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The effects of temperature and food availability on growth, flexibility in metabolic rates and their relationships in juvenile common carp

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ABSTRACT

Flexibility in phenotypic traits can allow organisms to handle environmental changes. However, the ecological consequences of flexibility in metabolic rates are poorly understood. Here, we investigated whether the links between growth and flexibility in metabolic rates vary between two temperatures. Common carp *Cyprinus carpio* were raised in three temperature treatments [the 18 °C, 28 °C and 28 °C-food control (28 °C-FC)] and fed to satiation of receiving food either once or twice daily for 4 weeks. The morphology and metabolic rates (standard metabolic rate, SMR; maximum metabolic rate, MMR) were measured at the beginning and end of the experiment. The mean total food ingested by fish in the 28 °C-FC treatment was the same as that by fish in the 18 °C treatment at each food availability. The final SMR (not MMR and aerobic scope, AS = MMR − SMR) increased more in the 28 °C and 28 °C-FC treatments with twice-daily feedings than once-daily feedings. Fish in the 28 °C treatment had a higher specific growth rate (SGR) than fish in the 28 °C-FC and 18 °C treatments at both food availabilities. However, no differences in feeding efficiency (FE) were found among the three treatments in fish fed twice daily. The flexibility in SMR was related to individual differences in SGR, not with food intake and FE; individuals who increased their SMR more had a smaller growth performance with twice-daily feedings at 28 °C, but it did not exist at 18 °C. Flexibility in SMR provides a growth advantage in juvenile common carp experiencing changes in food availability and this link is temperature-dependent.

1. Introduction

Natural habitats vary greatly in conditions such as temperature, food availability due to seasonal cycling, daily rhythm or human activity, all of which could cause animals to encounter changing environments over their lifetime. The capacity of animals to regulate their phenotypic traits (e.g., morphology, physiology and behavior) is called phenotypic flexibility, which might provide an advantage for individual fitness when environmental conditions change (Piersma and Drent, 2003; Bolnick et al., 2011; Auer et al., 2015a). When considering challenges caused by ongoing global climate change and habitat modification, it is necessary to examine how individuals with various levels of phenotypic flexibility respond to a rapidly changing environment; it is also necessary to identify how various levels of phenotypic flexibility affect both ecological consequences and fitness of individuals within a population (Hofmann and Todgham, 2010; Auer et al., 2015a).

Temperature has been called an 'ecological master factor' among the abiotic environmental factors (Brett, 1971). Animals are subjected to large diurnal and seasonal changes in temperature in their natural habitats (Claireaux et al., 2006; Schulte, 2015). As a consequence of global warming and abnormal atmospheric circulation, key physiological functions that are related to the fitness of individuals, such as thermal tolerance, growth and metabolic capacity, could be affected by the changes in temperature that fluctuate greater than before (Hofmann and Todgham, 2010; Pang et al., 2016). Such changes in temperature could also affect the habitat distribution of food sources by causing large temporal and spatial patchiness (Shulman, 1974; Xu et al., 1999), which could result in some individuals to experience high food availability and other individuals experience low food availability. Both temperature and food availability are believed to have important influences on the growth of animals (Van Ham et al., 2003; Handeland et al., 2008; Peng et al., 2014; Pang et al., 2016). Fast growth, especially during the larval and juvenile stages, is often perceived as beneficial because faster organ development and increases in body size could enhance individual survival, maturity, reproduction and fitness for certain animals (Arendt, 1997).

Metabolic rate, usually estimated by measuring oxygen consumption rate in fish species, represents the rate at which an animal oxidizes

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substrates to produce energy to fuel all of its biological processes, and it has two energy bounds (referring to minimum and maximum rate) (Careau et al., 2008; Metcalfe et al., 2016). Minimum metabolic rate is the minimum energy required to sustain life and is analogous to standard metabolic rate (SMR) in ectotherms (e.g., fishes) (Fry, 1971). In contrast, maximum metabolic rate (MMR) is the rate that represents the upper boundary supporting aerobic energy metabolism at a given temperature (Fry, 1971; Norin and Malte, 2011; Norin and Clark, 2016). Subtracting SMR from MMR calculates the aerobic scope (AS), which represents the remaining capacity for other energy-requiring activities (i.e., locomotion, digestion, growth and reproduction) (Claireaux and Lefrançois, 2007; Guderley and Portner, 2010; Clark et al., 2013). Energy metabolism of animals is thought to have an important influence on their fitness (Careau et al., 2008; Auer et al., 2015b); SMR is usually positively related to growth (Reid et al., 2012; Van Leeuwen et al., 2012; Zeng et al., 2017a), survival (Jackson et al., 2001) and reproduction (Sadowska et al., 2013). SMR also exhibits high flexibility in response to food availability. Generally, an individual SMR increases when food availability is higher and decreases when food availability is lower (Van Leeuwen et al., 2012; Auer et al., 2015a; Zeng et al., 2017b), which suggested flexibility in SMR could confer a growth advantage in animals that experience changes in food availability (Auer et al., 2015a; Zeng et al., 2017b). However, to our knowledge, studies that investigate whether all individuals within a population possess the same pattern of flexibility in SMR for MMR and AS in response to food availability under different temperatures are lacking.

In the present study, we used juvenile common carp, *Cyprinus carpio*, a freshwater omnivorous and eurythermic cyprinid species, as the experimental model. This fish species is native to eastern Europe and Asia. It is now one of the most abundant fish species in China (Pang et al., 2016) and is widely distributed throughout the world (Koehn, 2004). Here, we first examined individual variation in metabolic flexibility in response to changes in food availability and its ecological implications for somatic growth. Then, we investigated whether the relationship between flexibility in metabolic rates (i.e., SMR, MMR and AS) and growth performance changes with temperature. The temperatures (18 °C and 28 °C) employed in the present study encompass the typical spectrum of seasonal fluctuation in the Yangtze River and its main tributary (e.g., the Jialing River) in China (Long et al., 2007; Zeng et al., 2009).

