The effects of meal size on postprandial metabolic response and post-exercise metabolic recovery process in juvenile black carp (*Mylopharyngodon piceus*)

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The effects of meal size on postprandial metabolic response and post-exercise metabolic recovery process in juvenile black carp (*Mylopharyngodon piceus*)

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**ABSTRACT**

The effects of meal size on the postprandial metabolic response and of digestion on the post-exercise metabolic recovery process were investigated in juvenile black carp (*Mylopharyngodon piceus*). Experimental fish were forcibly fed with compound feed (meal sizes: 0.5%, 1% and 2% body weight). Then, the postprandial oxygen consumption rate and excess post-exercise oxygen consumption (EPOC) of the experimental fish were measured. Both the duration and the peak of oxygen consumption rate (PMR) increased with increasing meal size. The peak post-exercise metabolic rate of digesting fish were significantly higher, whereas EPOC magnitude and its duration were significantly smaller or (shorter) than those in the fasting fish. It is suggested that (1) this fish fulfills the increased energy demand during the digestive process by increasing PMR and by prolonging SDA duration with increasing meal size and (2) digesting fish might decrease their anaerobic exhaustive activity but increase the post-exercise recovery capacity.

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**KEYWORDS**

Meal size; specific dynamic action; excess post-exercise oxygen consumption; *Mylopharyngodon piceus*

**Introduction**

The increased metabolic expenditure due to feeding is commonly referred to as specific dynamic action (SDA), which represents the total energy used for food capture, handling, ingestion, digestion, absorption and assimilation of a meal, as well as protein synthesis and deposition, in animals (Jobling 1981; McCue 2006; Secor 2009). Many studies have revealed that SDA in fish is heavily influenced by a variety of factors such as body size (Hunt Von Herbing and White 2002; Luo and Xie 2008), dietary composition (Fu et al. 2005a; Luo and Xie 2008), temperature (Vanella et al. 2010; Pang et al. 2011), dissolved oxygen content (Jordan and Steffensen 2007; Zhang et al. 2010), exercise training (Li et al. 2013, 2016a) and meal size (Fu et al. 2005b, 2006; Wang et al. 2012). With increasing meal size, an elevated peak of oxygen consumption rate ($O_2$), a prolonged SDA duration and an increase in energy expended on SDA were
often found in fish (Fu et al. 2005b, 2006; McCue 2006; Wang et al. 2012). However, there is no general consensus on the effects of meal size on the SDA coefficient of fish (Secor and Diamond 1997; Secor and Faulkner 2002; Fu et al. 2005b; Li et al. 2009; Wang et al. 2012). Now it is widely accepted that the postprandial metabolic responses to the change in meal sizes may be related to the feeding habits of animal species (Secor 2001; Fu et al. 2009a). Therefore, more data regarding the effect of meal size on SDA in species of fish with different foraging strategies, such as frequently foraging cyprinid fish, could provide practical information for applications to fish culture (Li et al. 2012b).

Exhaustive exercise often occurs during food acquisition, predator avoidance and passing through the waterfall during fish migration and involves short bouts of high intensity swimming that is primarily powered by white muscle fibers and supported by anaerobic metabolism in fish (Milligan 1996; Kieffer 2000). ‘Excess post-exercise oxygen consumption’ (EPOC) refers to the increased O₂ following exhaustive exercise in animals (Gaesser and Brooks 1984; Lee et al. 2003a). The magnitude of EPOC is the index used most widely by researchers to evaluate the anaerobic metabolic capacity (Fu et al. 2007, 2009b; Li et al. 2012b). The peak post-exercise O₂ following exhaustive exercise might be limited by aerobic metabolic capacity and has been employed for the purpose of measuring maximum metabolic rate (MMR) for some fish species (Gaesser and Brooks 1984; Fu et al. 2009b; Zeng et al. 2010; Li et al. 2013). The duration of EPOC is also of great ecological significance and might influence the survival rate of animals due to the recovery time following exhaustive exercise being closely related to the frequency and the intensity of the next exercise (Milligan 1996; Lee et al. 2003a,b). Thus, the investigation of post-exercise recovery processes, such as EPOC, may provide useful information for fish culture applications and understanding fish physiology as well.

