

## The behavioural, digestive and metabolic characteristics of fishes with different foraging strategies

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### SUMMARY

To test the hypothesis that digestion has a more notable physiological effect on ambush foragers than on active foragers, we investigated the behavioural, digestive and metabolic characteristics, as well as the postprandial locomotory capacity, of four species of juvenile fish distributed along the Yangtze River, China, with distinct foraging strategies. The ambush foraging southern catfish (*Silurus meridionlis*) had the fewest movements per minute (MPM), lowest per cent time spent moving (PTM), slowest critical swimming speed ( $U_{crit}$ ), lowest maintenance metabolism ( $\dot{V}_{O_{2rest}}$ ) and lowest maximum locomotory metabolism ( $\dot{V}_{O_{2max}}$ ). However, the southern catfish had the highest feeding level and maximum feeding metabolism ( $\dot{V}_{O_{2peak}}$ ) and the greatest decrease in  $U_{crit}$  after consumption of a large meal. Thus, this fish is highly adapted to its ambush behavioural strategy and sedentary life style. In the herbivorous grass carp (*Ctenopharyngodon idellus*), a low digestive capacity led to little change in postprandial locomotory performance, which benefits its frequent grazing behaviour. In this species, the greater amount of energy spent on routine activity and avoiding predators versus  $U_{crit}$  might be related to its herbivorous life style and high predation risk. The active foraging crucian carp (*Carassius auratus*) adopts a unique high energy cost strategy that allows for high capacity in both routine activity and digestion, and the great flexibility of its cardio-respiratory capacity (increased  $\dot{V}_{O_{2max}}$  after feeding) guarantees a small decrease in  $U_{crit}$  even after maximum feeding. Finally, the sluggish foraging darkbarbel catfish (*Pelteobagrus vachelli*) has low digestive and locomotory capacity, but its energy-efficient venomous defence strategy may be related to its abundance. These results show that the digestive, behavioural and metabolic strategies differ among these fish species. The locomotory capacity in the sedentary fishes decreased profoundly after feeding, whereas it decreased little or not at all in the active fishes. The maintenance of high locomotory capacity after eating in the active fishes is probably related to a large metabolic capacity, a lower digestive capacity or an improvement in cardio-respiratory capacity after feeding.

Key words: ambush and active foragers, energy expenditure, feeding metabolism, foraging mode, locomotory capacity, metabolic ceiling.

### INTRODUCTION

Animals can be classified as ambush (i.e. sit-and-wait) foragers, active foragers or herbivores according to their foraging mode (Cooper, 1995). Researchers have suggested that foraging mode might be closely related to an animal's morphological, physiological and ecological characteristics and life-history traits (Huey and Pianka, 1981; Webb et al., 2003). Swimming performance, metabolic characteristics and digestive capacity may also change according to foraging behaviour in fishes and other animals (Perry, 1999; Newland et al., 2004). For example, Secor (Secor, 2001) suggested that the maximum feeding level and feeding metabolism were much higher in some sedentary ambush predators than in active foragers. Others reported that the maximum oxygen consumption rate after feeding ( $\dot{V}_{O_{2peak}}$ ) of some ambush fishes was similar to (or even higher than) maximum aerobic  $\dot{V}_{O_2}$  ( $\dot{V}_{O_{2max}}$ ) during maximum sustainable swimming (Priede, 1985; Armstrong et al., 1992; Fu et al., 2005a). However, little has been done to compare the swimming performance, metabolic characteristics and digestive capacity of fishes with different foraging modes. Previous studies on the foraging mode of fishes have focused on swimming efficiency and prey encounter rate of pelagic fishes (Miyasaka and Nakano, 1999; Asaeda et al., 2001), while the sit-and-wait foraging fishes have received little attention. Thus, the first aim of this study was

to determine whether significant differences in routine activity level, swimming performance, metabolic characteristics and digestive capacity exist among fishes with different foraging modes.

Feeding (hence digestion) and locomotion are the two most closely related activities involved in foraging behaviour. Although they differ in many aspects, they share the cardio-respiratory system required to obtain and supply oxygen and substrate (Hicks and Bennett, 2004). The outcome of the competition between these two activities might be different in fishes with distinct foraging modes because postprandial swimming has a different ecological relevance. Sedentary ambush fishes usually consume a large meal and then remain motionless for a long time while digesting, whereas active fishes must continue foraging for prey during digestion. Thus, the capacity for postprandial locomotion should be maintained in active foraging fishes. However, no comparative work exists examining the effect of feeding on locomotion in fishes with different foraging modes. Thus, the second aim of this study was to test whether digestion has different effects on the postprandial locomotory capacity in fishes with distinct foraging modes.

Newlands and colleagues (Newlands et al., 2004) suggested that the energy expenditure and return of various types of foraging behaviour are of importance in determining foraging mode in fishes. Theoretically, the differences in routine activity or locomotory

capacity among fishes with different foraging modes must closely relate to their energetic profiles. The positive relationship between locomotory capacity and metabolism (either resting or maximum metabolism) has long been accepted (Wieser, 1985). However, there is an apparent gap in the understanding of the energy expenditure for maintenance and the metabolic constraints on locomotory and digestive performance in different foraging fishes. Hence, our third aim was to study the metabolic strategy (i.e. metabolic ceiling, energy expenditure for maintenance and relative magnitude of the metabolic scope of digestion and locomotion) used by fishes with different foraging modes.