2. Materials and methods

2.1. Fish

Juvenile common carp (6.98 ± 0.11 g body mass; 6.42 ± 0.04 cm body length) were obtained from a local aquaculture farm and acclimatized to laboratory tanks with a controlled temperature of 23.0 ± 0.1 °C and a 14 L:10 D photoperiod. After two weeks, the rearing temperature for approximately half of the fish increased or decreased to 27.9 ± 0.1 °C or 18.0 ± 0.1 °C, respectively, at a rate of 2 °C per day (He et al., 2015). After reaching the prescribed temperature, fish were kept at the respective temperatures and acclimated for another two weeks prior to the experiment. Dechlorinated fresh water was used, and 20% of the water in the tanks was replaced every two days. The dissolved oxygen content was maintained above 7.0 mg L^{-1} using an air pump. During the holding period, fish were fed to satiation once daily with a commercial diet (composition: 41.2 ± 0.9% protein, 8.5 ± 0.5% lipids, 25.7 ± 1.2% carbohydrate, and 12.3 ± 0.4% ash; Tongwei Ltd., Sichuan, China), which was used throughout the entire study. The diet was in the form of spheres and could float on the water surface without dissolving for 12 h; uniform pellet sizes were used in the experiment and were acquired by filtering through a mesh screen due to a slight difference in the diameter of diet.

In the present study, all animal handling and experiments were conducted in accordance with both the ethical requirements and recommendations for animal care of the Key Laboratory of Animal Biology of Chongqing, China (Permit No. Zhao-20140622-01), and the requirements for environmental and housing facilities for laboratory animals in China (GB/T14925-2001). All of the experiments also complied with the local animal welfare laws of Chongqing City, China (e.g., Measures of Chongqing Municipality for the administration of experimental animals).

2.2. Experimental design

Fish generally have higher food intake rates at higher temperatures than at lower temperatures (Handeland et al., 2008; Pang et al., 2016), but the growth performance of fish might be different under the same food intake rate due to differences in SMR and food conversion efficiency. Hence, the present study included three temperature treatments, 18 °C, 28 °C and 28 °C-food control (28 °C-FC), with each treatment having two levels (high or low) of food availability. The mean diet mass of the 28 °C-FC treatment was the same as the 18 °C treatment at both levels of food availability. The high or low food availability was quantified by feeding frequency; high food availability meant two feedings per day (9:00 h and 18:00 h), and low food availability meant one feeding per day (9:00 h). In the present study, the mean total diets fed to individuals raised under low food availability conditions were 57.2% at 18 °C, 53.1% at 28 °C, and 51.5% at 28 °C-FC of the mean total diets fed to individuals raised under high food availability conditions in the same temperature treatment groups. The mean feeding level of twice daily were 2.29% at 18 °C, 4.51% at 28 °C, and 2.33% at 28 °C– FC of their initial body mass, whereas those of once daily were 2.69% 18 °C, 5.16% at 28 °C, and 2.82% at 28 °C-FC of their initial body mass. The fish (n = 40 per temperature treatment and food availability) in the 18 °C and 28 °C treatments were fed to satiation within 1 h of each feeding.

Fish fasted for 36 h before each measurement; they were measured for their morphology (body mass and body length) and metabolic rates (SMR and MMR) at the beginning and end of the experiment. The SMR of individual fish was determined using a continuous-flow respirometer (Fu et al., 2009; Killen et al., 2016). The MMR was induced by having fish endure exhaustive exercise, and oxygen consumption was measured immediately after exercise using an intermittent-flow respirometer (Auer et al., 2015b; Norin and Clark, 2016). After the initial measurements of metabolic rates, fish from each temperature treatment were randomly designated to one of two food availability categories and were placed into corresponding compartments for a continuous feeding period of 28 days.

2.3. Measurements of growth performance

The fish in both the 28 °C and 28 °C-FC treatments were raised in two independent-cycling tank systems, each consisting of 80 compartments, and the fish in the 18 °C treatment were raised in two additional independent-cycling tank systems, each consisting of 40 compartments. Each cycling tank system included a large tank, a temperature controller (C-1000A, Guangdong Resun Group Co. Ltd., Guangdong, China), a UV sterilizer (Atman-18w, Chuangxing Ltd., Zhongshan, China), and a biological filtration system. All environmental conditions (e.g., temperature, oxygen concentration and photoperiod) within a cycling tank system were the same as conditions during the acclimation period. To avoid influences caused by dominance hierarchies or competition for food, each fish was individually raised in a compartment during the experiment. The walls between neighboring compartments were composed of non-toxic mesh that allowed water to flow through to maintain dissolved oxygen concentrations in the systems. However, the food pellets were too large to pass through the mesh, ensuring that each fish consumed its own food and that the exact quantity of food consumed by fish at each feeding could be calculated. Each compartment was covered with mesh to prevent fish from escaping the

compartments. After 1 h of feeding, uneaten feed pellets and feces in each compartment were collected using a siphon. The body mass (0.01 g, using digital scale) and body length (0.1 cm, using vernier calipers) of fish were measured after the fish were slightly anesthetized with neutralized tricaine methanesulfonate (MS-222, 50 mg L^{-1}) at the beginning and end of the experiment. The following formulas were used to calculate the growth parameters:

$$\text{Food intake (FI, g kg}^{-1}\text{d}^{-1}) = I/[(M_2 + M_1)/2/1000]/T \quad (1)$$

$$\text{Specific growth rate (SGR,\%d}^{-1}) = (\ln M_2 - \ln M_1)/T \times 100 \quad (2)$$

$$\text{Feed efficiency (FE,\%)} = (M_2 - M_1)/I \times 100 \quad (3)$$

where M_1 and M_2 are the body masses (g) of an individual fish at the beginning and end of the experimental period (28 days), respectively; I (g) represents the total amount of food consumed by an individual fish; and T represents the experimental period of 28 days.

2.4. Measurements of metabolic rates

2.4.1. Standard metabolic rate

The present study used the oxygen consumption rate to calculate the SMR of the fish, and SMR measurements were collected at specific temperatures (18 °C or 28 °C). The SMR of individual fish was determined using continuous-flow respirometry, and each set-up consisted of ten respirometry chambers (with fish) and one blank respirometry chamber (without fish) (Killen et al., 2016; Zeng et al., 2017b). To avoid the influence of digestion on the measurements of SMR, the fish fasted for 36 h prior to data collection; this is an appropriate time for fish to evacuate any remaining gut contents. The oxygen consumption rate of each fish was measured 14 times during the following day (once per hour from 08:00 to 21:00). The mean of the lowest three measurements collected during this period was used as the SMR (Killen et al., 2016).

