



Effects of temperature and digestion on the swimming performance of juvenile Chinese bream

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ABSTRACT: Fish that are active foragers usually perform routine activities while digesting their food; thus, postprandial swimming capacity might be ecologically important. To test whether digestion affected swimming performance in an active forager and whether the possible effects varied with temperature, we investigated the critical swimming speed (U_{crit}) and the resting and active metabolic rate (MO_2) of fasted and fed juvenile Chinese bream *Parabramis pekinensis* after 30 d exposure to 3 temperatures (15, 20, and 25°C). In fasted fish, U_{crit} , resting and active MO_2 all increased with temperature. Digestion elicited a significant increase in MO_2 , which was enhanced at higher temperatures. Compared to fasted fish, fed fish exhibited significantly lower U_{crit} in both the 25 and 20°C groups, whereas no significant difference in U_{crit} was observed between fasted and fed fish in the 15°C group. Furthermore, digestion resulted in a significantly higher active MO_2 in the 15°C group, whereas no significant difference in active MO_2 was observed between fasted and fed fish in the 20 and 25°C groups. This suggests that the bream adopted an additive metabolic mode, i.e. digestion and swimming were performed independently at low temperatures, but shifted to a digestion-priority mode at higher temperatures due to a shortage of oxygen resulting from an increased digestive and locomotive oxygen demand. The present study contradicted our hypothesis that an active cyprinid with high swimming performance would give priority to locomotion when the oxygen supply was insufficient to meet the metabolic demands of both digestion and swimming.

KEY WORDS: Digestion · Metabolic mode · Metabolic priority · Swimming performance · Temperature

INTRODUCTION

Swimming is an important physiological activity for fish because it is closely related to food capture, predator avoidance and reproductive behavior (Brett 1964, Blake 2004, Kieffer 2010, Cai et al. 2014a). Fish may perform swimming activities while digesting their food, and the outcome of the competition between the processes of digestion and swimming has important ecological relevance because both activities are important fitness-determining physiological functions in fish species. This competition might be increasingly severe in active foragers and in those fish species living in a highly demanding habitat (e.g. high water

velocity or predation stress). Recently, the competition between digestion and swimming under a postprandial locomotion status has drawn the attention of scientists (Alsop & Wood 1997, Thorarensen & Farrell 2006, Altimiras et al. 2008, Fu et al. 2009, Jourdan-Pineau et al. 2010, Cai et al. 2014b). These 2 physiological activities can be performed independently—the so-called additive metabolic mode found in fish species such as the common carp *Cyprinus carpio* (Pang et al. 2011) and the European sea bass *Dicentrarchus labrax* (Altimiras et al. 2008, Jourdan-Pineau et al. 2010). Otherwise, the digestion process may defer to swimming (locomotion-priority mode), as in qingbo *Spinibarbus sinensis* (Pang et al. 2011), or vice

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versa (digestion-priority mode) as in goldfish *Carassius auratus* (Pang et al. 2011), rainbow trout *Oncorhynchus mykiss* (Alsop & Wood 1997) and Chinook salmon *O. tshawytscha* (Thorarensen & Farrell 2006).

The physiological mechanisms, ecological causes and selective agents underlying the different metabolic modes among fish species are largely unknown. We previously suggested that the metabolic mode employed might be related to the ecological habitat of the individual species (Pang et al. 2011); i.e. high performance swimmers evolved under selective stress for high swimming demand, and therefore digestion should give priority to swimming when the metabolic supply is insufficient to meet the metabolic demands (and vice versa). However, only 3 cyprinids have been investigated thus far with regards to metabolic mode. In this study, we investigated the metabolic mode in Chinese bream *Parabramis pекinensis*, a widely distributed cyprinid in China with high swimming performance (Yan et al. 2013).

It has been suggested that the metabolic mode may vary with environmental conditions such as temperature and dissolved oxygen levels in some (but not all) fish species (Pang et al. 2011, Zhang et al. 2012). The competition between digestion and swimming is resolved by their relative roles within a given species, and by the conservative capacities of the central cardio-respiratory system (oxygen supply) and the peripheral digestive and locomotory systems (metabolic demands). The change in metabolic mode results from a shift in the balance point between oxygen supply and the metabolic demands of digestion and locomotion in different environments.

