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The effects of temperature on metabolic interaction between digestion and locomotion in juveniles of three cyprinid fish (*Carassius auratus*, *Cyprinus carpio* and *Spinibarbus sinensis*)

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ABSTRACT

To test whether the effects of temperature on the metabolic mode changed among different fish species, we investigated the specific dynamic action (SDA) and swimming performance of fasting and fed fish at 15 and 25 °C in three juvenile Cyprinidae fish species: goldfish (*Carassius auratus*), common carp (*Cyprinus carpio*) and qingbo (*Spinibarbus sinensis*). Both taxon and temperature had significant effects on the resting oxygen consumption rate ($\dot{M}O_{rest}$), SDA and swimming performance ($p<0.05$). In addition, the effect of temperature differed significantly among the different species (interaction effect, $p<0.05$). Under the low temperature condition, digestion had no effect on either critical swimming speed (U_{crit}) or the active $\dot{M}O_2$ ($\dot{M}O_{active}$) for all fish species (additive metabolic mode). When the temperature was increased from 15 to 25 °C, the metabolic scope (*MS*) for digestion increased approximately 182, 49 and 17%, and the *MS* for locomotion increased approximately 129, 58 and 138% in goldfish, common carp and qingbo, respectively. The total metabolic demands for both digestion and locomotion (i.e., the sum of digestive *MS* and locomotive *MS*) increased approximately 143, 56 and 112% in goldfish, common carp and qingbo, respectively. The total *MS* for both digestion and locomotion (the difference between $\dot{M}O_{active}$ in fed fish and $\dot{M}O_{rest}$ in fasting fish) increased approximately 106, 58 and 78% in goldfish, common carp and qingbo, respectively. Thus, the *MS* for locomotion in fed goldfish decreased due to the large increase in digestive function at the high temperature, and the U_{crit} of fed goldfish decreased by 11% compared to that of fasting fish ($p<0.05$) (digestion-priory metabolic mode). The metabolic mode of qingbo changed to locomotion-priority mode, as illustrated by the large increase in locomotive *MS* in response to the increase in temperature. In the common carp, temperature had no effect on metabolic mode as illustrated by the parallel increases in cardio-respiratory capacity and metabolic capacity of digestive and locomotive organs. A discussion on the changes in metabolic mode in response to temperature and its possible relationship with the metabolic characteristics of a given fish species was also documented in this paper.

1. Introduction

As an important ecological factor, temperature has a profound effect on fitness-determining traits such as growth, metabolism, and locomotion performance (Jain and Farrell, 2003; Green and Fisher, 2004). Animals need to eat and move to varying degrees, both activities being known to increasing organisms' metabolic rate ($\dot{M}O_2$) of organisms independently. Digestion is an important physiological activity in animals because it provides energy and nutrients required for the animal's survival and growth. During digestion, the increase of $\dot{M}O_2$ is due to the specific dynamic action (SDA) of food and may primarily occur in gastrointestinal organs and the liver (Andersen and Wang, 2003). Studies found that temperature affects postprandial metabolic response with increased peak $\dot{M}O_2$ ($\dot{M}O_{peak}$) and decreased duration of the metabolic response (Peck et al., 2003; Wang et al., 2003; Secor et al., 2007; Luo and Xie, 2008). Swimming performance is another survival determining trait for fish because it is closely related to food gain and predator avoidance. The critical swimming speed (U_{crit}, i.e., water speed at which a fish can no longer maintain position or maximum sustainable swimming speed) is a widely used parameter for the evaluation of aerobic swimming performance. Previous research showed that the U_{crit} and active $\dot{M}O_2$ ($\dot{M}O_{active}$, the maximum $\dot{M}O_2$ during the U_{crit} test) increased significantly with the increase of temperature (Rome et al., 1990; Keen and Farrell, 1994; Claireaux et al., 2000, 2006; Jain and Farrell, 2003; Lee et al., 2003; MacNutt et al., 2006).