During all measurements, two sides of each chamber were covered with a darkened blind to minimize disturbance caused by seeing other fish because visual communication may trigger individuals to exhibit minor activity (Hu et al., 2015), which would affect the SMR measurements. Additionally, the respirometer was covered with an opaque plastic board to decrease disturbances from the laboratory environment or the experimenter to the fish. The dissolved oxygen concentration was measured to the nearest 0.01 mg L^{-1} at the outlet of each chamber using an oxygen meter (HQ_{30}, Hach Company, Loveland, CO, USA). The water flow rate through each chamber was determined by measuring the time required to fill a 50-mL volumetric flask from the outlet of the chambers. The water flow rate though the chambers was set at 2.1 L h^{-1} at the beginning of experiment and then increased to 3.2 L h^{-1} at the end of experiment; the adjustment accounted for fish growth and ensured that oxygen could be measured and oxygen concentrations remained above 80% saturation. The mean time required for a 99% water exchange in the chamber was between 18 and 39 min at flow rates between 2.1 and 3.2 L h^{-1} (Steffensen, 1989); thus, the 1-h interval was sufficient to measure the metabolic rate that represented the physiological status of the fish during that time period. The SMR ($\dot{M}O_2$, mg O_2 h^{-1}) of the fish was determined using the following formula:

$$\dot{M}O_2 = (C_{O2control} - C_{O2fish}) \times v \quad (4)$$

where $C_{O2control}$ and C_{O2fish} are the oxygen concentrations (mg L^{-1}) in the outflow water of the control chamber and fish chamber, respectively; and v (L h^{-1}) is the flow rate of water through the chamber.

2.4.2. Maximum metabolic rate

After the measurements of SMR, individual MMR was induced by exhaustive exercise in a circle-chasing apparatus, and the post-exercise oxygen consumption of each fish was measured immediately using an intermittent-flow respirometer (volume of 520 mL), which was submerged in a large acrylic bath with a controlled temperature (18 °C or 28 °C). This intermittent-flow respirometer included a micropump that forced inner water to circulate slowly around the respirometer and mixed the oxygen concentration of the inner water when it closed. Briefly, each individual fish was moved from its chamber to the exercise apparatus (Φ = 52 cm, ~50 cm s^{-1} in water speed, 10 cm in water depth) and was then exercised to exhaustion (usually < 3 min) against the circle current (1800 L h^{-1}) created by a short length of tubing attached to a pump in the centre (Φ = 28 cm) of the exercise apparatus (Fu et al., 2009; Zeng et al., 2010; Auer et al., 2015b). Fish were considered physically exhausted when they lost equilibrium and were no longer responsive to manual chasing (Milligan, 1996; Hyndman et al., 2003). Following exhaustive exercise, the fish were immediately moved within 15 s to the respirometer, and the dissolved oxygen concentration in the respirometer was measured once every 10 s during a period of 6 min. After the measurement, each individual fish was transferred to a small bucket and anesthetized slightly with MS-222 (50 mg L^{-1}), and its body mass (0.01 g) and body length (0.1 cm) were measured before it was moved back to its individual compartment. Deoxygenated water was emptied from the respirometer so it could be refilled with fresh oxygenated water before measuring the MMR of the next fish. MMR ($\dot{M}O_2$, mg O_2 h^{-1}) was calculated based on the depletion of oxygen according to the following equation:

$$\dot{M}O_2 = (S_t - S_0) \times v \times 3600 \quad (5)$$

where S_t and S_0 (slope, mg L^{-1} s^{-1}) are decreases in the oxygen concentration of the water per second with and without fish in the respirometer, respectively; these two values were calculated from the linear regressions between time (seconds) and oxygen concentration (mg L^{-1}). v (L) is the volume of the respirometer minus the volume of the fish. The AS (mg O_2 h^{-1}) was calculated by subtracting SMR from MMR (AS = MMR − SMR) and factorial aerobic scope (FAS) was calculated by dividing MMR by SMR.

2.5. Statistical analyses

Because metabolic rates can be affected by body mass (M) (in the present study: SMR = 0.237 × $M^{0.889}$, R^2 = 0.594, P < 0.001; MMR = 0.523 × $M^{1.017}$, R^2 = 0.809, P < 0.001), the metabolic rates and body mass were both $\log_{10}$-transformed prior to examining the relationship between double-log-transformed body mass and metabolic rate. Mass-independent estimates of individual metabolic rate, i.e., the residuals from the regression, were used in subsequent analyses. For use in tables and figures, individual metabolic rates (i.e., SMR and MMR) were standardized to a mean body mass of 8.96 g, by calculating the residuals of the least squares regression using the following equation (Killen et al., 2016):

$$\text{Log}_{10}\text{SMR} = \text{Log}_{10}b + a\text{Log}_{10}M + \varepsilon \quad (6)$$

where letters a and b are constants, and M is body mass (g) and ε is the residual variation. The residuals of each individual from this regression were added to the fitted value for an animal of 8.96 g (the mean body mass of all fish used in the present study based on two measurements of metabolic rates, n = 406) to obtain adjusted estimates of metabolic rate.

We then examined whether adjusted metabolic rates (SMR, MMR and AS) and body mass changed over the experimental period under the different treatments. This model included metabolic rates (SMR, MMR and AS) and body mass as the dependent variables and measurement time (initial vs. final), temperature and food availability as fixed categorical effects. We also tested whether temperature treatment and food availability influenced the growth parameters (FI, SGR and FE) during the experimental period with the model included temperature treatment and food availability as fixed categorical effects and diet mass and growth parameters (FI, SGR and FE) as the dependent variables.

Duncan's multiple range test or independent *t*-test was performed after the models reported the significant differences among the treatments. Finally, we used Pearson's correlation to examine the relationships between growth parameters (FI, SGR and FE) and change in metabolic rates (the adjusted SMR, MMR, AS and FAS were presented in percentage of the initial value, e.g., ΔSMR: 100 × (final SMR − initial SMR) / initial SMR) under different treatments of temperature and food availability.

Some individuals jumped onto the floor and thus, injured themselves or consistently consumed less than one-third of their mean daily ration; these fish were excluded from data analysis. Final fish numbers were 60, 66 and 77 for the 18 °C, 28 °C and 28 °C-FC treatments, respectively. All correlation and linear model analyses were performed using SPSS, version 19.0 (SPSS Inc., Chicago, IL, USA). P values < 0.05 were considered statistically significant, and all data are presented as the means ± 1 S.E.