To address our research objectives, we selected four species of juvenile fish with distinctly different foraging modes: a sit-and-wait carnivorous southern catfish (*Silurus meridionalis*), an active grazing herbivorous grass carp (*Ctenopharyngodon idellus*), a sluggish omnivorous darkbarbel catfish (*Pelteobagrus vachelli*) and an active omnivorous crucian carp (*Carassius auratus*). The first three species are the most abundant species with their respective foraging mode in the Yangtze River (Ding, 1994). The crucian carp is a highly adaptable species with a wide distribution throughout the world, including the Yangtze River. We measured the number of movements per minute (MPM) and the per cent time spent moving (PTM) to identify foraging mode and demonstrate activity levels; the resting  $\dot{V}_{O_2}$  ( $\dot{V}_{O_{2rest}}$ ) to represent maintenance energy expenditure;  $\dot{V}_{O_{2max}}$  to represent the metabolic ceiling; and the critical swimming speed (maximum sustainable swimming speed,  $U_{crit}$ ) and stamina (duration at a fixed swimming speed) to represent the aerobic and anaerobic swimming capacity, respectively; and the maximum feeding level and the postprandial metabolic response to represent the digestive capacity.

## MATERIALS AND METHODS

### Experimental animals, diets and acclimation

Juvenile southern catfish (*S. meridionalis* Chen; 17.72±0.39 g,  $N=100$ ), crucian carp (*C. auratus* Linnaeus; 6.01±0.15 g,  $N=100$ ), grass carp (*C. idellus* Valenciennes 1844; 8.77±0.17 g,  $N=100$ ) and darkbarbel catfish (*P. vachelli* Richardson 1846; 7.06±0.18 g,  $N=100$ ) were obtained from local fisheries and acclimated in a rearing system for at least 30 days before the experiment. The body size of southern catfish was larger than that of the other three species because of its fast growth rate. Therefore, it was difficult to find experimental animals with a body size similar to that of the other tested species. The dechlorinated fresh water temperature was maintained at 25.0±0.5°C, and the oxygen content was kept above 7 mg l<sup>-1</sup>. During the acclimation period, the crucian carp and the grass carp were fed to satiation with a formulated diet, and the southern catfish and the darkbarbel catfish were fed fillets of freshly killed loach (*Misgurnus anguillicaudatus*) once daily. The chemical composition of the formulated diet was 61.45% moisture, 14.91% protein, 1.62% lipid and 8.70% digestible carbohydrate, resulting in 5.02 kJ g<sup>-1</sup> of bio-available energy. The loach flesh was 78.20% moisture, 15.71% protein, 3.17% lipid and 0.07% digestible carbohydrate, resulting in 4.97 kJ g<sup>-1</sup> of bio-available energy. The dietary bio-available energy was calculated as 23.6 kJ g<sup>-1</sup> protein, 39.5 kJ g<sup>-1</sup> lipid and 17.2 kJ g<sup>-1</sup> starch. Analyses of chemical composition were conducted following standard methods (Association of Official Analytical Chemists, 1995).

### Assessment of foraging mode and routine activity: PTM and MPM

To measure PTM and MPM, 12 fish from each species were transferred to 48 individual observation chambers (120 l) and

acclimatised for 3 days. The chambers were cylindrical unplasticised polyvinyl chloride (UPVC) tanks with lids. Because of the relatively low biomass-to-water volume ratio in the observation chamber (3.95–10.36 g/120 l), the water was partially replenished daily (20%) with slight aeration. Fish were observed through a window on the lid at 09:00, 15:00 and 21:00 h on the fourth day after they were transferred to the observation chamber. Individual fish were observed continuously for 15 min. To compensate for the disturbance of fish by the observer's presence, the first 5 min of each observation was omitted from further analyses. We defined movement as motion of the tail fin. Movement was considered to cease when the tail fin rested for more than 1 s. The tail fin was selected because it concurrently shows motion with any kind of body activity (other than opercular activity) in these four species, and its motion is easy to measure precisely. The following data were recorded: whether the fish showed movement during the whole observation period, total number of movements, and the duration of movement. The total number of movements was recorded by a hand tally counter, and the duration of the movement was recorded by a stopwatch. The PTM (%) and MPM (times min<sup>-1</sup>) were calculated over the entire 10 min observation period.