Under natural conditions, fishes (especially those frequently foraging species) often need to perform multiple tasks at the same time and undertake different activities simultaneously, such as digestion and exercise (Hicks and Bennett 2004; Thorarensen and Farrell 2006). Plenty of studies have revealed that feeding has a significant effect on steady swimming performance and aerobic metabolic capacity in fish when the two physiological functions occur simultaneously (Alsop and Wood 1997; Li et al. 2010a, 2010b; Nie et al. 2017a). However, little information is available on the interaction between the post-exercise recovery process (i.e. EPOC) and the digestion in fish (Fu et al. 2009b; Li et al. 2012a, 2012b). Whether changes in metabolic recovery processes during digestion have significant fitness outcomes for fish is unclear, and hence, more data regarding the anaerobic capacities of postprandial fishes with different foraging habits are needed.

In this study, juvenile black carp (Mylopharyngodon piceus), a warm-water and frequent-foraging cyprinid fish species, was selected as the experimental animal because it is widely distributed in the middle and upper reaches of the Yangtze River and is one of the four most important cultured fish species in Chinese aquaculture history (the four major Chinese carp) (Ding 1994; Liu et al. 2004). So far, the SDA and EPOC in juvenile M. piceus have not been explored. The aims of this study are to (1) investigate whether meal size has effects on postprandial metabolic response and (2) test whether feeding has a significant effect on post-exercise metabolic recovery process in juvenile M. piceus.
Materials and methods

Experimental animals

Juvenile *M. piceus* (Cypriniformes: Cyprinidae) were taken from a local fisheries hatchery in Beibei, Chongqing, China. Prior to the experiment, the fish were acclimated for four weeks in a laboratory cement pit system (180 cm × 120 cm × 60 cm) with recirculating water. During the acclimation period, the dechlorinated freshwater temperature of the system was maintained at 25.0 ± 0.5°C, and the oxygen content was kept above 7 mg L⁻¹ by using an airpump. Fish were fed to satiation twice daily, at 09:00 and 18:00, on a commercial diet (Tongwei, China) (composition: 41.2 ± 0.9% protein; 8.5 ± 0.5% lipid; 25.7 ± 1.2% carbohydrate and 12.3 ± 0.4% ash) under constant light.

Measurement of O₂

The O₂ of the fish was measured by using a continuous-flow respirometer with 15 chambers (see the structure in Fu et al. 2005a). The following formula was used to calculate the O₂ (mg O₂ kg⁻¹ h⁻¹):

\[ O₂ = \frac{\Delta O₂ \times v}{m} \] (1)

in which \( \Delta O₂ \) is the difference in oxygen concentration (mg O₂ L⁻¹) between the experimental chamber and the control chamber (chamber without fish), \( v \) is the rate of water flow in the 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 using an oximeter (HQ30d, Hach Company, Loveland, CO, USA). The flow rate of water through the respirometer chamber was measured by collecting the water that was expelled from each chamber. The flow rate of each chamber was adjusted to assure 70% saturation of the dissolved oxygen in the water exiting the chamber to avoid undue stress on the physiology of the fish (Blaikie and Kerr 1996; Fu et al. 2005a). All of the experiments were conducted under constant light to minimize the effect of the circadian rhythm on O₂ (Blaikie and Kerr 1996; Fu et al. 2005a; Li et al. 2013).