3. Results

3.1. Changes in body mass and metabolic rates

Log-transformed metabolic rates (SMR, MMR and AS) increased with log-transformed body mass in the 18 °C, 28 °C and 28 °C-FC treatments under the two food availabilities. Fish in all three treatments showed an increase in body mass under both food availabilities, and no differences in the initial body mass or metabolic rates were detected between the two food availabilities (Fig. 1, Table 1). However, the final body mass was largest in fish in the 28 °C treatment compared to those in both the 28 °C-FC and 18 °C treatments with twice-daily feedings, while the final body mass of fish was smallest in the 28 °C-FC compared to those in both the 28 °C and 18 °C treatments with once-daily feedings (Fig. 1A). Fish in all three treatments had larger final body mass with twice-daily feedings than with once-daily feedings. After standardization, fish increased their SMR in the 18 °C and 28 °C treatments with twice-daily feedings, and in the 18 °C treatments with once-daily feedings (Fig. 1B, Table 1). The final SMR were largest for fish in the 28 °C treatment compared to those in the 18 °C and 28 °C-FC treatments under both food availabilities (Fig. 1B), while the fish in the 18 °C treatment had the smaller final MMR compared to those in the 28 °C and 28 °C-FC treatments under both food availabilities (Fig. 1C). However, no change was found in AS in the three temperature treatments during the experiment (Fig. 1D). The final FAS was smaller than the initial value in the 18 °C under both food availabilities, and no changes were found between the initial and final FAS in the 28 °C and 28 °C treatments under both food availabilities (Fig. 1E, Table 1).

The extent to which the SMR, MMR and AS changed was larger in fish fed twice a day than in fish fed once a day in the 28 °C treatment (Fig. 2A–C, Table 2), but no difference was found in the FAS between two food availabilities in the 28 °C treatment (Fig. 2D). The fish in the 18 °C and 28 °C treatments had a larger change in SMR (ΔSMR) compared to that in the 28 °C-FC treatments with twice-daily feedings, while the fish had a larger ΔSMR in 18 °C treatments than those in both the 28 °C and the 28 °C-FC treatments with once-daily feedings (Fig. 2A). The change in MMR (ΔMMR) was larger in the 28 °C treatment than the 18 °C and 28 °C-FC treatments with twice-daily feedings, but no difference in ΔMMR was found among the three temperature treatments with once-daily feedings (Fig. 2B). The change in AS (ΔAS) was larger in the 28 °C and 28 °C-FC treatments than the 18 °C treatment with twice-daily feedings, while no difference was found in ΔAS among the three temperature treatments with once-daily feedings (Fig. 2C). Fish in the 28 °C and 28 °C-FC treatments had a larger change in FAS (ΔFAS) compared to fish in the 18 °C treatment with two food availabilities (Fig. 2D, Table 2).

The negative relationships were found between ΔSMR and ΔFAS irrespective of temperature and food availability (all $P < 0.01$, Table 3). As to other parameters of metabolic rate, only ΔSMR correlated negatively with ΔAS in the 28 °C treatment with twice-daily feedings (Table 3).

3.2. Growth performance

The FI was 69.0%, 71.2% and 74.3% for fish in the 18 °C, 28 °C and 28 °C-FC treatments with once-daily feedings, respectively, compared to fish fed twice daily; fish in the 28 °C treatment had the largest FI compared to fish in the 18 °C and 28 °C-FC treatments with two food availabilities (Fig. 3A, Table 2). As expected, fish in all three temperature treatments had a larger SGR when fed twice daily compared to those fed once daily (Fig. 3B, Table 2). When fed twice daily, the SGR was highest in fish in the 28 °C treatment compared to fish in both the 18 °C and 28 °C-FC treatments. In fish fed once daily, those in the 28 °C-FC treatment had a smallest SGR compared to those in the 18 °C and 28 °C treatments. In addition to the 18 °C treatment, the FE of fish in the 28 °C and 28 °C-FC treatments were lower in fish fed once daily than in fish fed twice daily (Fig. 3C, Table 2). No difference in FE was found in fish fed twice daily among the three temperature treatments, but in fish fed once daily, the FE was smallest in fish in the 28 °C-FC treatment compared to those in both the 18 °C and 28 °C treatments (Fig. 3C).

Among the growth parameters, the SGR was positively related to FE in the 18 °C, 28 °C and 28 °C-FC treatments under both food availabilities (Table 4, all $P < 0.001$). In contrast, negative correlations were found between FE and FI in the 28 °C-FC treatment under both food availabilities and in the 18 °C treatment with once-daily feedings (Table 4, all $P < 0.01$). The SGR was positively correlated to FI in fish in the 18 °C treatment that were fed twice daily (Table 4).

3.3. Relationships between growth performance and flexibility in metabolic rates

The negative relationships were found between SGR and ΔSMR, and between SGR and ΔMMR in the 28 °C treatment with fish fed twice daily and in the 28 °C-FC treatment with fish fed once daily, respectively (Table 5). Additionally, SGR also correlated negatively with change in metabolic rates (MMR, AS and FAS) in the 28 °C treatment with fish fed once daily (Table 5).

4. Discussion

The present study found that SMR and MMR in the 18 °C and 28 °C treatments increased by different levels in response to increased food availability. The extent of change in metabolic rates was larger in fish with high food availability than in fish with low food availability, but it was temperature-dependent. Individuals in the 28 °C treatment who increased their SMR more had a smaller SGR under high food availability conditions, while those whose SMR or FAS were inflexible or decreased had a larger SGR. However, these situations disappeared in the low food availability conditions in either the 18 °C or 28 °C treatments. For fish with larger growth rate under the high food availability conditions, their higher growth performance was attributed to the improved digestive capacity, as indicated by the FE but not the FI.