Temperature has a profound effect on all physiological functions, including cardio-respiratory capacity, digestion and swimming performance (Fry 1971, Kieffer et al. 1994, Luo & Xie 2008, Zeng et al. 2009). Furthermore, oxygen availability also changes with temperature, which may profoundly affect metabolic competition in fish species (Pang et al. 2011). Therefore, we selected 3 experimental temperatures to test whether the metabolic mode changed with temperature in Chinese bream. This species spends more than 30% of its time moving in either a fasting or digesting status, i.e. it is an active forager that frequently forages or swims while digesting food. Furthermore, its habitat exhibits profound seasonal thermal changes and daily fluctuations. We selected 15, 20 and 25°C, which simulate the mean of summer, autumn and winter temperatures of local water bodies. Our aim was to test whether digestion had a significant effect on the swimming performance of this active forager, and if so, whether such effects varied with temperature.

MATERIALS AND METHODS

Experimental animals and acclimation

Juvenile Chinese bream were obtained from a local farmer and kept in 20°C de-chlorinated, fully aerated tap water tanks for 2 wk prior to the experiment. The photoperiod was maintained at 12:12 h light:dark cycle, and the oxygen level was kept above 8 mg l⁻¹. One-tenth of the water in each tank was replaced daily with fresh water. Throughout the experimental period, the fish were fed twice daily (at 09:00 and 17:00 h) to satiation with a commercial food (Tongwei; dietary composition: 41.2 ± 0.9% protein; 8.5 ± 0.5% lipid; 25.7 ± 1.2% carbohydrate and 12.3 ± 0.4% ash). The uneaten food and feces were removed with a siphon 1 h after feeding. All of the 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.

Experimental design

Three experimental temperatures (15, 20 and 25°C) were used. After acclimation, juvenile Chinese bream were transferred from the general holding tanks to experimental tanks. The water temperature was kept constant (20°C), increased (to 25°C) or decreased (to 15°C) by 1°C d⁻¹ until it reached the experimental treatment temperature (Pang et al. 2011). The fish were maintained at the experimental temperature for 30 d and fed to satiation twice daily as during the acclimation period.

For the fasting experiment group, after 1 d of fasting, 8 fish from each temperature group were introduced into a swim tunnel and held for 2 h at a water speed of 3.5 cm s⁻¹ for acclimation (0.5 body length [BL] s⁻¹, which was enough for full water exchange but elicited no apparent swimming activity) (Pang et al. 2011). The metabolic rate (MO₂, mg O₂ kg⁻¹ h⁻¹) was then measured and recorded as 'resting MO₂' (see details in 'Experimental facility and measurements' below). Individual fish were then tested using a ramp-*U*_{crit} test (Jain & Farrell 2003). This test involved increasing the water speed to 50% of the critical swimming speed (*U*_{crit}) as determined by a pilot experiment (35 cm s⁻¹ at 15 or 20°C, and 42 cm s⁻¹ at 25°C) over a 2 min period, after which time the water speed was increased in 7 cm s⁻¹ increments every 20 min until the fish became exhausted. Testing was terminated when the fish failed to move off

the rear honeycomb screen of the swimming chamber after 20 s (Jain & Farrell 2003, Lee et al. 2003, Pang et al. 2011). The maximum measured MO_2 during the ramp- U_{crit} test was defined as 'active MO_2 '. Dissolved oxygen concentration values were measured throughout the whole ramp- U_{crit} test using a HQ30 oxygen probe (Hach).

For the fed fish, another 8 fish were selected from each temperature treatment group, slightly anesthetized with neutralized tricaine methane sulfonate (MS-222, 30 mg l⁻¹) and force-fed with approximately 3% body-mass, meal-sized diets (satiated feeding) by a gavage protocol (Altimiras et al. 2008, Li et al. 2010). The fed fish were then transferred to the swimming chamber and allowed to recover for 2 h; following recovery, U_{crit} was measured in the same manner as for the fasting groups. The 2 h recovery period was determined by the digestion process of Chinese bream (the duration of the digestion process is 8 h, and the post-prandial metabolic response peaks approximately 4 h after feeding, thus the metabolic competition between digestion and swimming is likely most severe during U_{crit} testing).