### Assessment of metabolic strategy: $\dot{V}_{O_{2rest}}$ and $\dot{V}_{O_{2max}}$ of fasting and maximum fed fish

$\dot{V}_{O_2}$  for individual fish was measured using a continuous-flow respirometer (Fu et al., 2005a). The following formula was used to calculate the  $\dot{V}_{O_2}$  (mg O<sub>2</sub> h<sup>-1</sup>) of individual fish:

$$\dot{V}_{O_2} = \Delta O_2 \times v, \quad (1)$$

where  $\Delta O_2$  is the difference (mg O<sub>2</sub> l<sup>-1</sup>) in oxygen concentration between an experimental chamber and the control chamber (chamber without fish) and  $v$  is the water flow rate in the experimental chamber (l h<sup>-1</sup>). To account for variations in oxygen consumption rate due to size differences among the fish,  $\dot{V}_{O_2}$  was adjusted to a standard body mass of 1 kg using a mass exponent of 0.75 (Reidy et al., 2000; Fu et al., 2005a). Standardised  $\dot{V}_{O_2}$  was calculated using the following formula:

$$X_s = (1/m)^{0.75} X_m, \quad (2)$$

where  $X_s$  is the standardised  $\dot{V}_{O_2}$  (mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>),  $X_m$  is the measured  $\dot{V}_{O_2}$  per fish (mg O<sub>2</sub> h<sup>-1</sup>) calculated by Eqn 1, and  $m$  is the body mass of the fish (kg). Dissolved oxygen concentration was measured at the outlet of the chamber by an oxymeter (HQ20, Hach Company, Loveland, CO, USA). The flow rate of water through the respirometer chamber was acquired by measuring water flow for a standardised time period.

Each fish (see Table 2 for sample size) was placed in the respirometer chamber and allowed to acclimate for 1 week before the experiment was conducted. After the fish had been fasted for 48 h, the  $\dot{V}_{O_2}$  was measured four times at 2 h intervals and used as  $\dot{V}_{O_{2rest}}$  (Fu et al., 2005a). The  $\dot{V}_{O_{2max}}$  was measured using the chasing method as described previously (Fu et al., 2006). Briefly, the experimental fish were chased to exhaustion with a hand net in a circular trough (the process usually lasted 3–5 min) and then immediately placed into a respirometer chamber. The water flow rate was about 0.6 l min<sup>-1</sup>, and 99% of the water was replaced within 1 min in the 0.1 l chamber (Steffensen, 1989). The first measurement of oxygen consumption was made 1 min after the fish was placed in the chamber. Maximal oxygen consumption was usually observed

immediately (1–4 min) after the fish was placed in the chamber, but the measurement was continued for 30 min.

#### Assessment of digestive strategy: postprandial $\dot{V}_{O_2}$ responses to different feeding levels

The postprandial  $\dot{V}_{O_2}$  responses were measured using the continuous-flow respirometer at relative feeding levels of 0, 0.5, 1, 2, 4 and 8% body mass in the darkbarbel catfish and 0, 0.5, 1, 2 and 4% body mass in the crucian carp and the grass carp with either fish fillets or the formulated diet. The maximum feeding level was 8% body mass for the darkbarbel catfish and 4% body mass for both carp species. Because in each treatment group only the fish that finished their food in 30 min during the trial were used for the experiment, the number of fish was 6, 7, 7, 6 and 5 in the control, 0.5, 1, 2 and 4% body mass crucian carp groups, respectively, and 8 in all the grass carp and the darkbarbel catfish groups. The effects of feeding level (Fu et al., 2005a), temperature (Luo and Xie, 2008a) and body size (Luo and Xie, 2008b) on postprandial  $\dot{V}_{O_2}$  response in southern catfish were studied extensively in our previous research; therefore, we did not repeat those parts of the experiments in the current study.

The fish were placed in the respirometer chamber and allowed to acclimate for 1 week before the experiment.  $\dot{V}_{O_2}$  was measured after a 48 h fasting period. A prescribed quantity of fish fillet or formulated diet was then offered. Immediately after the fish had completed feeding, the chambers were closed, and the  $\dot{V}_{O_2}$  was measured at 2 h intervals for 12 h for the crucian carp and grass carp, and 36 h for the darkbarbel catfish. The maximum feeding level and duration of the experiment were determined in a pilot experiment. A sample of each diet was collected and dried to a constant mass at 70°C for composition analysis.

#### Assessment of locomotory capacity: $U_{crit}$ and stamina before and after feeding

$U_{crit}$  and stamina were measured using gravity-driven swimming tunnels (Zhang et al., 2007). In brief, a hydraulic pressure was established between the upper holding reservoir and lower receiving tank. The hydraulic pressure was maintained by a fixed vertical height difference between the water levels of the two tanks. The water flow velocity in the swimming tunnels was dictated by parallel variable valves that could independently adjust the resistance and flow of the water entering the swimming tunnels. The inner diameter and the length of the swimming tunnel were 10 cm and 60 cm, respectively. The maximum velocity of the water flow was about 42 cm s<sup>-1</sup>. A honeycomb plate was fixed to either side of the swimming tunnel, helping to reduce turbulence and eddies. The swimming tunnel was situated in a thermally controlled water bath, and the experimental water temperature in the swim chamber was maintained at 25.0±0.5°C in this study.