4.1. Temperature and food availability effects on metabolic rates and growth

Under the same food availability, the final body mass and SGR were both higher in fish fed twice daily in the 28 °C treatment compared to those in the 18 °C treatment (Fig. 1A), which is consistent with previous studies (Handeland et al., 2008; Peng et al., 2014; Pang et al., 2016). Individuals with a larger SGR had a higher FE, and vice versa, but this was independent of water temperature and food availability. The high temperature could induce the increase in an individual's SMR when compared to the lower temperature, but juvenile common carp enhanced their FI to meet, or even exceed, their daily metabolic

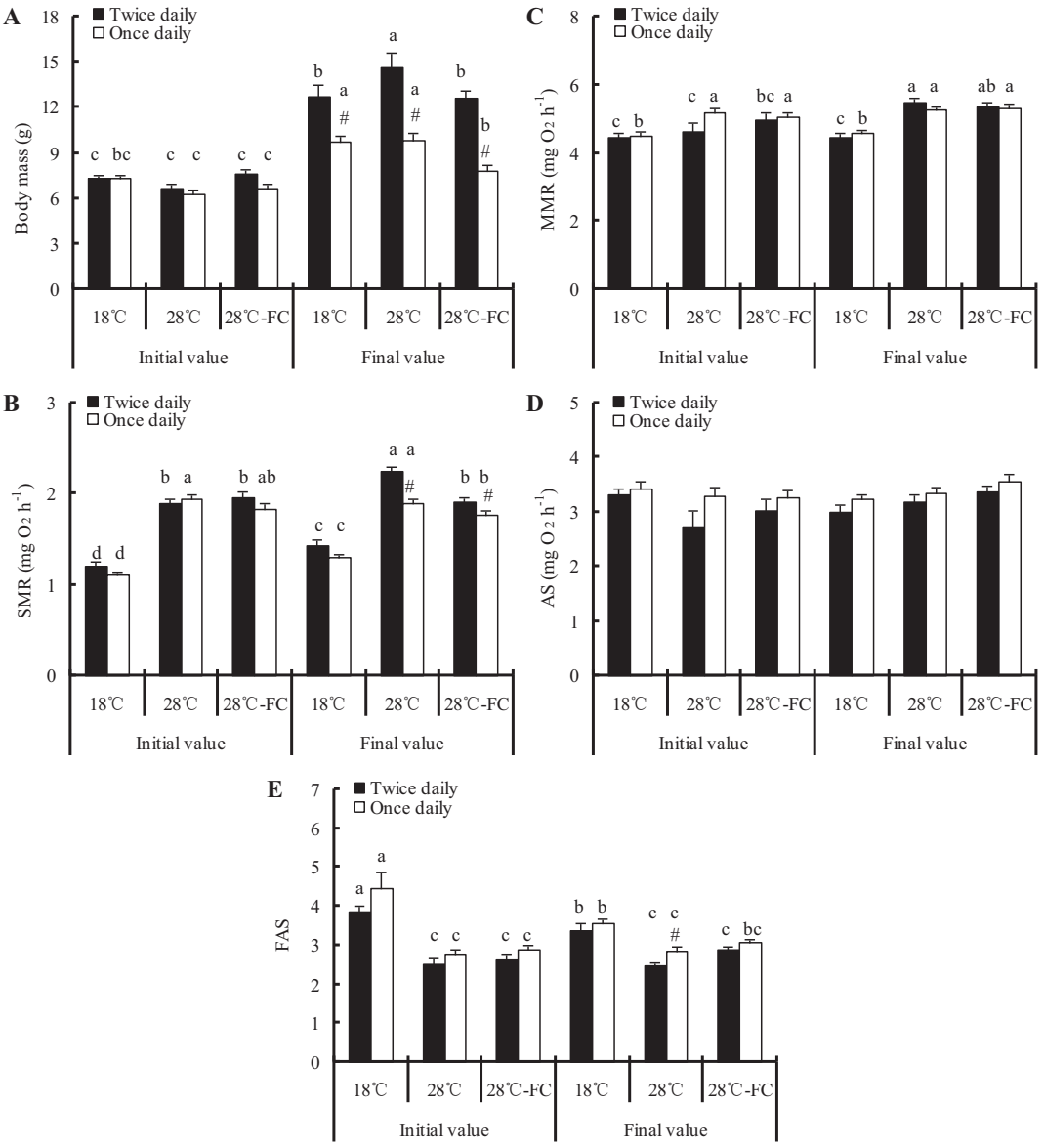

Fig. 1. Comparisons of body mass and metabolic rates between different temperature treatments in juvenile common carp at the beginning and end of experiment under two food availabilities. Bars with different lowercase letters indicate a significant difference between temperature treatments within a given food availability ($P < 0.05$), and the symbol (#) means a significant difference between food availabilities within a given temperature treatment ($P < 0.05$). SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope; FAS = factorial aerobic scope; and FC = food control. Error bars = SEM.

maintenance and hence, may allocate a greater proportion of ingested energy to growth in the higher temperature category. In contrast to the previous study on common carp (Pang et al., 2016), we found that no significant difference in FE was detectable between fish in the 18 °C and 28 °C treatments, suggesting that assimilation performance (i.e., protein synthesis) of fish was retained over the temperature range (18–28 °C) used in the present study. Additionally, the mean FE (50.2% and 45.6% at 18 °C and 28 °C, respectively) values in the present study were greatly smaller than those (102.1% and 70.1% at 15 °C and 25 °C, respectively) found in the previous study under the same conditions of twice-daily satiation feeding (Pang et al., 2016). This might be because the moisture levels (mean 13%) of the diet in the present study were higher than that of the previous study (dry diet, Pang et al., 2016) though the composition of diet was the same in these two studies.

Table 1
The effects of measurement time, temperature and food availability on the body mass and metabolic rates of juvenile common carp based on the General Linear Model.