Experimental facility and measurements

A Brett-type swim tunnel respirometer was used to measure fish U_{crit} and MO_2 as a function of swimming speed (for details of the respirometer, see Li et al. 2010 and Pang et al. 2011). Fish were placed downstream of the propeller in a swimming chamber with an area of approximately 20 cm². The water temperature in the swimming chamber was controlled within $\pm 0.2^\circ\text{C}$ by a water bath connected to a stainless steel heat exchanger. U_{crit} was calculated for individual fish using Brett's equation (Brett 1964):

$$U_{crit} = v + (t/T) \Delta v \quad (1)$$

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 constant period of swimming per speed (20 min), and t is the time that the fish swam at the final speed (min). All absolute U_{crit} values (cm s⁻¹) were converted to body length per second (BL s⁻¹), which denotes relative U_{crit} .

A small fraction of the water from the sealed respirometer was siphoned past the probe of the HQ30 oximeter in a chamber thermoregulated by a water bath. The water oxygen concentration (mg l⁻¹) was recorded once every 2 min. In open mode, the respirometer was supplied with fully aerated and thermoregulated water that circulated in a reservoir

tank. In closed mode, the standardized MO_2 of an individual swimming fish was calculated from the depletion of oxygen according to the following equation (Fu et al. 2009):

$$MO_2 = 60 \text{ slope } V/m^{0.75} \quad (2)$$

where slope is the decrease in the water oxygen content per minute (mg O₂ min⁻¹) obtained from linear regressions of time (min) and water oxygen content (mg l⁻¹) using a statistical program (Excel 2003). Only slopes with $r^2 > 0.95$ were considered in the analysis. V is the total volume of the respirometer (3.5 l) minus the volume of the fish, and m is the body mass of the fish (kg). The water oxygen content in the respirometer was never allowed to fall below 85% oxygen saturation (Claireaux et al. 2006).

Data analysis

All values are presented as means \pm SE; results were considered significant at $p < 0.05$. The effect of temperature and digestion on U_{crit} (body length as the covariate), resting MO_2 and active MO_2 (body mass as the covariate) was determined by a 2-way ANCOVA. The effect of temperature, swimming speed, and digestion on MO_2 was determined by a 3-way repeated measures ANOVA. The ANOVA was followed by a Duncan multiple-comparison test or a t -test when it was necessary to determine the difference between the values of the different treatment groups.

RESULTS

Resting MO_2

Neither body mass nor body length significantly differed among the fish in the experimental groups (Table 1). Both temperature and digestion showed significant effects on resting MO_2 ($p < 0.001$) (Table 2). In fasted fish, resting MO_2 increased with temperature, and a significant difference was found among all 3 temperature groups ($p < 0.001$) (Fig. 1a). After feeding, the fish in all groups showed a significant increase in resting MO_2 ($p < 0.001$), and the digestion-elicited MO_2 increment increased with temperature (interaction effect, $p = 0.007$).

U_{crit}

Both temperature and digestion showed significant effects on U_{crit} ($p < 0.05$). In fasted fish, U_{crit} increased

Table 1. Body sizes of Chinese bream *Parabramis pekinensis* (mean \pm SE, n = 8) used in the temperature experiments

	Fasted		Fed	
	Body mass (g)	Body length (cm)	Body mass (g)	Body length (cm)
15°C	7.07 \pm 0.32	7.36 \pm 0.12	8.27 \pm 0.43	7.71 \pm 0.11
20°C	7.62 \pm 0.58	7.34 \pm 0.16	7.52 \pm 0.23	7.59 \pm 0.17
25°C	8.53 \pm 0.36	7.71 \pm 0.12	8.74 \pm 0.32	7.89 \pm 0.10
df	2,21	2,21	2,23	2,23
F	3.271	2.899	3.347	1.336
p	0.058	0.077	0.055	0.284

with temperature (Fig. 1b). After feeding, U_{crit} in both the 25 and 20°C temperature groups decreased significantly, whereas U_{crit} in the 15°C temperature group showed no significant change after feeding.

Active MO₂

Temperature had a significant effect on the active MO₂ ($p < 0.001$). In fasted fish, the active MO₂ values of the 25 and 20°C temperature groups were significantly higher than that of the 15°C temperature group ($p < 0.05$) (Fig. 1c). After feeding, only the 15°C temperature group showed a significantly higher active MO₂ compared to fasted fish; digestion had no effect on active MO₂ in the other 2 temperature groups.

Swimming speed: MO₂ profile

MO₂ increased significantly with swimming speed in all groups ($p < 0.001$) (Fig. 2). Digestion caused a significant increase in MO₂ when the fish swam at any given speed in the 15°C temperature group; however, compared to fasted fish, fed fish in the 25 and 20°C temperature groups only showed a significantly higher MO₂ at low swimming speeds.

