means $\pm$ S.E.). The D-15 °C indicates the diel fluctuating temperature group measured at 15 °C, and the D-25 °C indicates the diel fluctuating temperature group measured at 25 °C (a, b, c, d indicate significant differences among groups, $p < 0.05$).

3.2.2. Effect of temperature on the fast-start escape response

V_{max} was lowest in the 15 °C group and significantly lower in this group than in both the 20 °C group and the diel-fluctuating temperature group measured at 25 °C (Fig. 4). There were no significant differences among the other constant-temperature groups and the diel-fluctuating temperature group measured at either 15 or 25 °C. Similar to V_{max}, A_{max} was lowest in the 15 °C group and significantly lower in this group than in the 20 °C group. The R of the 15 °C group was significantly longer than that of diel-fluctuating temperature group measured at 15 °C, whereas the latter was significantly longer than that of the 20 and 25 °C groups as well as that of the diel-fluctuating temperature group measured at 25 °C.

3.3. Growth performance

Neither body mass nor body length differed among the four temperature groups at the beginning of the experiment (Table 2). After 30 d growth, both the final weight and final length of the constant-temperature groups (15, 20, 25 °C) increased significantly with temperature, whereas both variables in the diel-fluctuating temperature group had values between those of (and not significantly different from) the 15 and 20 °C groups. The SGR of the 15 °C group was significantly lower than those of the other three groups ($p < 0.05$), with no significant differences among the other three groups. The FR of 15 °C group was significantly lower than those of the 20 and 25 °C groups ($p < 0.05$), whereas the FR of the diel-fluctuating temperature group was significantly higher than those of all the other groups ($p < 0.05$). FE was significantly lower in the 15 °C group than in all the other groups ($p < 0.05$), with no significant differences observed among the other three groups.

3.4. Effect of temperature on SDA

Body mass did not differ among the four temperature treatment groups before the SDA experiment (Table 1). MO_{2rest} in each of the three constant-temperature groups increased significantly with temperature (Table 3) ($p < 0.05$). MO_{2rest} neither differed significantly
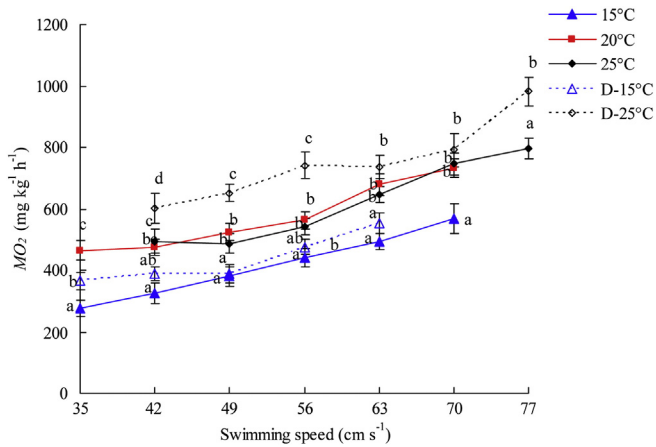
Fig. 3. MO_2 during the critical swimming performance of Chinese bream acclimated at different temperatures The D-15 °C indicates the diel fluctuating temperature group measured at 15 °C, and the D-25 °C indicates the diel fluctuating temperature group measured at 25 °C (a, b, c, d indicate significant differences among groups within the same swimming speed, $p < 0.05$).

between the 15 °C group and the diel-fluctuating temperature group measured at 15 °C, nor differed between the 25 °C group and the diel-fluctuating temperature group measured at 25 °C. MO_2 increased significantly after food consumption (Fig. 5). Similar to MO_{2rest}, MO_{2peak} in the three constant-temperature groups increased significantly with temperature ($p < 0.05$). The MO_{2peak} in the diel-fluctuating temperature group measured at 15 °C did not differ significantly from that of the 15 °C group, and the MO_{2peak} in the diel-fluctuating temperature group measured at 25 °C did not differ significantly from that of either the 20 or 25 °C group (Table 3). Duration ranged from 7 to 9.38 h, with no significant differences among groups. SDA magnitude decreased from 6.16 to 3.33 kJ kg^{-1} as the acclimation temperature decreased from 25 to 15 °C; however, there were no significant differences among the three constant-temperature groups. The SDA magnitude of the diel-fluctuating temperature group measured at 25 °C was significantly larger than that measured at 15 °C.