Parameters	Time	Temperature	Food	Time × Temperature	Time × Food	Temperature × Food
Body mass (g)	$F = 227.24$, $P < 0.001$	$F = 1.887$, $P = 0.153$	$F = 73.17$, $P < 0.001$	$F = 8.471$, $P < 0.001$	$F = 49.468$, $P < 0.001$	$F = 3.489$, $P = 0.031$
SMR (mg O_2 h^{-1})	$F = 10.532$, $P = 0.001$	$F = 180.98$, $P < 0.001$	$F = 17.27$, $P < 0.001$	$F = 7.105$, $P = 0.001$	$F = 5.638$, $P = 0.018$	$F = 0.138$, $P = 0.871$
MMR (mg O_2 h^{-1})	$F = 9.158$, $P = 0.003$	$F = 23.087$, $P < 0.001$	$F = 0.750$, $P = 0.387$	$F = 1.847$, $P = 0.159$	$F = 2.910$, $P = 0.081$	$F = 0.314$, $P = 0.731$
AS (mg O_2 h^{-1})	$F = 1.300$, $P = 0.255$	$F = 1.176$, $P = 0.310$	$F = 6.798$, $P = 0.009$	$F = 3.580$, $P = 0.029$	$F = 0.349$, $P = 0.555$	$F = 0.369$, $P = 0.692$
FAS	$F = 2.366$, $P = 0.125$	$F = 46.293$, $P < 0.001$	$F = 9.660$, $P = 0.002$	$F = 7.239$, $P = 0.001$	$F = 0.256$, $P = 0.613$	$F = 0.297$, $P = 0.744$

SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope; and FAS = factorial aerobic scope.

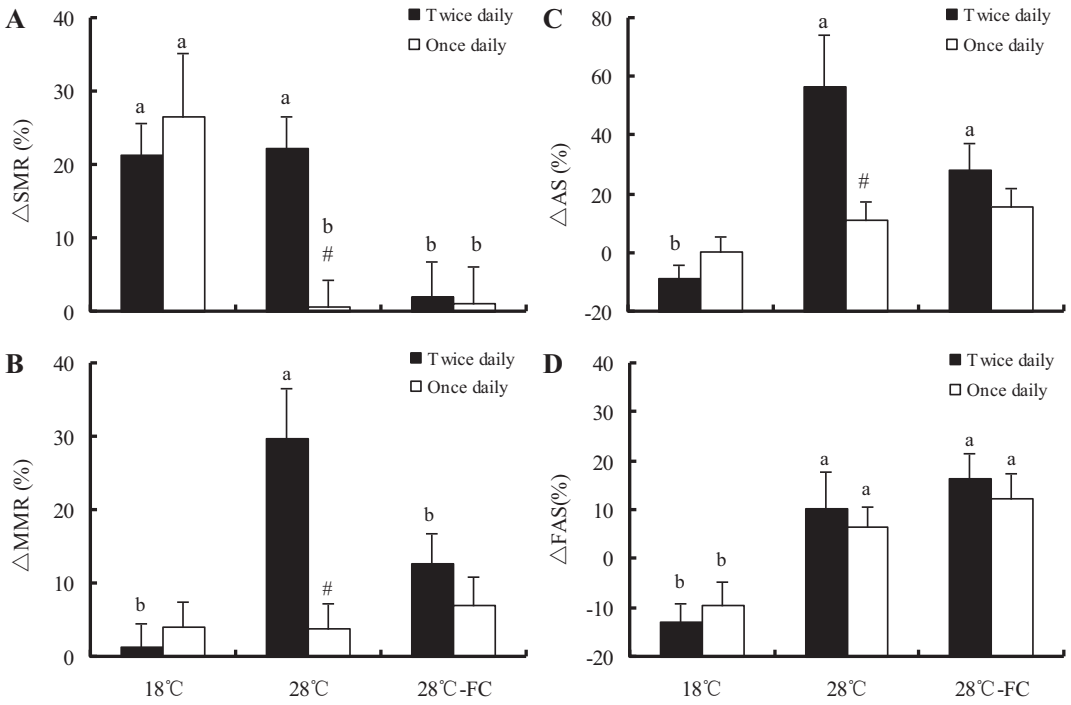

Fig. 2. Comparisons of change in metabolic rates between different temperature treatments in juvenile common carp under two food availabilities. Bars with different lowercase letters represent a significant difference between temperature treatments within a given food availability ($P < 0.05$), and the symbol (#) means a significant difference between food availabilities within a given temperature treatment ($P < 0.05$). SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope; FAS = factorial aerobic scope; and FC = food control. Error bars = SEM.

Individuals had a larger FI at 28 °C than at 18 °C under the once-daily feeding condition, but no difference in final body mass was found between these two treatments (Fig. 1A). This phenomenon may partly be due to lower maintenance metabolism (Zeng et al., 2010) and lower activity levels of fish raised at lower temperatures (Schurmann and Steffensen, 1994) that could reduce the daily energy cost of living in fish. It is also possible that individual fish raised in the 18 °C treatment had the same FE to fish in the 28 °C treatment, which might result in a higher proportion of energy allocation to growth at low temperature.

Under the same FI, no differences in final body mass or SGR were found between fish fed twice daily in the 18 °C and the 28 °C-FC treatments (Fig. 1A), which is consistent with a previous study on juvenile turbot (Van Ham et al., 2003). This result was due to the food conversion performance, as indicated by the FE values for these two treatments, though the SMR, which was standardized to the mean body mass, was much higher in fish in the 28 °C-FC treatment than that of fish in the 18 °C treatment (Fig. 1B). In fish fed once daily, the final body mass was larger in the 18 °C treatment than in the 28 °C-FC treatment under the same FI because fish in the 18 °C treatment had larger FE and thus, larger SGR than fish in the 28 °C-FC treatment, despite the differences in their SMR. In addition, inadequate food intake at high temperatures (e.g., the 28 °C-FC treatment in the present study) could reduce individual mitochondrial respiratory capacity (Salin et al., 2016) and negatively affect the organism's performance (i.e., growth) (Schulte, 2015). As discussed above, our results suggested that low food availability could intensify the deviation and impairment of the growth trajectory in the fish at the higher temperature and possibly reduce their fitness in the face of ongoing global warming.

4.2. Links between growth and flexibility in metabolic rates under different temperatures

The cause-effect links between SMR and growth in fish has been debated for many years. Earlier studies thought that variation in SMR was the cause of individual variation in growth (Yamamoto et al., 1998; Alvarez and Nicieza, 2005; Reid et al., 2012), but recent studies documented that the food consumption might actually cause variation in growth that is related to metabolic rates rather than be a consequence of variation in metabolic rates (Van Leeuwen et al., 2012; Rosenfeld et al., 2015). As expected from the former perspective, the relationships between SMR and growth should all be positive, with different extents of correlation despite food availability. Indeed, a

Table 2
The effects of temperature and food availability on the growth parameters and change in metabolic rates in juvenile common carp based on the General Linear Model.