Experimental procedures or protocols

Effect of gavage treatment on the O₂

A gavage protocol (see the details in Li et al. 2013) was performed because the fish did not eat food voluntarily in the respirometer chamber. To evaluate the effect of gavage treatment on the O₂ in juvenile *M. piceus*, 12 fish of similar size (8.42 ± 0.31 g) were randomly divided into two groups (ungavaged group and sham-gavaged group, 6 fish in each group). All the experimental fish were transferred into the respirometer chamber after 24 h of fasting and allowed to acclimate for another 48 h. Fish from the sham-gavaged group were gently removed from the respirometer chamber and anesthetized (neutralized MS222, 50 mg L⁻¹) for approximately 2 to 3 min in a small container until they lost normal reflexes. The tip of a syringe (1 mL) without a needle was then inserted into the proximal intestine. However, no food was injected into the proximal intestine of the fish in the sham-gavaged group. The fish were subsequently returned to the
continuous-flow respirometer chamber. The fish in the ungavaged group were not subjected to the procedure. The O$_2$ was measured at 2-h intervals for 18 h.

**Effect of meal size on the postprandial O$_2$ response**

To investigate the effect of the meal size on the postprandial O$_2$ response in juvenile *M. piceus*, 24 fish of similar size (8.27 ± 0.35 g) were randomly divided into 0.5%, 1.0% and 2.0% (2.0% body mass was the maximum meal size for voluntary feeding during acclimation) relative meal size groups (8 fish in each group). All the experimental fish were transferred into the respirometer chamber after 24 h of fasting and allowed to acclimate for another 48 h. O$_2$ was measured 3 times in 2-h intervals before treatment and the means were defined as the resting metabolic rate (RMR) (Fu et al. 2005b; Li et al. 2010b). All fish were gently removed from the respirometer chamber, and a gavage treatment was performed (see above). Compound feed at a relative meal size of 0.5, 1.0 and 2.0% body mass (pellet feed diluted at a ratio of 1:1.5 with water) was injected into the proximal intestine of fish in different meal size groups in a 1-min period. The fish were subsequently returned to the continuous-flow respirometer chamber. O$_2$ values of all experimental fish were measured at 2-h intervals for 18 h at the same day.

We quantified the following parameters for the description of SDA: (1) RMR, the mean of three O$_2$ values before force-feeding; (2) the peak O$_2$ (PMR), which is defined as the maximum observed O$_2$ uptake rate in the SDA process; (3) the time to peak metabolic rate, which is calculated as the time post-feeding when O$_2$ was at PMR; (4) the factorial metabolic scope, which is calculated as the PMR divided by RMR; (5) the duration, which is calculated as the time from feeding to when O$_2$ returned to within the standard error of the RMR of a given fish; (6) the energy expended during SDA, which is calculated as the total O$_2$ above RMR during the duration of SDA; and (7) the SDA coefficient (%), which is the energy expended on SDA and quantified as a percentage of the energy content of the compound feed (7.07 kJ g$^{-1}$). The oxygen consumption was converted to energy using a conversion factor of 13.54 J (mg O$_2$)$^{-1}$.

**Effect of feeding on EPOC**

The EPOCs were measured at relative meal sizes of 0% (fasting group) and 2.0% (feeding group) body mass in juvenile *M. piceus* (8.62 ± 0.46 g). After 24 h of fasting, seven fish in each group were placed in the respirometer chamber and allowed to acclimate for another 48 h. Then, the fish in the fasting group underwent a sham-gavage treatment and the fish in the feeding group were forcedly fed (gavage) with approximately 2.0% body mass (maximum meal size) of meal-sized compound feed. From the experiment on the postprandial O$_2$ response detailed above, we found that the maximal postprandial O$_2$ was achieved at 3 h in the 2.0% relative meal size group. The pre-exercise O$_2$ was measured 3 h post-feeding in the fasting and the feeding groups when each fish achieved its peak postprandial O$_2$ according to the data obtained from the above experiment. Afterwards, the individual fish was gently removed from the respirometer chamber and exercised by manual chasing for 1–2 min to an exhausted state in a circular container (73 cm in diameter, with a water velocity of approximately 65 cm s$^{-1}$) (Wood 1991; Wilkie et al. 2001; Fu et al. 2009b). After being chased, the fish
were placed immediately back to the respirometer chamber. The measured flow rate was approximately 0.4 L min⁻¹, with a 99% exchange of water achieved within 1 min in the 0.08-L chamber (Steffensen 1989). O₂ values were measured at 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55 and 60 min post-exercise.