4. Discussion

In the present study, we found that temperature acclimation had prominent effects on thermal tolerance. The narrower thermal scope and lower CT_{max} of Chinese bream relative to other fish species in Three Gorge Reservoir together with the conservation of CT_{max} with temperature acclimation, suggest that this species may face a relatively greater physiological challenge under climate change. Routine energy expenditure and digestion performance, as indicated by MO_{2rest} and MO_{2peak}, increased linearly with temperature. However, most swimming and growth performance parameters showed no change with the temperature change from 25 to 20 °C, although they did decline sharply with the further decrease to 15 °C. These results suggest that 20–25 °C may be the optimal thermal range for most physiological processes in Chinese bream. The observed maintenance of most U_{crit} levels at low temperature may be related to the particular morphological and biochemical regulation of this species under low temperature demonstrated in the previous studies (He et al., 2014). Fish under the diel-fluctuating temperature regime (20 ± 5 °C) showed a wider thermal scope as a consequence of lower CT_{min} and CT_{max} but exhibited no improvement in SGR despite a higher FR than in the 20 °C group.

4.1. Effects of temperature acclimation on thermal tolerance

CT_{max} and LT_{max} varied from 31 to 37 °C, whereas CT_{min} and LT_{min} varied from 0 to 8 °C, depending on the acclimation temperature. As expected, these values are lower than those measured in tropical fish

species such as rohu (*Labeo rohita*) (Chatterjee et al., 2004) but higher than those of cold-water fish species such as rainbow trout (*Oncorhynchus mykiss*) (Currie et al., 1998). Interestingly, the heat tolerance indicators of Chinese bream were much lower than those of most fish species in the Three Gorges Reservoir. For example, at the same acclimation temperature range as used in the present study (15 to 25 °C), CT_{max} has been shown to vary from 37 to 39 °C in qingbo (*Spinibarbus sinensis*) (Wang, 2009) and from 34 to 39 °C in darkbarbel catfish (*Pelteobagrus vachelli*) (Wang, 2009). CT_{max} varied from 34 to 38 °C in southern catfish (*Silurus meridionalis*) at acclimation temperatures between 10 and 20 °C (Wang et al., 2008) and was measured at 39.8 °C at a 25 °C acclimation temperature in common carp (*Cyprinus carpio*) (Chatterjee et al., 2004). However, unlike the CT_{max}, the CT_{min} values of Chinese bream were similar to those of the aforementioned fish species. Since thermal tolerance scope is the difference between CT_{max} and similar CT_{min}, the lower CT_{max} and similar CT_{min} lead to a narrower thermal tolerance scope than the aforementioned fish species. For example, the tolerance scope of Chinese bream was 30.3, 28.8 and 28.84 °C in 15, 20 and 25 °C acclimated temperature, respectively. While the thermal tolerance scope was 31.1 °C in rohu acclimated at 25 °C (Chatterjee et al., 2004), was 33.3 °C in crucian carp (*Carassius auratus*) acclimated at 25 °C (Wang and Wu, 1994), was 28.9 °C in rainbow trout acclimated
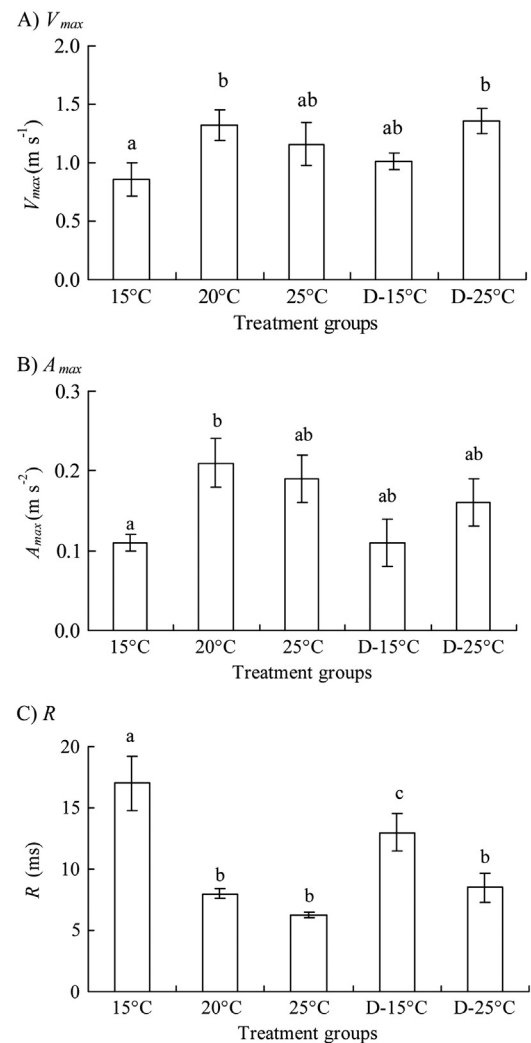