Parameters	Temperature	Food availability	Temperature × Food availability
ΔSMR	$F = 7.637$, $P = 0.001$	$F = 1.551$, $P = 0.214$	$F = 2.921$, $P = 0.056$
ΔMMR	$F = 4.611$, $P = 0.011$	$F = 6.951$, $P = 0.009$	$F = 5.231$, $P = 0.006$
ΔAS	$F = 7.818$, $P = 0.001$	$F = 4.413$, $P = 0.037$	$F = 3.945$, $P = 0.021$
ΔFAS	$F = 11.265$, $P < 0.001$	$F = 0.104$, $P = 0.747$	$F = 0.273$, $P = 0.761$
FI (g kg^{-1} d^{-1})	$F = 150.17$, $P < 0.001$	$F = 130.90$, $P < 0.001$	$F = 5.490$, $P = 0.005$
SGR (% d^{-1})	$F = 126.82$, $P < 0.001$	$F = 97.870$, $P < 0.001$	$F = 3.141$, $P = 0.045$
FE (%)	$F = 0.958$, $P = 0.385$	$F = 29.775$, $P < 0.001$	$F = 5.525$, $P = 0.005$

SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope; and FAS = factorial aerobic scope. FI = food intake; SGR = specific growth rate; and FE = feeding efficiency.

Table 3
The relationships between change in SMR (ΔSMR) and changes in metabolic rates (ΔMMR, ΔAS and ΔFAS) in juvenile common carp under different temperature treatments.

Temperature	Food availability	Parameters	*r*	*P*
18 °C	Twice daily	ΔMMR	0.339	0.067
		ΔAS	− 0.044	0.817
		ΔFAS	− 0.675	< 0.001**
	Once daily	ΔMMR	− 0.171	0.365
		ΔAS	− 0.286	0.126
		ΔFAS	− 0.618	< 0.001**
28 °C	Twice daily	ΔMMR	0.049	0.785
		ΔAS	− 0.348	0.047*
		ΔFAS	− 0.500	0.003**
	Once daily	ΔMMR	0.264	0.138
		ΔAS	− 0.136	0.451
		ΔFAS	− 0.644	< 0.001**
28 °C-FC	Twice daily	ΔMMR	0.156	0.344
		ΔAS	− 0.140	0.395
		ΔFAS	− 0.642	< 0.001**
	Once daily	ΔMMR	0.313	0.056
		ΔAS	− 0.141	0.400
		ΔFAS	− 0.660	< 0.001**

SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope; FAS = factorial aerobic scope; and FC = food control.
** $P < 0.01$.
* $P < 0.05$.

positive relationship between SMR and growth was found under high food availability, but no correlations, and even a negative relationship, were detected under low food availability (Auer et al., 2015a; Zeng et al., 2017b), indicating that the relationship between SMR and growth may be causal and dependent on the level of food availability (Auer et al., 2015a). The present study documented that both the final body mass and metabolic rates (i.e., SMR) were higher in fish fed twice daily than in fish fed once daily; the relationship between flexibility in SMR and growth were negative in fish fed twice daily at 28 °C, but the same positive correlation did not exist in most fish fed twice daily or once daily at 18 °C (Table 4). Our results suggest that food availability may partially contribute to the variation in metabolic rates and growth of individuals and hence, phenotypic flexibility in juvenile common carp under conditions of different food availability.

The present study found that the correlations between flexibility in metabolic rate (i.e., SMR) and growth were negative in juvenile common carp with higher food availability in the 28 °C temperature, but not in fish with lower food availability at two temperatures, suggesting that temperature might affect the growth advantage conferred by flexibility in metabolic rate under conditions of changing food availability. In our study, juvenile common carp were fed daily with two levels of food availability over a total period of 28 days. During the period of feeding, individuals may maintain their up-regulated digestive tract performance (or organ size, which is related to SMR), though a portion of consumed energy must be spent on digestion and assimilation (i.e., specific dynamic action, SDA) (Secor, 2009). Increases in metabolic rate reflects underlying elevations in digestive and assimilative abilities (Secor, 2009; Armstrong and Bond, 2013) and mitochondrial efficiency (Monternier et al., 2014), and these physiological processes are thought to be closely correlated with individual growth (Auer et al., 2015a). Temperature has a great influence on maintenance metabolism, digestion of meals and growth of juvenile common carp (Pang et al., 2011, 2016), but the negative relationship between flexibility in SMR and growth could only be existed in conditions of high food availability at 28 °C. This phenomenon might be because fish with higher flexibility in SMR were raised under conditions of higher food availability, but their larger extent of increment in basic metabolism and more energy expenditure on SDA inevitably reduced proportion of energy from diet that allocated to their growth, and hence exhibited lower growth performance when compared to those whose SMR were