Under natural conditions, animals often need to carry out digestion and locomotion simultaneously (Alsop and Wood, 1997; Andersen and Wang, 2003). The physiological design of their cardio-respiratory systems must accommodate these simultaneous demands either by according emphasis to one of them or by somehow sharing it (Hicks and Bennett, 2004). In some animals, digestion and locomotion can be performed simultaneously (i.e., there were no interactive effects between digestion

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and locomotion) (additive metabolic mode); for example, in monitor lizards (*Varanus exanthematius*), a postprandial increase in resting $\dot{M}O_2$ was maintained at all levels of locomotion (Bennett and Hicks, 2001). However, for most fish species, it may be important to exert physiological priorities so that one activity can be emphasized at the expense of the other. Either the swimming performance will be impaired to sustain the SDA or *vice versa*. For example, in postprandial rainbow trout (*Oncorhynchus mykiss*) and Chinook salmon (*Oncrhynchus tshawytscha*), the elevated $\dot{M}O_2$ due to digestion was maintained throughout a U_{crit} test, and the fed fish ended up having a profoundly lower U_{crit} but similar maximum $\dot{M}O_2$ compared with fasting fish (digestion-priority) (Alsop and Wood, 1997; Thorarensen and Farrell, 2006). However, in sablefish (*Anopoma fimbria*), a comparison of power-performance curves for fed and fasting fish found that the fed fish can allocate their oxygen supply preferentially to locomotor muscles and suppress the oxygen demand of digestion when swimming (locomotion-priority) (Furnell, 1987).

These apparently contrasting results regarding the competition between digestion and locomotion may be related to the great variation in capacity of the central cardio-respiratory system, the peripheral digestive and locomotor systems among different species (Fu et al., 2009). Recent studies have found that the water dissolved oxygen level, exercise training and starvation all have profound effects on the metabolic mode in fish species (Jourdan-Pineau et al., 2010; Li et al., 2010; Fu et al., 2011). The reason lies in the relative status of oxygen availability, cardiovascular performance and muscle metabolic capacity. A recent study in southern catfish (*Silurus meridionalis* Chen) found that the metabolic mode changed from an additive mode to a digestion-priority mode with the temperature increased from 15 to 33 °C (Pang et al., 2010). The authors suggested that the change of metabolic mode is due to the lower oxygen availability and higher peripheral digestive and locomotive metabolic capacities at the high temperature. Only one fish species has been investigated thus far with respect to the effect of temperature on the metabolic mode between digestion and locomotion. Fish species show great variation in the metabolic and respiratory capacity of digestive, locomotive and the cardio-respiratory system. Furthermore, the digestion and locomotion processes may show different responses to a change in water temperature. Thus, it would be interesting to investigate the effect of temperature on metabolic mode among different fish species.

In this study, we selected three fish species of Cyprinidae: goldfish (*Carassius auratus*), common carp (*Cyprinus carpio*) and qingbo (*Spinibarbus sinensis*). The goldfish is a highly adaptive species with a wide distribution throughout the world, while the common carp and qingbo are the most abundant fish species in the Yangtze River of China (Duan et al., 2002). The three Cyprinid species are all active, omnivorous fishes, and they have a similar genetic background from the Barbini family (Kong et al., 2007). Thus, the possible statistical analysis noise from genetic and ecological effect in the present study was minimized. We first measured the fasting and postprandial $\dot{M}O_2$ response of three selected carps under different temperatures (15 and 25 °C). We then investigated the effect of digestion on U_{crit} and $\dot{M}O_{active}$ in all three fish species at different temperatures. The aims of this study were (1) to provide and compare SDA and U_{crit} data for Cyprinid fishes at different temperatures, (2) to test whether temperature had different effects on SDA and swimming performance among different fishes and (3) to test whether temperature had different effects on the metabolic mode among Cyprinid fish species.