Before measuring  $U_{crit}$ , the fish were acclimated at 1 body length s<sup>-1</sup> (BL s<sup>-1</sup>) water flow for 1 h. The water velocity was increased at an increment of 1 BL s<sup>-1</sup> every 15 min until the fish ceased swimming. The cessation of swimming was judged by the lack of resumption of swimming activity after the fish was subjected to the sudden change of water velocity between 1 BL s<sup>-1</sup> to the final testing velocity in three trials (failed to move off the rear grid).  $U_{crit}$  values were calculated as in Brett (Brett, 1964):

$$U_{crit} = U_f + (U_i \times t_f / t_i), \quad (3)$$

where  $U_f$  is the water velocity of the last fully completed increment,  $t_f$  is the time spent on the last water velocity increment,  $t_i$  is the

period for each completed water velocity increment (15 min), and  $U_i$  is the water velocity increment (1 BL s<sup>-1</sup>).  $U_{crit}$  was not corrected for the solid blocking effect because the cross-sectional area of the fish did not exceed 5% of that of the swimming tunnel.

After 48 h of fasting, the experimental fish were offered the prescribed diets. Because some fish did not consume their food during the given 30 min or vomited during the experimental process, the sample number in each treatment varied from 4 to 10 (Table 3).  $U_{crit}$  was measured for each fish at a prescribed hour after feeding when the fish had achieved its peak postprandial  $\dot{V}_{O_2}$  at a given feeding level (according to postprandial  $\dot{V}_{O_2}$  response data in this study or previous work) (Fu et al., 2005a; Luo and Xie, 2008a; Luo and Xie, 2008b). The grass carp, crucian carp and darkbarbel catfish were transferred to the swimming tunnel 1 h after feeding. The southern catfish, however, was transferred to a swimming chamber at 3, 5, 10, 12 and 12 h after feeding for the 2, 4, 8, 12 and 20% body mass groups, respectively.  $U_{crit}$  of fasting fish was measured as the control group.

Before stamina was measured, the fish were acclimated at 1 BL s<sup>-1</sup> water flow for 1 h. Then, water velocity gradually increased to 9 BL s<sup>-1</sup> for crucian carp and 6 BL s<sup>-1</sup> for southern catfish at increments of 1 BL s<sup>-1</sup>. The velocity of water flow was determined in a pilot experiment. The stamina test was terminated when the fish failed to move off the rear grid. The stamina was determined as the duration of time between the point when the specific velocity (9 BL s<sup>-1</sup> for the crucian carp and 6 BL s<sup>-1</sup> for the southern catfish) was achieved and the point when the fish ceased swimming. Feeding metabolism is generally considered to be an aerobic process. Thus, anaerobic locomotory capacity, indicated by variables such as anaerobic stamina, is unlikely to be affected by feeding metabolic processes such as digestion. We chose to measure only the stamina in the two extreme species in fasting status and after a maximum meal: the sedentary southern catfish and the active crucian carp were chosen because they have the lowest and highest  $U_{crit}$ , respectively. We predicted that postprandial digestion would have little effect on their anaerobic stamina.

#### Data analysis

We used STATISTICA 4.5 (StatSoft, Singapore) for the data analysis. The hypotheses were tested using ANOVA, followed by *post-hoc* multiple comparisons (least significant difference). *P* values <0.05 were considered statistically significant, and all the data are presented as means ± 1 s.e.m.

## RESULTS

#### Assessment of foraging mode and routine activity: PTM and MPM

Some experimental fish did not show any defined movement during the entire 10 min observation period. Among the 36 observations, in all four tested species, 36/36 crucian carp, 28/36 grass carp, 29/36 darkbarbel catfish and 2/36 southern catfish showed movement. Table 1 shows the PTM and the MPM for the four fish species. Both PTM and MPM showed significant differences among all the fishes tested (*P*<0.05).

#### Assessment of metabolic strategy: $\dot{V}_{O_{2rest}}$ and $\dot{V}_{O_{2max}}$ of fasting and maximum fed fish

The  $\dot{V}_{O_{2rest}}$  of the crucian carp was 24% higher than that of the grass carp (*P*<0.05; Table 2), and the latter was about 30% higher than the values for the darkbarbel catfish and the southern catfish (*P*<0.05). The  $\dot{V}_{O_{2max}}$  values of the crucian carp and the grass carp



Table 1. The number of movements per minute (MPM) and per cent time spent moving (PTM) of experimental fishes at 25°C

Species	Body mass (g)	Number of observations	Number of movements	MPM (min <sup>-1</sup> )	PTM (%)
Crucian carp	8.69±0.47	36	36	54.17±1.39 <sup>a</sup>	83.30±1.97 <sup>a</sup>
Grass carp	7.65±0.23	36	28	12.32±3.87 <sup>b</sup>	30.78±9.11 <sup>b</sup>
Darkbarbel catfish	3.95±0.15	36	29	4.09±2.20 <sup>c</sup>	4.97±2.57 <sup>c</sup>
Southern catfish	10.36±0.58	36	2	0.08±0.06 <sup>d</sup>	0.48±0.32 <sup>d</sup>

*N*=12, means ± s.e.m. Values in each column without a common superscript are significantly different (*P*<0.05).

were about 80% higher than that of the darkbarbel catfish (*P*<0.05), and the latter was 67% higher than that of the southern catfish (*P*<0.05).

