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Acclimation temperature alters the relationship between growth and swimming performance among juvenile common carp (*Cyprinus carpio*)

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ABSTRACT

Individual variation in growth, metabolism and swimming performance, their possible interrelationships, and the effects of temperature were investigated in 30 juvenile common carp (*Cyprinus carpio*) at two acclimation temperatures (15 and 25 °C). We measured body mass, critical swimming speed (U_{crit}), resting metabolic rate (RMR), active metabolic rate (AMR) and metabolic scope (MS) twice (28 days apart) in both temperature groups. Fish acclimated to 25 °C showed a 204% higher specific growth rate (SGR) than those acclimated to 15 °C due to a 97% higher feeding rate (FR) and a 46% higher feed efficiency (FE). Among individuals, SGR was positively correlated with the FR and FE at both low and high temperatures. All measured variables (U_{crit}, RMR and AMR) related to swimming except MS showed a high repeatability after adjusting for body mass (mass-independent). Fish acclimated to 25 °C had a 40% higher U_{crit} compared with 15 °C acclimated fish, which was at least partially due to an improved metabolic capacity. AMR showed a 97% increase, and MS showed a 104% parallel increase with the higher acclimation temperature. Residual (mass-independent) U_{crit} was positively correlated with residual RMR, AMR and MS, except for the residual RMR at high temperature. When acclimated to the lower temperature, both the residual and absolute U_{crit} were negatively correlated with FR and FE and, hence, with SGR, suggesting a functional trade-off between growth and locomotion in fish acclimated to low temperatures. However, when acclimated to the higher temperature, this trade-off no longer existed; absolute U_{crit} was positively correlated with SGR because individuals with rapid growth exhibited greatly increased body mass. The higher metabolic capacity at 25 °C showed a positive effect on both swimming performance and growth rate (because of improved digestive efficiency) under the high-temperature condition, which we did not anticipate. Overall, these results indicate that temperature alters the relationship between growth and swimming performance of juvenile common carp. This change may be an adaptive strategy to seasonal temperature variation during their life history.

1. Introduction

Somatic growth is one of the most fundamental biological processes necessary for survival, enabling an organism to increase its body size and energy storage from an ovum to a multicellular, reproductive adult (Arnott et al., 2006). Fast growth is often perceived as beneficial, especially in the juvenile stages, because vital organs develop faster, and the potential benefits of a large body size, such as improved competitive ability and overwinter survival, can accrue more quickly (Arendt, 1997; Arnott et al., 2006). Swimming is another survival-determining trait for fish because it is closely related to food capture, predator avoidance and reproductive behaviour (Reidy et al., 2000). The critical swimming speed (U_{crit}) is the water velocity at which a fish can no longer maintain its position (Brett, 1964; Svendsen et al., 2010). Although fish rely on anaerobic metabolism to varying degrees while reaching their U_{crit} (Nelson et al., 1996), U_{crit} is highly correlated with an animal's active metabolic rate (AMR, i.e., the maximum metabolic rate during the U_{crit} test) and is widely accepted as an indicator of aerobic swimming performance (Lee et al., 2003; Reidy et al., 2000). Researchers have found that in some fish species, individuals with larger body size and/or faster swimming speed survive and reproduce better than their smaller and slower competitors (Arendt, 1997; Billerbeck et al., 2001; Sogard, 1997). However, growth and swimming performance are limited by many external conditions, such as temperature and food abundance (Guderley, 2004), as well as internal factors, such as hormonal status and genetic capacity (Barton, 2002; Li et al., 2007). Thus, adaptive variation in growth and swimming performance may also be associated with energy acquisition and output.

Both growth and swimming performances often exhibit wide and consistent variations among individuals of the same fish species, and these variations are possibly linked to their energy metabolism (Auer et al., 2015a; Killen et al., 2013; Kolok and Farrell, 1994). An animal's standard metabolic rate (or resting metabolic rate, RMR) represents

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the minimal level of energy required to maintain its basic functions (Priede, 1985), and individuals with a high RMR can support greater energy output for growth and/or locomotion (Biro and Stamps, 2010). However, individuals with a high RMR may be at a growth disadvantage when food becomes scarce (Auer et al., 2015a). They may also have a lower metabolic scope (MS, i.e., AMR-RMR) for swimming if their AMR is not equivalently increased (Arnott et al., 2006). Although some fish species may not be highly active in pursing their prey, their ability to compete for food may still be related to swimming performance. Therefore, swimming capacity is a crucial factor for successful foraging, which is a prerequisite for growth, whereas feeding and growth supply the energy for swimming. Therefore, the effects of growth and swimming performances could interact at the species level. On the one hand, swimming performance is positively correlated with body mass (Fry and Cox, 1970; Hammer, 1995), and faster growth may therefore lead to a greater improvement in swimming performance. On the other hand, several studies have reported a trade-off between growth rate and swimming speed in some fish species (Álvarez and Metcalfe, 2007; Arnott et al., 2006; Billerbeck et al., 2001; Gregory and Wood, 1998, 1999; Killen et al., 2014; Kolok and Oris, 1995). It may be better to be large and fast, but it may also be difficult to become large without becoming slow because of internal (e.g., hormonal status and genetic capacity) and external (i.e., environmental variables) limitations. Therefore, understanding and testing the complex interactions between growth and locomotion are important and of interest to the field of ecophysiology.