Table 2. Effect of temperature and digestion on critical swimming performance (U_{crit}) and resting and active oxygen consumption rate (MO₂) in Chinese bream *Parabramis pekinensis* based on a 2-way analysis of covariance

	df	Resting MO ₂		U_{crit}		Active MO ₂	
		F	p	F	p	F	p
Covariate	1,41	0.225	0.638	9.453	0.004	0.007	0.932
Temp. (T)	2,41	32.20	<0.001	4.932	0.011	14.22	<0.001
Digestion (D)	1,41	59.06	<0.001	0.482	0.491	0.423	0.519
T \times D	2,41	3.381	0.044	5.119	0.010	5.110	0.010

DISCUSSION

Swimming performance

The U_{crit} of the Chinese bream *Parabramis pekinensis* in our experiments was between 9.67 and 10.86 BL s⁻¹ depending on experimental temperature; swimming resulted in a 4- to 6-fold increase in MO₂ compared to the resting status of the fish. These are among the highest values documented in cyprinids (Yan et al. 2013). However, after consumption of a satiated meal in this study, postprandial MO₂ only increased by 50% compared to fasted individuals, which is one of the lowest postprandial metabolic increases among all published data (Jobling et al. 1981, Alsop & Wood 1997, Pang et al. 2011). Chinese bream is thus a typical model of the so-called locomotion–metabolic type of fish (i.e. fish species with a high locomotive but low digestive metabolism; Priede 1985). Chinese bream frequently forage on grass of low nutritive value in either open water bodies with a high risk of predation or in rivers with rapid currents. Laboratory observation revealed that both fed and fasting Chinese bream spend more than 30% of their time spontaneously moving (J. Peng & S. J. Fu pers. obs.). Thus, selection may favor high swimming performance over digestive performance in this species.

In this study, all variables increased significantly with the increase in experimental temperature. However, thermal sensitivity varied profoundly among the different variables. With a temperature increase from 15 to 25°C, resting MO₂ increased by 106% and active MO₂ increased by 43%, whereas U_{crit} only increased by 12%. The change in resting MO₂ is similar to other cyprinids such as goldfish and common carp (100 to 130%), but higher than qingbo and crucian carp *Carassius auratus* (ca. 50% for both species; Pang et al. 2011, He et al. 2014). Although anaerobic metabolism is involved to some extent during U_{crit} measurement, it is generally acknowledged that U_{crit} is largely an aerobic swimming indicator and closely related to maximum aerobic capacity, i.e. active MO₂. Thus, U_{crit} theoretically possesses a positive relationship with active MO₂. In the present study, the unparallel change between U_{crit} and active MO₂ lay in the decreased swimming efficiency at higher temperature as a result of increased resting MO₂. Furthermore, energy expenditure (hence MO₂) increased exponentially with swimming

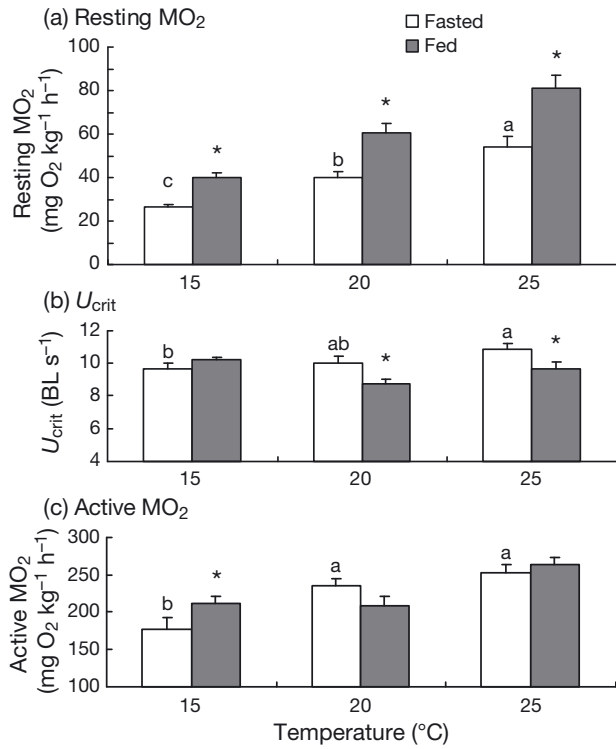


Fig. 1. Effects of temperature and digestion on (a) resting oxygen consumption rate (MO₂), (b) critical swimming speed (U_{crit}), and (c) active MO₂ in juvenile Chinese bream *Parabramis pekinensis*. Data are mean ± SE (n = 8); see Table 1 for information on fish sizes. Letters above white bars indicate significant differences among experimental temperatures in fasted fish; (*) above shaded bars denotes a significant difference (p < 0.05) in variables between fasted and fed fish in a given temperature treatment group. BL: body lengths