#### Assessment of digestive strategy: postprandial $\dot{V}_{O_2}$ response to different feeding levels

The maximum feeding levels were about 4% body mass for the crucian carp and the grass carp and about 8% body mass for the darkbarbel catfish. The postprandial  $\dot{V}_{O_2}$  response was most notable in the crucian carp, which showed the highest  $\dot{V}_{O_{2peak}}$  (173.2 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>, 148% higher than that of  $\dot{V}_{O_{2rest}}$ ) and shortest duration (2–8 h depending on feeding levels; Fig. 1). The postprandial  $\dot{V}_{O_2}$  response was lowest in the grass carp, which also exhibited the lowest  $\dot{V}_{O_{2peak}}$  (83.6 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>, 49% higher than that of  $\dot{V}_{O_{2rest}}$ ) and a relatively short duration (8–10 h). The  $\dot{V}_{O_2}$  response in the darkbarbel catfish was lower than that of the crucian carp, but it exhibited a long duration at the higher feeding level (such as the 4% and 8% body mass, respectively).

Feeding level had a profound effect on  $\dot{V}_{O_2}$  response in all the fishes tested in this study. In the crucian carp,  $\dot{V}_{O_2}$  peaked significantly (*P*<0.05) at 2 h after feeding and returned to the pre-fed level within 6–8 h after feeding depending on feeding level. For the darkbarbel catfish, the postprandial  $\dot{V}_{O_2}$  responses to lower feeding levels (0.5, 1 and 2% body mass) were low and hard to detect. However, both the 4 and 8% body mass groups showed prolonged postprandial  $\dot{V}_{O_2}$  elevation, which was about 70–80% higher than the control level and lasted for about 20 h. The  $\dot{V}_{O_2}$  of all the grass carp groups peaked at 2 h after feeding. The 0.5% body mass and control groups did not return to the pre-fed level. However, the 1, 2 and 4% feeding level groups returned to the pre-fed level within 6–8 h after feeding.

#### Assessment of locomotory capacity: critical swimming speed ( $U_{crit}$ ) and stamina before and after feeding

$U_{crit}$  of the fasting crucian carp was more than 60% higher than the levels found in the grass carp and the darkbarbel catfish, and  $U_{crit}$  of the darkbarbel catfish was more than 50% higher than that of the southern catfish (*P*<0.05, Table 3).  $U_{crit}$  had a tendency to decrease with increased feeding level in all the fish species studied. However, there was no significant change in  $U_{crit}$  in both the grass carp and the darkbarbel catfish. In the southern catfish,  $U_{crit}$  decreased 34% after consumption of the maximum meal, and  $U_{crit}$  values at the maximum feeding level (20%) and the 12% body mass feeding level groups were significantly lower than those of all the other groups (*P*<0.05). There was no significant difference among the other groups of southern catfish. In the crucian carp,  $U_{crit}$  decreased significantly even after consuming at 0.5% feed level (*P*<0.05), but there was no significant difference among the 0.5, 1 and 2% feeding level groups. The maximum meal (4%) elicited a 12% decrease in  $U_{crit}$  compared with the fasting group, which was significantly lower than the  $U_{crit}$  of the control and the 1% feeding levels.

The effect of maximum feeding level on stamina was investigated only in the southern catfish and the crucian carp. The velocity of the water flow was 9 BL s<sup>-1</sup> for the crucian carp (body mass 6.08±0.10 g) and 6 BL s<sup>-1</sup> for the southern catfish (body mass 18.73±0.42 g). The maximum feeding levels were 21.33±1.33% for southern catfish and 4.44±0.00% for the crucian carp. The stamina values of crucian carp fed at the maximum feeding level and without food were 40.77±13.01 s (*N*=9) and 36.27±6.54 s (*N*=7), respectively. The stamina values of the southern catfish fed at the maximum feeding level and without food were 51.00±3.61 s (*N*=9) and 36.13±4.65 s (*N*=6), respectively. There was no significant difference in the stamina