Temperature has been called the 'ecological master factor' for fish (Brett, 1971), and important physiological functions, such as growth, metabolism and swimming performance, can have temperature optima at which these functions occur at maximum efficiency (Clark et al., 2013; Kellogg and Gift, 1983; Lee et al., 2003; Pang et al., 2013; Pörtner and Farrell, 2008). The relationships between temperature and growth rate (Handeland et al., 2008; Kellogg and Gift, 1983) or swimming speed (Lee et al., 2003; Pang et al., 2013; Zeng et al., 2009) are known to follow bell-shaped curves, i.e., ascending as temperatures rise from levels below their optimal temperature and descending as temperatures rise above their optimal temperature. The improved physiological functions at higher temperatures are due to elevated biochemical reaction rates (Franklin, 1998), metabolic capacities (Pang et al., 2010) and enzyme activities (Pelletier et al., 1993a). However, different physiological functions have various thermal sensitivities (Yan et al., 2012; Zeng et al., 2009) and reaction norms (Angilletta et al., 2003). Thus, the relationships between different physiological functions may be altered between different environmental temperatures (Killen et al., 2013). Therefore, fish may have developed different growth and swimming strategies to cope with different and variable environmental conditions, such as temperature (Auer et al., 2015a; Pang et al., 2010, 2014).

In this study, we selected juvenile common carp (*Cyprinus carpio*), an omnivorous, rapidly growing, warm-water cyprinid, as our experimental animal. The common carp is native to eastern Asia and is widely distributed throughout the world. It is one of the most abundant fish species in the Yangtze River and is an important cultured fish species in China. Studies of individual variation in the physiological performance of fish may provide insight into how selection has influenced diversity in phenotypic traits (Marras et al., 2010). In this study, we aimed to (1) investigate the variation in individual growth and swimming performance in juvenile common carp, (2) verify the relationship between growth and swimming performance and (3) test whether the possible relationship varies with acclimation temperature. To address our research aims, we measured body mass, U_{crit}, RMR, AMR and MS twice (before and after a 28-day experimental period) in 30 fish acclimated to either 15 or 25 °C. We calculated the specific growth rate (SGR) and measured the feeding rate (FR) and feed efficiency (FE) during this period. The temperatures applied in this study, (15 and 25 °C) are similar to the seasonal temperature fluctuations (winter and summer, respectively) in the Yangtze River of China (Pang et al., 2014).

2. Materials and methods

2.1. Experimental fish and holding protocol

Juvenile common carp (5–10 g, $n = 400$) were obtained from a local hatchery on the Yangtze River (Bishan, Chongqing, China). Prior to the experiment, the fish were kept for 2 weeks in a laboratory cement pit system (180 cm × 120 cm × 60 cm) with recirculating water. During this period, the temperature of the fresh dechlorinated water used was maintained at 20 ± 0.5 °C (actual range), the water oxygen content was above 7.5 mg L^{-1}, the pH ranged from 6.5 to 7.3, and ammonia-N varied from 0.005 to 0.025 ppm. The photoperiod was maintained at 12 h light:12 h dark. The fish were fed to satiation daily at 18:00 with a commercial dry floating diet (Tongwei Group, Chengdu, China; composition: 41.2% protein, 8.5% lipid, 25.7% carbohydrate and 12.3% ash).

2.2. Experimental protocol

After 2 weeks in the recirculating water system, 60 similarly sized fish were transferred individually into 60 separate compartments (20 cm × 15 cm × 15 cm) immersed in four similar indoor recirculating water systems (two systems for each temperature group, 15 fish in each system) at the two treatment temperatures (15 and 25 °C). The water temperature was 20 °C when the fish were transferred and was then decreased or increased at 1 °C d^{-1} until reaching the prescribed temperature for a 21-day temperature acclimation period. During the temperature treatment period (including the 5-day temperature adjustment period and the 21-day temperature acclimation period), the fish at 15 and 25 °C were individually fed approximately 0.5 and 1.0%, respectively, of their body mass as a maintenance ration (see the previous paragraph for dietary composition) daily at 9:00.

During the experimental period, the experiment temperatures were maintained at 15 and 25 °C for 28 days, and all fish were individually fed to satiation twice daily (at 9:00 and 18:00) with a commercial diet of floating pellets of similar size (9.52 ± 0.06 mg per pellet). Uneaten food and faeces were removed 1 h after feeding using a siphon, and food consumption was calculated based on the number and average weight of the pellets. Body mass, length, U_{crit}, RMR, AMR and MS were individually measured twice (before and after a 28-day experimental period). To reduce the influence of undigested food on the physiological status of the fish, all experimental fish were fasted for 24 h before any measurements.

2.3. Measurements of growth performance

At the beginning and end of the 28-day experimental period, experimental fish were lightly anaesthetized (neutralized MS222, tricaine methanesulfonate, 50 mg L^{-1}) for approximately 2 min, and body mass, length, width and depth (body width and depth for correcting U_{crit}) were then measured to the nearest 0.01 g (body mass) or 0.01 cm (body length, width and depth). The following growth performance parameters were calculated:

$$\mathrm{Feeding\,rate}\left(\mathrm{FR},\%\mathrm{body\,mass\,d}^{-1}\right) = 100 \times \mathrm{F_c}/[(\mathrm{W_0}+\mathrm{W_t})/2]/\mathrm{t} \tag{1}$$

$$\mathrm{Feed\,efficiency}\,(\mathrm{FE},\%) = 100 \times (\mathrm{W_t}-\mathrm{W_0})/\mathrm{F_c} \tag{2}$$

$$\mathrm{Specific\,growth\,rate}\left(\mathrm{SGR},\%\mathrm{d}^{-1}\right) = 100 \times [\ln(\mathrm{W_t}) - \ln(\mathrm{W_0})]/\mathrm{t} \tag{3}$$

where $\mathrm{F_c}$ represents the total amount of food consumed by the fish (g), $\mathrm{W_0}$ and $\mathrm{W_t}$ are the initial and final body mass (g) of the experimental fish, respectively, and t is the experimental period (d).