We quantified the following parameters for the description of EPOC: (1) Pre-exercise metabolic rate (mg O₂ h⁻¹ kg⁻¹): oxygen consumption before exercise; (2) Peak post-exercise metabolic rate (mg O₂ h⁻¹ kg⁻¹): the observed maximum oxygen consumption during the exercise recovery process; (3) Change in metabolic rate (mg O₂ h⁻¹ kg⁻¹): the difference between peak post-exercise metabolic rate and pre-exercise metabolic rate; (4) Time to peak post-exercise metabolic rate (min): the time post-exercise when the O₂ was at peak post-exercise metabolic rate; (5) Duration (min): time from exercise to when post-exercise O₂ was not significantly different from pre-exercise O₂; (6) EPOC magnitude (mg O₂ kg⁻¹): the excess oxygen consumption above the pre-exercise O₂ during the recovery process.

Statistical analysis

Excel (Microsoft office 2003) and SPSS 17.0 were used for data analysis. Values were expressed as the mean ± SE, and P < 0.05 was used as the level of statistical significance. The effect of the gavage procedure (between ungavaged and sham gavaged groups) on O₂ within each time point, the effect of feeding (between fasting and feeding groups) on the variables of excess post-exercise oxygen consumption and the differences between pre-exercise metabolic rates and peak post-exercise metabolic rates were assessed using the two independent sample t-test. The effects of meal size on the variables of postprandial metabolic response were assessed through a one-way analysis of variance (ANOVA). ANOVA was followed by a least-significant-difference multiple-comparison test when appropriate.

Results

Gavage treatment

There were no significant differences in the O₂ within each time point between the ungavaged and sham-gavaged groups (Figure 1). These results suggest that the gavage treatment has no significant effects on the measurement of the O₂ in juvenile *M. piceus*.

Postprandial O₂ response

Neither body mass nor RMR differed significantly among the three meal size groups at the beginning of the experiment (Table 1). The postprandial O₂ of fish in the three meal size groups increased immediately after feeding and then slowly returned to pre-fed levels (Figure 2). The duration increased markedly from 5.57 to 13.50 h when the relative meal size increased from 0.5% to 2.0% in this experiment (Table 1) (F₂,₂₃ = 14.973; P < 0.001). There were no significant differences in the time to PMR among the three meal size groups (Table 1). The 2.0% relative meal
size group showed significantly higher PMR and factorial metabolic scope compared to the 0.5% relative group (P < 0.05), whereas the PMR and the factorial metabolic scope of the 1.0% relative meal size group were not significantly different from the other two groups. Energy expended on SDA markedly increased (from 2.05 to 8.83 kJ kg\(^{-1}\)) as relative meal size increased from 0.5% to 2.0% (\(F_{2, 23} = 15.826; P < 0.001\)). However, the SDA coefficient was not significantly different among the three meal size groups (Table 1).

**Epoc**

There were no significant differences in body mass between the fasting and the feeding groups (Table 2). \(O_2\) immediately increased after exhaustive exercise and returned to the pre-exercise level in both the fasting and the feeding groups (Figure 3). The fish in the feeding group showed significantly higher pre-exercise metabolic rates, peak post-exercise metabolic rates and increment of metabolic