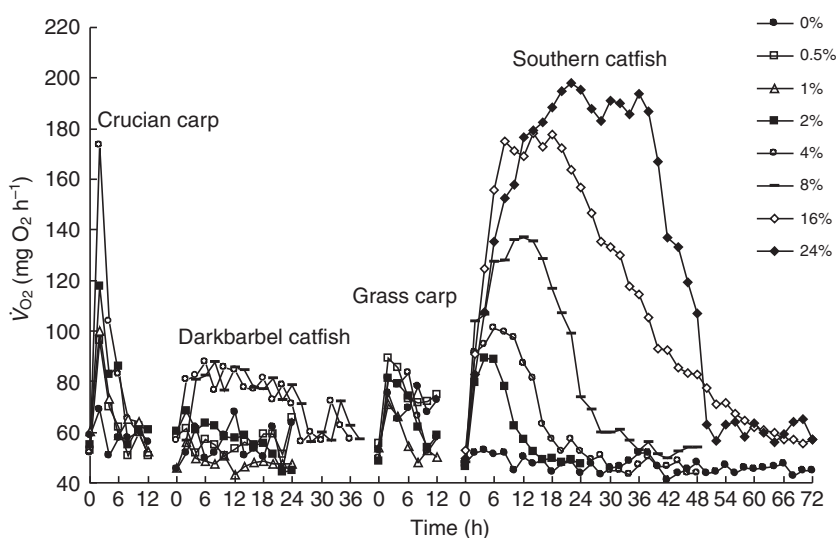


Fig. 1. The postprandial  $\dot{V}_{O_2}$  responses to different feeding levels in the crucian carp, the darkbarbel catfish, the grass carp and the southern catfish. Data on the southern catfish were from Fu et al. (Fu et al., 2005a). Food was consumed at 0 h. The number of fish used was 6, 7, 7, 6 and 5 in the control, 0.5, 1, 2 and 4% body mass crucian carp groups, respectively; 8 in all grass carp and darkbarbel catfish groups; and 6, 6, 6, 9, 3 and 2 in control, 2, 4, 8, 16 and 24% body mass southern catfish groups. The body masses were 5.67±0.16 g, 8.86±0.07 g, 7.05±0.29 g, and 44.12±1.82 g for crucian carp, grass carp, darkbarbel catfish and southern catfish, respectively. The  $\dot{V}_{O_2}$  was adjusted to a standard body mass of 1 kg using a mass exponent of 0.75.

Table 2. The  $\dot{V}_{O_{2rest}}$ , postprandial  $\dot{V}_{O_{2peak}}$  after the maximum meal and  $\dot{V}_{O_{2max}}$  elicited by exercise of the experimental fishes at 25°C

Species	N	Body mass (g)	$\dot{V}_{O_{2rest}}$ (mg O <sub>2</sub> kg <sup>-1</sup> h <sup>-1</sup> )	$\dot{V}_{O_{2peak}}$ (mg O <sub>2</sub> kg <sup>-1</sup> h <sup>-1</sup> )	$\dot{V}_{O_{2max}}$ (mg O <sub>2</sub> kg <sup>-1</sup> h <sup>-1</sup> )
Crucian carp	6	6.06±0.27 <sup>b</sup>	69.8±3.8 <sup>a</sup>	173.2±14.2 <sup>a</sup>	294.3±13.0 <sup>a</sup>
Grass carp	6	7.42±0.26 <sup>b</sup>	56.2±3.2 <sup>b</sup>	83.6±6.9 <sup>b</sup>	303.4±17.3 <sup>a</sup>
Darkbarbel catfish	6	6.03±0.44 <sup>b</sup>	44.0±3.0 <sup>c</sup>	97.2±7.1 <sup>b</sup>	166.5±13.2 <sup>b</sup>
Southern catfish	10	16.46±0.50 <sup>a</sup>	42.2±3.4 <sup>c</sup>	197.9	127.1±8.2 <sup>c</sup>

Means ± s.e.m. for rate of O<sub>2</sub> consumption at rest ( $\dot{V}_{O_{2rest}}$ ), maximum level after feeding ( $\dot{V}_{O_{2peak}}$ ) and maximum aerobic level after exhaustive chasing ( $\dot{V}_{O_{2max}}$ ). Values in each column without a common superscript are significantly different ( $P < 0.05$ ).

of fish between the maximum feeding level and control groups in both the southern catfish and the crucian carp.

### DISCUSSION

The main aims of this study were to test whether digestion has a different effect on the capacity for postprandial locomotion in fishes with different foraging modes, and whether the different effect related to the differences in behavioural, digestive and metabolic strategies that exist among fishes with distinct foraging modes. Fishes selected in this study showed significant differences in routine activity level, swimming performance, metabolic characteristics and digestive capacity. The active omnivorous (crucian carp) and the herbivorous (grass carp) fishes showed higher levels of activity and locomotory capacity, a higher metabolic ceiling and energy expenditure, and a lower feeding level compared with the sluggish (darkbarbel catfish) and the ambush (southern catfish) fishes. The locomotory capacity in the sedentary fish decreased profoundly after feeding, whereas it decreased little or not at all for active fishes. The effect of feeding on locomotory capacity was related not only to the change of postprandial  $\dot{V}_{O_2}$  but also to the special metabolic strategy, in accordance with the competition between digestive and locomotory metabolism (an increase in  $\dot{V}_{O_{2max}}$  and metabolic scope after eating; see below).

Digestion and locomotion are two primary physiological activities that organisms in nature must, to some extent, conduct simultaneously (Bennett and Hicks, 2001). Research on postprandial locomotion has been popular in recent years in both fishes and reptiles (Blaikie and

Kerr, 1996; Alsop and Wood, 1997; Bennett and Hicks, 2001). The present study is the first attempt to explain the change in locomotory capacity that occurs after an animal eats in an ecological context. Theoretically speaking, maintaining the capacity for locomotion is more important in active fishes than in sit-and-wait foragers because the former are more likely to encounter predators and need to be able to avoid capture, and they continue to hunt or graze while still digesting. However, typical active foraging fishes such as rainbow trout (*Oncorhynchus mykiss*) and chinook salmon (*Oncorhynchus tshawytscha*) always appear to prioritise oxygen delivery to meet the needs of digestion over oxygen delivery for postprandial locomotion, as demonstrated by a decrease of  $U_{crit}$  by 9–15% after a meal (Alsop and Wood, 1997; Thorarensen and Farrell, 2006). On the other hand, in the Atlantic cod (*Gadus morhua*), when swimming at a low speed after a moderate size meal, the  $\dot{V}_{O_2}$  of postprandial swimming fish was larger than the sum of  $\dot{V}_{O_2}$  elicited by feeding and swimming alone; i.e. the locomotion and digestion activity can process independently. However, because feeding levels had a significant effect on postprandial  $\dot{V}_{O_2}$  (Jobling 1981; Fu et al., 2005a), whether the additivity model adopted by cod can be maintained after a huge meal needs to be investigated further.