Fig. 4. The maximum liner velocity (V_{max}) (panel A), maximum liner acceleration (A_{max}) (panel B) and response latency (R) (panel C) of Chinese bream acclimated at different temperatures during the fast-start escape response (means ± S.E.). The D-15 °C indicates the diel fluctuating temperature group measured at 15 °C, and the D-25 °C indicates the diel fluctuating temperature group measured at 25 °C (a, b, c, d indicate significant differences among groups, $p < 0.05$).

Table 2
The growth performance of Chinese bream under different treatments (means ± S.E., N = 30).

Temperature groups	15 °C	20 °C	25 °C	15–25 °C	Significance
Initial mass (g)	6.56 ± 0.21	6.29 ± 0.23	6.54 ± 0.20	6.02 ± 0.21	F = 1.373 p = 0.255
Initial length (cm)	7.16 ± 0.08	7.12 ± 0.07	7.21 ± 0.07	7.01 ± 0.08	F = 1.081 p = 0.360
Final mass (g)	6.95 ± 0.21[a]	7.78 ± 0.28[b]	8.45 ± 0.21[c]	7.46 ± 0.22[ab]	F = 7.463 p < 0.001
Final length (cm)	7.29 ± 0.08[a]	7.54 ± 0.09[b]	7.76 ± 0.08[c]	7.47 ± 0.08[ab]	F = 5.659 p = 0.001
Specific growth rate (SGR, % d^{-1})	0.20 ± 0.03[a]	0.71 ± 0.06[b]	0.87 ± 0.11[b]	0.73 ± 0.07[b]	F = 16.07 p < 0.001
Feeding rate (FR, % body mass d^{-1})	1.69 ± 0.07[a]	2.62 ± 0.10[b]	2.59 ± 0.12[b]	3.03 ± 0.11[c]	F = 30.08 p < 0.001
Feeding efficiency (FE, %)	11.24 ± 1.25[a]	26.21 ± 1.67[b]	29.72 ± 4.27[b]	24.41 ± 2.32[b]	F = 9.334 p < 0.001

[a] Values in each row that do not share a common superscript letter are significantly different from one another ($p < 0.05$).
[b] Values in each row that do not share a common superscript letter are significantly different from one another ($p < 0.05$).

Table 3
Effects of experimental treatments on the SDA of juvenile Chinese bream following the consumption of a meal (1.5% body weight) (means ± S.E., N = 8).