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**Table 1.** Effect of meal size on several variables of postprandial metabolic response in juvenile *Mylopharyngodon piceus* (mean± S.E.).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>0.5</th>
<th>1.0</th>
<th>2.0</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>F(_{2, 23}) = 0.007; P = 0.993</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>8.24 ± 0.42</td>
<td>8.26 ± 0.38</td>
<td>8.31 ± 0.52</td>
<td>F(_{2, 23}) = 0.007; P = 0.993</td>
</tr>
<tr>
<td>RMR (mgO(_2) kg(^{-1}) h(^{-1}))</td>
<td>208.55 ± 4.86</td>
<td>205.11 ± 9.89</td>
<td>194.01 ± 6.60</td>
<td>F(_{2, 23}) = 1.049; P = 0.368</td>
</tr>
<tr>
<td>Meal size (% body mass)</td>
<td>0.50 ± 0.00(^a)</td>
<td>1.02 ± 0.01(^b)</td>
<td>2.00 ± 0.01(^a)</td>
<td>F(_{2, 23}) = 17,337.811; P &lt; 0.001</td>
</tr>
<tr>
<td>Energy ingested (kJ kg(^{-1}))</td>
<td>35.09 ± 0.18(^b)</td>
<td>72.19 ± 0.54(^a)</td>
<td>141.51 ± 0.43(^a)</td>
<td>F(_{2, 23}) = 17,337.798; P &lt; 0.001</td>
</tr>
<tr>
<td>Duration (h)</td>
<td>5.75 ± 0.80(^b)</td>
<td>9.25 ± 1.30(^b)</td>
<td>13.50 ± 0.82(^b)</td>
<td>F(_{2, 23}) = 14.973; P &lt; 0.001</td>
</tr>
<tr>
<td>Time to peak metabolic rate (h)</td>
<td>2.25 ± 0.25</td>
<td>3.00 ± 0.53</td>
<td>3.00 ± 0.53</td>
<td>F(_{2, 23}) = 0.887; P = 0.427</td>
</tr>
<tr>
<td>PMR (mgO(_2) kg(^{-1}) h(^{-1}))</td>
<td>257.52 ± 4.70(^b)</td>
<td>274.01 ± 8.39(^a)</td>
<td>282.89 ± 7.83(^a)</td>
<td>F(_{2, 23}) = 3.714; P = 0.042</td>
</tr>
<tr>
<td>Factorial metabolic scope</td>
<td>1.24 ± 0.04(^b)</td>
<td>1.35 ± 0.05(^a)</td>
<td>1.46 ± 0.04(^a)</td>
<td>F(_{2, 23}) = 6.188; P = 0.008</td>
</tr>
<tr>
<td>Energy expended on SDA (kJ kg(^{-1}))</td>
<td>2.05 ± 0.60(^b)</td>
<td>4.04 ± 0.67(^a)</td>
<td>8.83 ± 1.21(^a)</td>
<td>F(_{2, 23}) = 15.826; P &lt; 0.001</td>
</tr>
<tr>
<td>SDA coefficient (%)</td>
<td>5.87 ± 1.74</td>
<td>5.58 ± 0.91</td>
<td>6.24 ± 0.78</td>
<td>F(_{2, 23}) = 0.071; P = 0.932</td>
</tr>
</tbody>
</table>

Note: Values in each row without a common superscript indicate a significant difference (P < 0.05).
rates than those in the fasting group ($T_{12} = 4.387, 4.315$ and $2.476; P = 0.001, 0.001$ and $0.029$) (Table 2). There were no significant differences in the time to peak post-exercise metabolic rate between the fasting and the feeding groups. However, the duration was much shorter in the feeding group than in the fasting group. The EPOC magnitude of the feeding group was significantly lower than that of the fasting group ($T_{12} = -3.817; P = 0.002$) (Table 2).