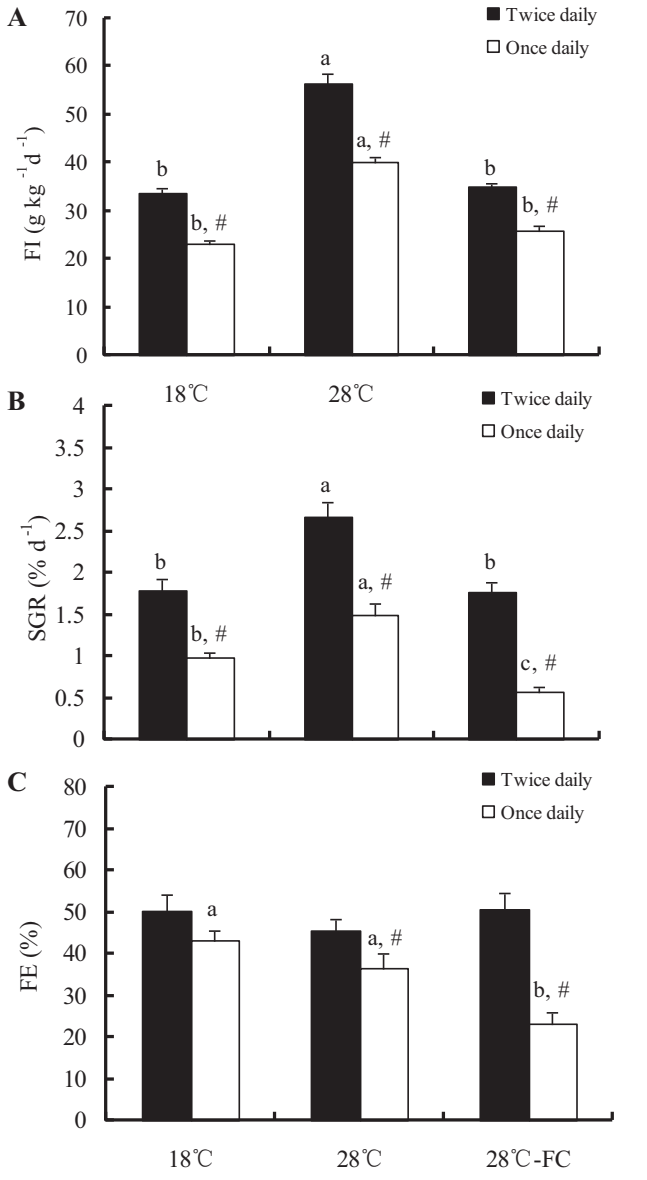

Fig. 3. Comparisons of growth parameters between different temperature treatments in juvenile common carp under two food availabilities. Bars with different lowercase letters represent a significant difference between temperature treatments within a given food availability ($P < 0.05$), and the symbol (#) means a significant difference between food availabilities within a given temperature treatment ($P < 0.05$). FI = food intake; SGR = specific growth rate; FE = feeding efficiency; and FC = food control. Error bars = SEM.

inflexible or decreased.

Previous studies have documented that individuals with higher SMR tended to have higher MMR or AS (Norin and Malte, 2012; Pang et al., 2015; Pang et al., 2016), which suggests that individuals with higher aerobic capacity have higher energetic maintenance costs. These findings are consistent with the hypothesis proposing a mechanistic link between internal organ mass and metabolic rate (Daan et al., 1990; Norin and Malte, 2012). When considering the flexibility in metabolic rate, it could be deduced that individuals with higher SMR flexibility may have the same approximate degree of AS (or MMR) flexibility under the same environmental conditions, producing the same positive correlation between flexibility in SMR and flexibilities in AS and MMR. However, in the present study, our data did not support such inference which showed that no links between ΔSMR and ΔMMR (or ΔAS in most cases) were found in the three temperature treatments under two food

Table 4
Pearson's correlations between growth parameters with two food availabilities in juvenile common carp under different temperatures.

Temperature	Twice daily			Once daily	
		FE	FI	FE	FI
18 °C	SGR	$r = 0.978^{**}$ $P < 0.001$	$r = 0.417^{*}$ $P = 0.022$	$r = 0.963^{**}$ $P < 0.001$	$r = -0.233$ $P = 0.216$
	FE		$r = 0.256$ $P = 0.172$		$r = -0.477^{**}$ $P = 0.008$
28 °C	SGR	$r = 0.903^{**}$ $P < 0.001$	$r = 0.138$ $P = 0.444$	$r = 0.946^{**}$ $P < 0.001$	$r = 0.187$ $P = 0.254$
	FE		$r = -0.255$ $P = 0.152$		$r = -0.109$ $P = 0.511$
28 °C-FC	SGR	$r = 0.938^{**}$ $P < 0.001$	$r = -0.121$ $P = 0.462$	$r = 0.929^{**}$ $P < 0.001$	$r = -0.179$ $P = 0.284$
	FE		$r = -0.431^{**}$ $P = 0.006$		$r = -0.483^{**}$ $P = 0.002$

FI = food intake; SGR = specific growth rate; FE = feeding efficiency; and FC = food control.
** $P < 0.01$.
* $P < 0.05$.

Table 5
The relationships between the specific growth rate (SGR) and change in metabolic rate in juvenile common carp under different temperature treatments.

Temperature	Food availability	Change in Metabolic rates	*r*	*P*
18 °C	Twice daily	ΔSMR	0.114	0.548
		ΔMMR	0.186	0.120
		ΔAS	0.120	0.529
		ΔFAS	−0.132	0.486
	Once daily	ΔSMR	−0.117	0.538
		ΔMMR	0.282	0.131
		ΔAS	0.289	0.121
		ΔFAS	0.260	0.165
28 °C	Twice daily	ΔSMR	−0.545	0.001**
		ΔMMR	0.051	0.776
		ΔAS	0.254	0.154
		ΔFAS	0.343	0.051
	Once daily	ΔSMR	0.052	0.775
		ΔMMR	−0.461	0.007**
		ΔAS	−0.554	0.001**
		ΔFAS	−0.387	0.026*
28 °C-FC	Twice daily	ΔSMR	−0.258	0.113
		ΔMMR	−0.182	0.267
		ΔAS	−0.026	0.887
		ΔFAS	0.083	0.614
	Once daily	ΔSMR	−0.054	0.749
		ΔMMR	−0.333	0.041*
		ΔAS	−0.252	0.127
		ΔFAS	−0.126	0.450

SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope; FAS = factorial aerobic scope; and FC = food control.
** $P < 0.01$.
* $P < 0.05$.

availabilities (Table 3). Flexibility in metabolic rates is an important physiological mechanism for responding to changes in environmental conditions (e.g., food availability), allowing an individual to maximize its fitness in specific conditions (Auer et al., 2015a), and may potentially be a target of natural selection. Future studies should focus on whether phenotypic flexibility in metabolic rate of individuals remains constant across different environmental gradients and over time (Norin et al., 2016).

As shown in the present study, flexibility in metabolic rate could confer a growth advantage that potentially maximizes an individual's growth under conditions of changing food availability, and the benefit from this flexibility mechanism is temperature-dependent. In natural habitats, animals have to inevitably cope with inconsistent changes across a diverse set of environmental factors, which is reflected through their phenotypic flexibility of traits and related capacities (Auer et al., 2015b). Additionally, individuals within a population exhibit considerable phenotypic flexibility in traits, with different extents of response to changing environments, but differences in the pattern of phenotypic flexibility in traits may be consistent across different contexts and over a long time. Given the ongoing global climate change and the high degree of habitat modification currently experienced by many animals (Hofmann and Todgham, 2010; Pörtner and Peck, 2010; Bolnick et al., 2011), more work is needed to understand the mechanisms underlying the context-dependent links between key physiological traits (i.e., swimming capacity and metabolic rate) and components (i.e., survival and reproduction) of fitness in the face of a rapidly changing environment.

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