Temperature groups	15 °C	20 °C	25 °C	15–25 °C		Significance
				15 °C	25 °C	
O_{2rest} (mg kg^{-1} h^{-1})	88.6 ± 4.9[a]	133.2 ± 9.3[b]	178.5 ± 15.4[c]	71.2 ± 5.6[a]	170.1 ± 6.6[c]	F = 27.01 p < 0.001
O_{2peak} (mg kg h^{-1})	159.6 ± 7.3[a]	239.6 ± 14.1[b]	293.4 ± 20.6[c]	125.9 ± 9.3[a]	276.2 ± 9.7[bc]	F = 31.34 p < 0.001
Duration (h)	7.88 ± 0.72	7.00 ± 0.27	7.38 ± 0.91	8.00 ± 0.68	9.38 ± 0.60	F = 1.836 p = 1.144
SDA magnitude (kJ kg^{-1})	3.33 ± 1.11[ab]	4.74 ± 1.23[ab]	6.17 ± 1.09[b]	2.84 ± 0.55[a]	6.22 ± 0.94[b]	F = 2.397 p = 0.069

[a] Indicate significant differences among treatment groups ($p < 0.05$).
[b] Indicate significant differences among treatment groups ($p < 0.05$).
[c] Indicate significant differences among treatment groups ($p < 0.05$).

at 15 °C (Currie et al., 1998). Thus, the lower heat tolerance capacity and narrower thermal scope relative to other fish species within the same habitat suggest that local temperature elevations due to natural or artificial causes (global warming, eutrophication, and damming) will have more profound effects on Chinese bream than on other local fish species.

In the three constant-temperature acclimation groups, CT_{max}, CT_{min}, LT_{max} and LT_{min} all increased significantly with the increase in temperature from 15 to 25 °C. These findings are in agreement with the previous studies of other fish species, such as rohu and southern catfish (Das et al., 2005; Wang et al., 2008). CT_{max} and LT_{max} in the 25 °C group increased by approximately 5.5 and 4.3 °C, respectively, and CT_{min} and LT_{min} increased by 7 and 5.9 °C, respectively, over those of the 15 °C group, suggesting that the heat tolerance of Chinese bream is lower than its cold tolerance under temperature change. The lower plasticity of heat tolerance might contribute to the physiological challenge of water temperature elevation in this species.

All four thermal tolerance indicators of the diel-fluctuating temperature group were lower than those of the 25 °C group but higher than those of the 15 °C group. However, when compared with the fish in the 20 °C group, the diel-fluctuating temperature group exhibited a wider thermal tolerance scope, as indicated by their (non-significantly) higher CT_{max} and lower CT_{min} values. In the recent years, aerobic scope, which is the difference between resting and maximal metabolism, has been widely used for evaluation of how well fish populations will survive a warmer future (Jodie et al., 2013). It because that aerobic scope can evaluate how much energy can be allocated to different physiological processes such as growth, reproduction and so on. In this study, the aerobic scope of diel fluctuating temperature measured at 25 °C showed the highest value (958 mg kg^{-1} h^{-1}), then followed by 20 °C (669 mg kg^{-1} h^{-1}) and 25 °C (654 mg kg^{-1} h^{-1}) temperature groups.

The aerobic scope of fish in 15 °C group and diel fluctuating temperature group measured at 15 °C were the lowest (535 mg kg^{-1} h^{-1} and 481 mg kg^{-1} h^{-1}, respectively). It suggested that Chinese bream may handle the physiological processes more easily at higher temperature, which is contrary to the result of other thermal tolerance indicators. The underlying mechanisms need further investigation.