**Discussion**

**Effect of meal size on the postprandial O$_2$ response for juvenile M. piceus**

In this study, as relative meal size increased from 0.5% to 2%, both duration and PMR showed a gradual increase (from 5.75 h and 257.52 mgO$_2$ kg$^{-1}$ h$^{-1}$ to 13.50 h and 282.89 mgO$_2$ kg$^{-1}$ h$^{-1}$, respectively) in juvenile *M. piceus*. This result is in agreement with those of most published studies; fish usually fulfill the increased energy requirement during the
digestive process by means of a prolonged SDA and/(or) increased PMR with an increase in meal size (Jobling 1981; Fu et al. 2005b, 2006). However, with the increase in meal size and a corresponding increase in the energy requirement, whether duration or PMR changes more profoundly is closely related to fish species with different feeding habits (Fu et al. 2005b; Li et al. 2012b). For example, sit-and-wait carnivorous southern catfish (*Silurus meridionalis*) and Chinese catfish (*Silurus asotus*), exhibited significant increases both in PMR and in the duration of SDA with the increase in meal size (Fu et al. 2005b, 2006). Such strategy might favor a rapid digesting process and hence higher consumption and growth rates. On the other hand, Pang et al. (2009) found that an active omnivorous crucian carp (*Carassius auratus*) showed profoundly increased PMR but an unchanged duration of SDA with the increase of the meal size. The researchers believed that the digesting strategy was conducive to rapid digestion and absorption after feeding to prepare for re-feeding (Pang et al. 2009). Different from the above two strategies, however, the omnivorous rock carp (*Procypris rabaudi*) displayed an increased duration of SDA but an unchanged PMR when the meal size increased, which suggested that digesting process is slower in this fish species (Li et al. 2012b). Interestingly, in this study, both duration and PMR showed a gradual increase in juvenile *M. piceus* with the increase of the meal size. Such postprandial metabolic response to meal size might be beneficial for a rapid digesting process and hence a higher growth rate in this fish. Similar results have been found in juvenile darkbarbel catfish (*Pelteobagrus vachelli*) and snakeheads (*Channa argus*) in which these fishes exhibited increased PMR and duration of SDA with the increase in meal size (Li et al. 2009; Wang et al. 2012).

**Figure 3.** Excess post-exercise oxygen consumption (EPOC) response in fasting and feeding *Mylopharyngodon piceus* (mean± SE). The dashed lines denote pre-exercise metabolic rates of the fasting group and the feeding group.
In this study, the SDA coefficient of juvenile *M. piceus* was approximately 5–6%, which is lower compared to the results of other fishes, which usually range from 5% to 25% (Tandler and Beamish 1980; Ross et al. 1992; Fu et al. 2005b, 2006; Secor 2009; Li et al. 2012b). The low SDA coefficient in juvenile *M. piceus* may be related to the meal type used in this study. Indeed, formulated diets are easier to digest than natural foods, such as fish and krill. Similar to most studies on fishes, the meal size did not have a significant effect on the SDA coefficient for juvenile *M. piceus*. This is because the energy expended during SDA is linearly correlated with the relative size of the meal and thus the SDA coefficient of fish does not usually vary with meal size (Beamish, 1974; Tandler and Beamish 1980; Chakrabarty et al. 1992; Ross et al. 1992; Fu et al. 2005b; Li et al. 2012b). However, several studies on fishes have found that the SDA coefficients of smaller meal size groups are significantly greater than some of the larger meal size groups because the start-up costs of processing a meal are considerably large, which has a profound effect on total energy expenditure, especially after a small meal (Boyce and Clarke 1997; Robertson et al. 2002; Fu et al. 2006; Wang et al. 2012).

**Effect of feeding on post-exercise metabolic recovery for juvenile *M. piceus***

In this study, the peak post-exercise metabolic rate and the change in metabolic rate for juvenile *M. piceus* were 541.43 mgO$_2$ kg$^{-1}$ h$^{-1}$ and 362.31 mgO$_2$ kg$^{-1}$ h$^{-1}$, respectively, which are lower than those of active crucian carp (1053 mgO$_2$ kg$^{-1}$ h$^{-1}$ and 802 mgO$_2$ kg$^{-1}$ h$^{-1}$, respectively) and grass carp (1032 mgO$_2$ kg$^{-1}$ h$^{-1}$ and 841 mgO$_2$ kg$^{-1}$ h$^{-1}$, respectively), but higher than those of sit-and-wait southern catfish (354 mgO$_2$ kg$^{-1}$ h$^{-1}$ and 234 mgO$_2$ kg$^{-1}$ h$^{-1}$, respectively) (Fu et al. 2009b). This result is reasonable since the PMR is usually limited by aerobic metabolic capacity, which is usually higher in active fish species than in sluggish sedentary species. The higher peak post-exercise metabolic rates and the larger O$_2$ increments of cyprinid fish species are helpful to a quick recovery process and hence are associated with the frequent feeding habits and predator escape capacities in active fish species. The moderate post-exercise metabolic response compared to other cyprinid fish species is expected based on the foraging mode of this fish species (i.e. a benthic carnivorous fish species feeding on mollusks such as screws which are all with poor locomotor performance).