speed, resulting in a more profound increase in active MO₂ than U_{crit} with the increase in experimental temperature.

The nonparallel increase between resting MO₂ and swimming performance was unexpected. The high swimming performance may be driven by a high selective stress for swimming demand. Thus, swimming performance might be more closely related to maintenance metabolism than to digestive performance at varied acclimation temperatures. However, the active MO₂, and hence U_{crit}, increased much less than the resting MO₂. This suggests that the increased maintenance metabolism may contribute more than locomotion to physiological function. For example, postprandial MO₂ increased by 100% with a temperature increase from 15 to 25°C, similar to the resting MO₂ in Chinese bream. This result may indicate that the digestive capacity of Chinese bream improved more than swimming performance as the temperature became optimum. However, when considering the metabolic increase solely on the basis

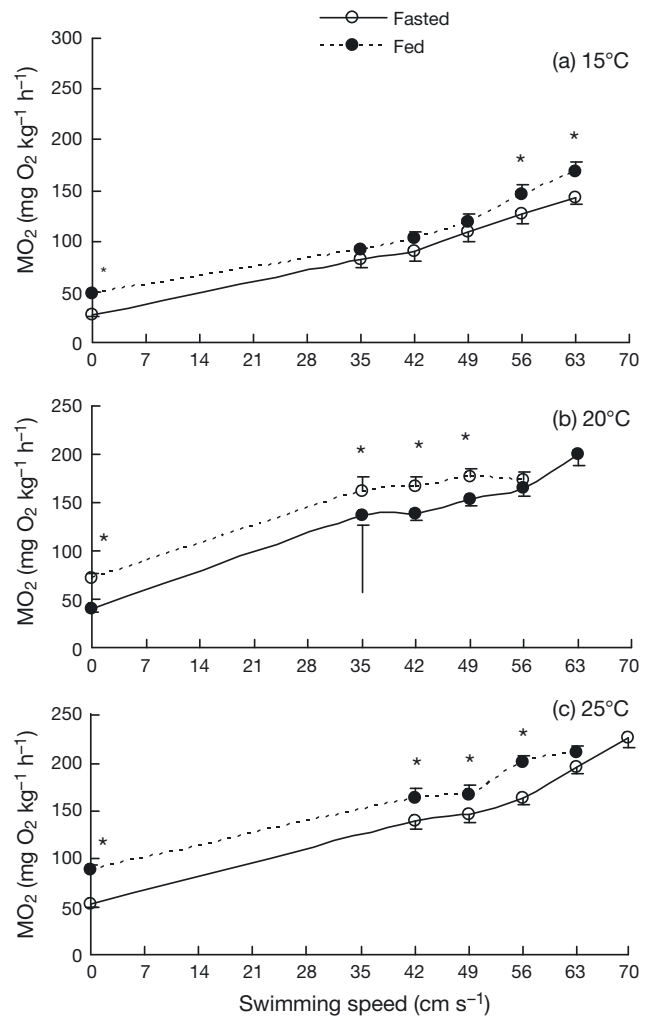


Fig. 2. Effects of digestion on oxygen consumption rate (MO₂) of Chinese bream *Parabramis pekinensis* at progressively increasing water velocities under experimental temperatures of (a) 15°C, (b) 20°C and (c) 25°C. Data are mean ± SE (n = 8). (*) denotes a significant difference (p < 0.05) in MO₂ between fasted and fed fish at a given swimming speed; see Table 1 for information on fish sizes

of digestion or locomotion, Chinese bream demonstrated a similar low digestive performance among the experimental temperatures, whereas the high swimming performance was mostly maintained at the low temperature. This is the reason that swimming performance cannot improve considerably as the temperature increases—swimming performance is more conservative at low temperatures. This is in agreement with a previous study that documented that Chinese bream gill morphology remained unchanged at low temperatures, while it (and hence the respiratory capacity) was reduced in other cyprinids (Chen 2011). In addition, while the glycogen recruitment and lactate clearance capacity decreased

at low temperatures in crucian carp, Chinese bream demonstrated unusually higher glycogen recruitment and lactate clearance capacities at low temperatures (He et al. 2014).