4.2. Effects of temperature on swimming performance

4.2.1. Effects of temperature on U_{crit}

U_{crit} decreased from 79 to 71 cm s^{-1} and $MO_{2active}$ decreased from 832 to 611 mg kg^{-1} h^{-1} as the temperature decreased from 25 to 15 °C. This decrease in steady swimming performance with a decreasing temperature is in agreement with the previous studies. For example,
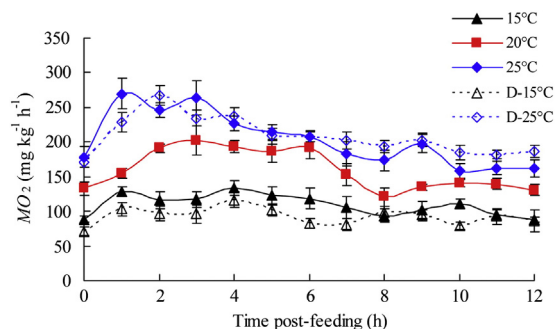

Fig. 5. Postprandial oxygen consumption responses of Chinese bream acclimated at different temperatures and fed to satiation, at different temperatures (means ± S.E., N = 8). The D-15 °C indicates the diel fluctuating temperature group measured at 15 °C, and the D-25 °C indicates the diel fluctuating temperature group measured at 25 °C ($p < 0.05$).

with a decrease in acclimation temperature from 25 to 15 °C, goldfish (*Carassius auratus*), common carp and qingbo showed 31%, 25% and 20% decreases in U_{crit}, respectively, and 56% 38%, and 57% decreases in $MO_{2active}$, respectively (Pang et al., 2011), whereas grass carp (*Ctenopharyngodon idellus*), crucian carp and sharp-jaw barbell (*Onychostoma sima*) showed 29.7%, 36.7% and 34.2% decreased in U_{crit}, respectively (Yan et al., 2013). However, the 11% and 27% decreases in U_{crit} and $MO_{2active}$, respectively, in Chinese bream are much less than those of all other fish species. It is widely accepted that U_{crit} is mainly limited by an organism's oxygen uptake capacity, energy utilization efficiency during swimming, transport and utilization of substrate, and lactate clearance capacity. Thus, in the present study, the maintenance of high steady swimming performance at low temperature was partly due to the significant improvement in swimming efficiency at low temperature (15 °C), as suggested by the much lower MO_2 at all swimming speeds, relative to the other two constant-temperature groups. Furthermore, the gills of Chinese bream showed no morphological changes at lower temperatures, whereas most other cyprinids exhibit a pronounced reduction in the gill functional respiratory surface. Our result suggests that Chinese bream retain most of their respiratory capacity at low temperatures (Chen, 2011). Finally, Chinese bream showed both an unusual improvement in tissue lactate clearance rate and higher lactate tolerance at low temperature, potentially also contributing to the high steady swimming performance observed at low temperature (He et al., 2014).

The $MO_{2active}$ in the diel-fluctuating temperature group measured at 25 °C was significantly higher than in the 25 °C group. This result indicates that the diel-fluctuating temperature regime improved cardiorespiratory capacity and, therefore, oxygen uptake capacity. However, the improved oxygen uptake capacity of fish in the diel-fluctuating temperature group did not yield an improvement in U_{crit}. This result may be due to the large observed variation in U_{crit} values and resulting high statistical noise, potentially masking differences between the two groups (note that body length in the diel-fluctuating temperature group was slightly lower than in the 25 °C group). Furthermore, the higher MO_2 of fish in the diel-fluctuating temperature group than in the 25 °C group at all swimming speeds suggests that decreased swimming efficiency might also explain the lack of observed difference in U_{crit} between these two groups. The underlying mechanism requires further investigation.