2. Materials and methods

2.1. Experimental animals and acclimation

Experimental juvenile goldfish (5–12 g, n = 100), qingbo (4–10 g, n = 100) and common carp (5–10 g, n = 100) were obtained from local farmers and kept in dechlorinated, 20 °C, fully aerated tap water tanks for 2 weeks prior to the experiment. The fish were fed to satiation once daily at 20:00 h with a formulated diet. The chemical composition of the formulated diet was 58.2% moisture, 16.6% protein, 1.9% lipid and 9.7% digestible carbohydrate, resulting in 6.3 kJ g^{-1} of bio-available energy. The dietary bio-available energy was calculated as 23.6 kJ g^{-1} protein, 39.5 kJ g^{-1} lipid and 17.2 kJ g^{-1} carbohydrate (Fu and Xie, 2004). The uneaten food and feces were cleared using a siphon 1 h after feeding. The water temperature was maintained at 20.0 ± 0.5 °C, and water oxygen content was maintained above 6.0 mg L^{-1}. The ammonia-N ranged from 0.005–0.025 mg L^{-1}, and the tanks were kept under constant light conditions (Luo and Xie, 2008).

Two acclimation temperatures (15 and 25 °C) were used in this experiment. After being held in 20 °C water for 2 weeks, 2 groups of juvenile fish were transferred from the general holding tanks to each of the 2 acclimation tanks (length × width × height, 1.5 m × 0.6 m × 0.5 m). The water temperature was 20 °C when the fish were transferred, and then it was increased or decreased at 1 °C day^{-1} until it reached the prescribed temperature. The fish were maintained at the experimental temperature for 21 days. During the acclimation period, fish were fed once every day to satiation.

2.2. Measurement of fasting and postprandial $\dot{M}O_2$

The $\dot{M}O_2$ for individual fish (either fasting or fed) was measured using a continuous-flow respirometer (Fu et al., 2005). The following formula was used to calculate the $\dot{M}O_2$ (mg kg^{-1} h^{-1}) of individual fish:

$$\dot{M}O_2 = \Delta O_2 \times v / m \quad (1)$$

where ΔO_2 is the difference in oxygen concentration (mg L^{-1}) between the experimental chamber and the control chamber (chamber without fish), v is the water flow rate in the experimental chamber (L h^{-1}) and m is the body mass of the fish (kg). The dissolved oxygen concentration was measured at the outlet of the chamber by an oximeter (HQ20, Hach Company, Loveland, CO, USA). The flow rate of water through the respirometer chamber was measured by collecting the water outflow from each tube. The flow rate of each chamber was adjusted to assure 80% saturation of dissolved oxygen concentration in the outlet water to avoid undue stress on physiological processes.

2.3. Measurement of U_{crit} and swimming $\dot{M}O_2$

A Brett-type swimming tunnel respirometer (Brett, 1964) was used to measure U_{crit} and the $\dot{M}O_2$ as a function of swimming speed (see detail inFu et al., 2005). The respirometer was constructed from clear plastic poly-methyl-methacrylate (PMMA). A circulating water flow was generated in the tunnel (total volume 3.5 L) by an acrylic propeller attached to a variable speed pump. Two honeycomb screens were secured at both ends of the swimming chamber to reduce turbulence and to ensure uniform water velocity across the swimming chamber. A video camera was used to calibrate the water velocity to the voltage output from the pump controller. The fish were placed downstream of the propeller in a swimming chamber with a 19.9 cm^2 cross-sectional area. The water temperature in the swimming chamber was controlled within ± 0.2 °C using a water bath connected to a stainless steel heat exchanger. U_{crit} was calculated for individual fish using Brett's equation (Brett, 1964):

$$U_{crit} = V + (t / T)\triangle V \quad (2)$$

where V is the highest speed at which the fish swam during the full time period of the experiment (cm s^{-1}); V is the velocity increment (0.5 body length s^{-1}; 6 cm s^{-1}), T is the prescribed period of swimming per speed (20 min) and t is the time that the fish swam at the final speed (min).

The O_2 concentration was measured continuously throughout the ramp-U_{crit} test as a function of swimming speed. The respirometer could switch between an open mode and a closed mode to replenish the oxygen and to measure the $\dot{M}O_2$, respectively. In the open mode, the respirometer was supplied with fully aerated and thermoregulated water