In the present study,  $U_{crit}$  of the sit-and-wait southern catfish did not decrease significantly when it was fed a meal under 8% body mass compared with the fasting fish. However, when the feeding level increased to 20%,  $U_{crit}$  showed a 34% decrease. The value was much larger than all published data about the effect of feeding on  $U_{crit}$  (Alsop and Wood, 1997; Thorarensen and Farrell, 2006). The

Table 3. Effect of feeding level (%) on critical swimming speed ( $U_{crit}$ ) of the experimental fishes at 25°C

		0	0.5	1	2	4*	8*	12	20*
N	Crucian carp	9	7	7	6	6			
	Grass carp	8	6	8	10	9			
	Darkbarbel catfish	10	8	8	8	6	7		
	Southern catfish	8			7	4	4	7	6
Feeding level (%)	Crucian carp	0	0.55±0.00	1.12±0.01	2.20±0.02	4.43±0.01			
	Grass carp	0	0.54±0.03	1.15±0.08	2.47±0.13	3.93±0.05			
	Darkbarbel catfish	0	0.57±0.02	1.01±0.03	2.03±0.03	4.04±0.05	7.98±0.04		
	Southern catfish	0			2.00±0.00	4.00±0.00	8.00±0.00	14.76±0.87	19.43±0.59
Body mass (g)	Crucian carp	6.09±0.13	6.06±0.10	5.96±0.10	6.18±0.18	6.14±0.09			
	Grass carp	8.64±0.38	8.61±0.63	9.27±0.21	8.93±0.32	8.36±0.38			
	Darkbarbel catfish	7.46±0.38	6.84±0.30	7.71±0.58	6.78±0.38	7.22±0.33	6.75±0.15		
	Southern catfish	17.18±0.45			18.72±0.54	20.59±0.93	18.45±1.29	17.48±1.47	17.38±1.47
Body length (BL, cm)	Crucian carp	5.46±0.04	5.71±0.08	5.37±0.06	5.55±0.09	5.55±0.11			
	Grass carp	7.94±0.14	8.08±0.11	8.14±0.14	8.11±0.13	7.84±0.13			
	Darkbarbel catfish	7.69±0.16	7.55±0.13	7.75±0.19	7.44±0.17	7.57±0.16	7.46±0.07		
	Southern catfish	13.20±0.12			12.54±0.22	13.13±0.29	12.50±0.44	12.36±0.51	12.01±0.51
$U_{crit}$ (BL s <sup>-1</sup> )	Crucian carp	7.44±0.16 <sup>a</sup>	6.82±0.14 <sup>b,c</sup>	6.96±0.10 <sup>b</sup>	6.67±0.16 <sup>b,c</sup>	6.52±0.09 <sup>c</sup>			
	Grass carp	4.51±0.16	4.32±0.14	4.13±0.10	4.23±0.16	4.08±0.09			
	Darkbarbel catfish	4.63±0.10	4.50±0.13	4.65±0.20	4.48±0.21	4.24±0.10	4.18±0.12		
	Southern catfish	3.00±0.06 <sup>a</sup>			2.96±0.06 <sup>a</sup>	2.88±0.24 <sup>a</sup>	2.76±0.13 <sup>a</sup>	2.29±0.08 <sup>b</sup>	1.99±0.19 <sup>b</sup>

Means ± s.e.m. Values in each row without a common superscript are significantly different ( $P < 0.05$ ). 4\* means 4% is the maximum feeding level for crucian carp and grass carp, 8\* means 8% is the maximum feeding level for darkbarbel catfish and 20\* means 20% is the maximum feeding level for southern catfish.

low  $U_{crit}$  of fasting fish, the trapezoid-shaped postprandial  $\dot{V}_{O_2}$  profile of fish after a large meal and the higher maximum feeding level suggest that the aerobic locomotory capacity was almost totally lost for a substantial period of time after the consumption of a large meal in the southern catfish. Because the southern catfish has a habit of digesting food while lying motionless at the bottom of a river and it belongs to the highest trophic level in its habitat, it is unlikely that it needs a large locomotory capacity, whereas digestion is necessary. The allocation of most of the metabolic capacity for digestion in the sit-and-wait southern catfish might favour fast digestion and growth (Priede 1985; Fu et al., 2005a; McGraw, 2007). However, regarding the question of whether digestion has a more profound effect on the capacity for postprandial locomotion in sit-and-wait fishes than it does in other fishes, more comparative work on species with different foraging modes using a full range of feeding levels needs to be conducted before a satisfactory conclusion can be made (Blaike and Kerr, 1996; Thorarensen and Farrell, 2006). Sit-and-wait fishes, such as the pike (*Esox lucius*) and other kinds of sedentary catfish, might be a suitable model for future study.