4.2.2. Effects of temperature on unsteady swimming performance

At high acclimation temperature, Chinese bream exhibited high V_{max} and short R, in agreement with the previous studies in crucian carp, grass carp and common carp (Yan et al., 2013; Penghan et al., 2014). The decreased V_{max} at low temperatures may be due to the increased water viscosity and, therefore, the increased drag force when swimming (Temple and Johnston, 1997); reduced metabolic power and skeletal muscle contractility (Randall and Brauner, 1991; Day and Butler, 2005); decreased biochemical reaction rates (Franklin, 1998); and lower contents of certain energy substrates (PCr and ATP) in cold-water fish (Kieffer et al., 1994; Kieffer, 2000). The short R may be due to faster signal transmission in the neural system and improved metabolic status under high temperatures (He et al., 2014). The R of fish in the diel-fluctuating temperature group measured at 15 °C was significantly shorter than in the 15 °C group, possibly due to the better internal tissue conditions in the former.

4.3. Effects of temperature on SDA and growth performance

Body temperature varies as a function of ambient temperature in ectotherms, and an increase in body temperature within a certain range usually results in higher respiratory and digestive performance. Similar to the previous studies (Luo and Xie, 2008; Pang et al., 2011), Chinese bream acclimated to a higher temperature showed a higher postprandial metabolic response, suggesting greater digestive performance.

Furthermore, the postprandial metabolic response of the diel-fluctuating temperature group measured at 15 °C (or 25 °C) was similar to that of the 15 °C (or 25 °C) constant-temperature group. This finding suggests that the digestion process, as indicated by postprandial metabolic response, was strongly dependent on temperature. SDA magnitude increased with an increasing temperature, consistent with the previous studies (Luo and Xie, 2008; Pang et al., 2011).

The effects of temperature on growth performance in fish have long been observed (Pauly, 1980; Pörtner et al., 2001; EI-Sayed and Kawanna, 2008). In the present study, there was no significant difference in *SGR* between fish of the 20 and 25 °C groups. However, *SGR* decreased by 77% as the acclimation temperature decreased to 15 °C due to lower *FR* (35% decrease) and *FE* (57% decrease). The impairment in growth rate as a consequence of decreased *FR* and (or) *FE* under low temperatures has also been documented in other fish species, such as Baltic salmon (*Salmo salar* L) (Koskela et al., 1997). There were no differences in any of the growth performance parameters between the 20 and 25 °C groups, suggesting that this temperature range is suitable for Chinese bream growth.

It has been hypothesized that fish may show improved growth performance under thermal cycles than under constant temperatures, as the former temperature regime results in greater food consumption and processing efficiency than constant-temperature conditions (Diana, 1984). Similarly, in our study, the *SGR* of the fluctuating temperature group showed a higher *FR* than in all the constant-temperature groups. However, *SGR* did not differ between the diel-fluctuating temperature group and the 20 °C group. This similarity may exist because Chinese bream acclimated at fluctuating temperatures ingested more food but also expended more energy to cope with the temperature change, as this species is very sensitive to temperature variation.

In conclusion, Chinese bream showed a lower heat tolerance and a narrower thermal tolerance scope than all other fish species sharing a similar habitat under the same measurement condition in the present study. Fish in the diel-fluctuating temperature group showed a wider thermal tolerance scope than those in the 20 °C group due to a higher CT_{max}. Temperature had less of an effect on U_{crit} in Chinese bream than in other cyprinids, possibly due to greater swimming efficiency and certain unusual morphological, physiological or biochemical adaptive mechanisms in Chinese bream at low temperatures. Fish in the diel-fluctuating temperature group showed no change in steady swimming performance, except for a lower swimming efficiency measured at 25 °C relative to those of the constant-temperature group of the same temperature. Fish in the 15 °C group had lower V_{max} and shorter R relative to the other constant-temperature groups. The former also exhibited lower *SGR*, due to their low *FR* and *FE*, than the other constant-temperature groups. In contrast, fish in the diel-fluctuating temperature group had the highest *FR* among all groups but a similar *SGR* to the 20 °C group. Thus, the lower heat tolerance and narrower thermal scope of Chinese bream relative to other fish species that share the same habitat suggest that temperature elevations of local water bodies as a result of natural or artificial influences will have more pronounced effects on Chinese bream than on other local fish species.

Acknowledgments

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