Theoretically, animals have a potential maximum metabolic ceiling (i.e. MMR) due to the limitations of their cardio-respiratory systems (Peterson et al. 1990; Weiner 1993; Hammond et al. 2000). The MMR could be elicited individually by locomotion or under a postprandial swimming situation in fishes (Cutts et al. 2002; Fu et al. 2009b; Li et al. 2010a; b). For example, studies on grass carp and rock carp have found that the peak post-exercise MO$_2$ could use all of the cardio-respiratory capacity in fasting fish, because the digesting and the fasting fish showed similar peak post-exercise O$_2$ values, which are similar to the maximal metabolic rates during critical swimming speed (Fu et al. 2009b; Li et al. 2012b). However, in this study, the peak post-exercise O$_2$ elicited by exhaustive exercise in feeding fish was significantly greater than that of fasting fish and PMR for juvenile *M. piceus*. This is similar to such fish species as southern catfish, Chinese catfish, and crucian carp (Fu et al. 2009b; Li et al. 2012b). Additionally, the peak post-exercise O$_2$ (approximately 758 mg O$_2$ kg$^{-1}$ h$^{-1}$) for the fish of the feeding group after exhaustive exercise was lower than a value of maximal O$_2$ (approximately 1100 mg O$_2$ kg$^{-1}$ h$^{-1}$ in a
previous study) elicited by a test of critical swimming speed in feeding *M. piceus* (Nie and Fu 2017b). These results indicate that neither digestive processes, post-exhaustive exercise metabolic recovery processes, nor both together could use the entire aerobic metabolic scope of this fish. More interestingly, the peak post-exercise O$_2$ and the absolute change in digesting fish were higher than those of fasting fish, which is contrary to our expectations and has never been documented in fish species before. The reason for the up-regulation of post-exercise recovery capacity in digesting fish might be a quick recovery (as suggested by a much shorter duration in digesting fishes than in fasting ones), since the resumption of metabolic capacity would be helpful to survival in a natural setting.

Several previous studies have found that the postprandial EPOC magnitude was not significantly different between fasting and feeding groups in fishes such as grass carp and rock carp (Fu et al. 2009b; Li et al. 2012b). The maintenance of anaerobic metabolism during digestion might be crucial for active foraging modes and anti-predation strategies for these fish species of low trophic levels. In this study, the EPOC magnitude and duration were profoundly decreased after feeding in juvenile *M. piceus* with lower digestive capacity, which suggests that the digestion process reduces the anaerobic capacity of exercise. This process has been found previously in southern catfish, Chinese catfish and crucian carp (Fu et al. 2009b; Li et al. 2012a). The differences between fish species might be due to the digestive performance among different fish species and needs further investigation.

In conclusion, meal size has a significant effect on the postprandial metabolic responses of juvenile *M. piceus*, as both PMR and the duration of SDA increased with the increase of the meal size. Neither digestive processes, exhaustive exercise recovery processes, nor both together can occupy all of the aerobic capacity of this fish, which might be related to the low activity habits of juvenile *M. piceus*. Digesting fish showed lower EPOC magnitudes but higher changes in post-exercise metabolic rates and shorter durations, indicating a down-regulated anaerobic capacity paralleled with the up-regulated post-exercise recovery processes, which might be helpful to quick recovery times that result in more metabolic scope being available while digesting, since digestion occupies some aerobic scope.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

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Ethical approval

This study complied with the current law of the country in which it was performed and was approved by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (permit number Zhao-20,151,010-01). The study was performed in strict accordance with the recommendations in the Guide for the Care and Use of Animals at the Key Laboratory of Animal Biology of Chongqing, China. All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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