In the grass carp, it was not surprising to find that  $U_{crit}$  showed no significant change after a meal because maximum feeding level (4% body mass) only elicited a 50%  $\dot{V}_{O_2}$  increase compared with  $\dot{V}_{O_{2rest}}$  (i.e. it only accounted for 10% of total metabolic scope, as calculated by the difference between  $\dot{V}_{O_{2max}}$  and  $\dot{V}_{O_{2rest}}$ ). This finding makes sense because the grass carp, with a small maximum feeding level, must graze for low-energy plant tissue with some food in the gut (i.e. in digestive status) throughout the day to meet its energy and nutrient requirements.  $U_{crit}$  of the fasting grass carp was greater than that of the sedentary southern catfish, but it was similar to that of the sluggish darkbarbel catfish, possibly due to the fact that the herbivorous grass carp does not require a high  $U_{crit}$  to chase prey. Researchers have suggested that animals with a higher locomotory performance usually have a higher metabolic capacity and maintain a higher metabolic cost when at rest (Reinhold 1999; Chappell et al., 2007). However, the  $\dot{V}_{O_{2rest}}$  of the grass carp was significantly higher than that of the darkbarbel catfish despite their similar  $U_{crit}$ , which is partly due to their levels of routine activity (higher MPM and PTM in grass carp). Furthermore, other locomotory performance (in addition to  $U_{crit}$ ) such as the fast-start performance may be involved in the metabolic strategy. The fast-start performance was considered to be closely related to escape manoeuvres. Hence, the grass carp has a metabolic strategy that expends the most energy to maintain the locomotory performance involved in avoiding predators, some energy to maintain the locomotory performance related to grazing, and little energy for digestive performance.

In the crucian carp, the unanticipated profound postprandial  $\dot{V}_{O_2}$  increase was even larger than that in southern catfish if we take the feeding level into account. However, the  $U_{crit}$  only showed a 12% decrease, even though the metabolic scope exhibited a 45% decrease as calculated by  $\dot{V}_{O_{2peak}}$ ,  $\dot{V}_{O_{2max}}$  and  $\dot{V}_{O_{2rest}}$ . The reason for this discrepancy lies in the high flexibility of the crucian carp's cardio-respiratory system. Fu and colleagues (Fu et al., 2009) found that the  $\dot{V}_{O_{2max}}$  increased from about 300 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> in fasting fish to 400 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> in feeding fish. Hence, the metabolic scope for locomotion changed little after feeding in the crucian carp. This means that the metabolic strategy of the crucian carp is to maintain a high metabolic capacity, which can support high activity in both feeding and locomotion. The cost of such a strategy is illustrated by the  $\dot{V}_{O_{2rest}}$  data: the  $\dot{V}_{O_{2rest}}$  of the crucian carp was 25–60% higher than those of the other three fishes studied. With such a strategy and the short duration of the digestive process, feeding activity actually had little effect on locomotion from an ecological perspective.

In the darkbarbel catfish, the cellular metabolic capacity of the digestive organs is lower compared with that of the crucian carp and the southern catfish (Fig. 1), as suggested by the lower postprandial  $\dot{V}_{O_2}$  curve and the prolonged trapeziform profile that occurs after a large meal. Such a digestive strategy guarantees a high capacity for locomotion after feeding, which might be critical for searching for food while still digesting. The activity,  $U_{crit}$  and  $\dot{V}_{O_{2rest}}$  of the darkbarbel catfish were lower than those of the active crucian carp. The explanation for this difference can be found in the traits of the darkbarbel catfish. With its venomous pectoral fin, the darkbarbel catfish can catch prey (it usually searches for small prey at night) without having to swim fast, and with its yellow aposematic colouration, it does not require the higher locomotory capacity involved in avoiding predators and thus does not have to expend energy to avoid being eaten. The darkbarbel catfish, which has the protection of venom, uses some energy for foraging and uses less energy for both digestion and predator avoidance activities.

McLaughlin (McLaughlin, 1989) suggested that foraging modes are species-specific strategies that are correlated with a suite of behavioural, ecological, physiological and morphological characteristics. This premise was exhibited in the sit-and-wait southern catfish in the present study. It had a large feeding level and a high digestive capacity (suggested by the large postprandial  $\dot{V}_{O_{2peak}}$ ), a low activity level (as suggested by the low PTM and MPM), and a low swimming performance (as suggested by the  $U_{crit}$ ), and hence a lower energy expenditure (as suggested by the lower  $\dot{V}_{O_{2rest}}$ ). It also had great flexibility in its digestive physiological response to nutritional status (Fu et al., 2005b). All of these characteristics are highly adaptive to its sedentary ambush life style (Priede 1985; Armstrong et al., 1992) and ensure high energy efficiency (more than 60% of ingested energy is channelled into growth) and fast growth rate (they can reach 3–4 kg in the first year when food is abundant and usually reach maturation at about 5–7 years in the wild). It is not surprising that the southern catfish is the most successful ambush forager in its habitat. The crucian carp's higher metabolic cost strategy and additivity metabolic model ensure that it can cope with the physiological issues of digestion, locomotion and postprandial locomotion. For the grass carp and the darkbarbel catfish, the lower digestive capacity strategy allows them to maintain their locomotory capacity to forage for food.

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