Effect of digestion

We found no difference in U_{crit} between fasted and fed fish at 15°C; the active MO_2 of fed fish was higher than that of fasted fish, and the digestion-elicited MO_2 increase can be added to swimming MO_2 total until the U_{crit} is reached. These results indicate that at low temperature, digestion and locomotion can be performed independently, i.e. Chinese bream exhibit an additive mode at low temperatures. This characteristic may due to a high oxygen uptake capacity resulting from a lack of down-regulation of gill morphology (Chen 2011), high tissue metabolite recruitment (He et al. 2014), low digestive performance, and high environmental oxygen availability at low temperatures. This agrees with all 3 cyprinids and southern catfish measured at 15°C (Pang et al. 2010, 2011). However, cold-water fish species, low temperature-acclimated Chinook salmon (10°C), and rainbow trout (15°C) all showed a digestion-priority mode (Alsop & Wood 1997, Thorarensen & Farrell 2006).

With increased temperature, both the resting MO_2 of fed fish and the active MO_2 of fasted fish increased, whereas the active MO_2 of fed fish showed no increase. Thus, the oxygen uptake capacity (as indicated by the postprandial active MO_2), and hence metabolic supply, is not enough to balance the oxygen demand during postprandial locomotion. One physiological function must be sacrificed to the other to some extent at a higher temperatures; as previously demonstrated in southern catfish, qingbo, and goldfish (Pang et al. 2010, 2011). It has been suggested that for fish with a high digestive performance (e.g. southern catfish and goldfish), locomotion would yield priority to digestion, while for fish with high locomotive performance, digestion would give way to locomotion as competition between digestion and locomotion becomes severe (Pang et al. 2011). However, contrary to our expectation, locomotion was sacrificed to digestion at the higher temperatures in Chinese bream, as U_{crit} decreased by 12 and 11% at 20 and 25°C experimental temperatures, respectively. This finding may be related to some conservative morphological or physiological characteristics showing genetic constraints.

For some fish species, once nutrients from food have reached the digestive tissues, the metabolic processes

cannot be turned off, while other fish can regulate their physiological process by shifting oxygen delivery, metabolic fuel and/or waste products via blood flood (Alsop & Wood 1997, Altimiras et al. 2008). Furthermore, because none of the previous investigations of metabolic mode (including this study) measured the digestive performance (e.g. evacuation rate) during swimming, it is possible that digestion does yield its priority to locomotion. At 20 and 25°C, the MO_2 of both the fed and fasted fish showed no significant difference at 56 and 63 $cm\ s^{-1}$, suggesting that the digestion-induced MO_2 increment also decreased at high swimming speeds. A previous study on goldfish suggested that decreased swimming efficiency is a result of physiological and/or morphological changes in postprandial fish rather than a competition for oxygen supply, which resulted in the decreased U_{crit} during digestion (Fu et al. 2013). Nevertheless, because Chinese bream are capable of high swimming speeds, a decrease in U_{crit} of 11 or 12% may not have significant negative ecological consequences.

Concluding remarks

The physiological priority, and hence the metabolic mode, may be shaped during long-term evolution depending on the costs and benefits of maintaining either locomotion or digestion during postprandial swimming, which varies profoundly among species and environmental conditions. In this study, Chinese bream demonstrated a higher swimming performance but lower digestive capacity compared to most of other cyprinids. This species maintained most of its swimming performance but demonstrated very little digestive capacity at low temperatures. Thus, the feeding metabolism increased more profoundly than active MO_2 and U_{crit} as the temperature rose. The feeding metabolism was added to the swimming MO_2 up to the U_{crit} at 15°C, suggesting an additive metabolic mode, possibly due to low digestive and locomotive capacity but high oxygen availability at lower temperatures. However, feeding metabolism can only add to swimming MO_2 at low swimming speeds, and fed fish showed a significantly low U_{crit} . This suggests a digestion-priority mode, possibly due to the enhanced competition between digestion and locomotion for oxygen at high temperatures.

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