



Digesting or swimming? Integration of the postprandial metabolism, behavior and locomotion in a frequently foraging fish



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ARTICLE INFO

Article history:

Received 19 July 2016

Received in revised form 6 December 2016

Accepted 7 December 2016

Available online 12 December 2016

Keywords:

Digestion

Competition

Priority

Swimming performance

ABSTRACT

Fish that are active foragers usually perform routine activities while digesting their food; thus, their postprandial swimming capacity and related behavior adjustments might be ecologically important. To test whether digestion affect swimming performance and the relationships of digestion with metabolism and behavior in an active forager, we investigated the postprandial metabolic response, spontaneous swimming activities, critical swimming speed (Ucrit), and fast-start escape performance of both fasted and digesting (3 h after feeding to satiation) juvenile rose bitterling (*Rhodeus ocellatus*). Feeding to satiation elicited a 50% increase in the oxygen consumption rate, which peaked at 3 h after feeding and returned to the prefeeding state after another 3 h. However, approximately 50% and 90% of individuals resumed feeding behavior at 2 and 3 h postfeeding, respectively, although the meal size varied substantially. Digestion showed no effect on either steady swimming performance as suggested by the Ucrit or unsteady swimming performance indicated by the maximum linear velocity in fast-start escape movement. However, digesting fish showed more spontaneous activity as indicated by the longer total distance traveled, mainly through an increased percentage of time spent moving (PTM). A further analysis found that fasting individuals with high swimming speed were more inclined to increase their PTM during digestive processes. The present study suggests that as an active forager With a small meal size and hence limited postprandial physiological and morphological changes, the swimming performance of rose bitterling is maintained during digestion, which might be crucial for its active foraging mode and anti-predation strategy.

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1. Introduction

Feeding and swimming are two of the primary physiological activities of fish species. Feeding provides the energy for all physiological activities including swimming, whereas swimming capacity is closely related to the success of food capture. Fish usually perform routine activities while digesting their food (Fu et al., 2009); thus, changes in performance and behavior that result from digestion can have important ecological implications for wild fishes. The situation might be increasingly complicated in active foragers and/or in those fish species living in habitats with high swimming demands (e.g., high water velocity or predation stress) (Peng et al., 2014).

The influence of digestion on swimming behavior in fish is poorly understood. It has been suggested that foraging behavior may be reduced with increasing levels of satiation (Gill and Hart, 1994, 1996), resulting in a decrease in spontaneous swimming speed with increasing satiation (Robinson and Pitcher, 1989; Asaeda et al., 2001). The decreased spontaneous activities may favor an efficient digestion process,

more allocation of energy to growth, and a lower rate of encountering potential predators. However, for an active forager feeding on scattered low-energy food, the maintenance of postprandial activities might be ecologically important (Fu et al., 2009). Furthermore, some vital, routine tasks such as safeguarding territories and identification of potential predators which closely related to spontaneous swimming may also prevent a profound decrease of postprandial activities (Tudorache et al., 2009). Thus, the effect of feeding on spontaneous activities might differ among fish with different ecological habits (foraging mode, anti-predation strategy, etc.) and among environments with differences in flow regime, food abundance and/or predation stress.

Locomotion in fish can be described as steady or unsteady swimming. Steady swimming is defined as swimming in a straight line at a constant speed (Blake, 1983; Videler, 1993). It is important to hold position in a flow and to seek suitable habitats, among other functions (Plaut, 2001; Kieffer, 2010; Fu et al., 2013). Both steady swimming and digestion are assumed to be metabolized aerobically and hence may compete for oxygen during postprandial swimming specifically in low oxygen environments (Jourdan-Pineau et al., 2010; Zhang et al., 2012). Thus, the competition between digestion and swimming during postprandial locomotion has drawn the attention of scientists (Alsop

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and Wood, 1997; Thorarensen and Farrell, 2006; Altimiras et al., 2008; Fu et al., 2009; Jourdan-Pineau et al., 2010). The steady swimming performance indicated by the critical swimming speed (Ucrit, the water speed at which a fish can no longer maintain position, also called the maximum sustainable swimming speed) showed no change after feeding in fish species such as common carp (*Cyprinus carpio*) (Pang et al., 2011) and the European sea bass (*Dicentrarchus labrax*) (Altimiras et al., 2008; Jourdan-Pineau et al., 2010). In contrast, the Ucrit has been reported to decrease from 10% to 30% in fish species such as Chinese bream (*Parabramis pekinensis*) (Peng et al., 2014), goldfish (*Carassius auratus*) (Pang et al., 2011), rainbow trout (*Oncorhynchus mykiss*) (Alsop and Wood, 1997) and Chinook salmon (*Oncorhynchus tshawytscha*) (Thorarensen and Farrell, 2006). The ecological benefit and cost of maintaining a steady swimming performance while digesting may vary among fish species with divergent ecological habits and/or species that favor different habitats (Yan et al., 2013). It might be the selective agents underlying the differences of response of Ucrit to digestion, whereas the physiological mechanisms used by different fish species remain largely unknown.

Thus, the investigation of postprandial changes in swimming performance, behavior mode and other physiological performances from an integrative perspective in more fish species might provide useful information.

Unsteady swimming involves maneuvers, acceleration and deceleration (Blake, 1983; Videler, 1993) and is a major component of spontaneous swimming activity, which includes common behaviors such as safeguarding territories, searching for food, avoiding predators and mating. Among them, the fast-start escape swimming response is a form of burst swimming of less than approximately 1 s in duration that is considered to be fueled anaerobically (Webb, 1986; Domenici and Blake, 1997; Walker et al., 2005). The propulsive performance of the fast-start response can be evaluated through quantified distance-time parameters, such as maximum forward velocity (Vmax) and maximum linear acceleration (Amax) during the fast-start escape movement (see review by Domenici and Blake, 1997). Theoretically, there is no metabolic competition between digestion and the fast-start escape response. However, several feeding-elicited morphological consequences such as increased mass and changes in body shape may negatively affect fast-start performance. The relationship between feeding and fast-start has only been investigated in an ambush predator, southern catfish (*Silurus meridionalis*), in which feeding to satiation resulted in a profound impairment in the fast-start response (Yan et al., 2015). The decreased fast-start performance while digesting is reasonable because southern catfish usually consume large meals, hide without moving while digesting, and have low predation stress. The effects of feeding on the fast-start response in active foraging fish species and its relationships with other physiological activities and behaviors need further investigation.

The maintenance of both steady and unsteady swimming performance and the corresponding adjustment of behavior mode might be closely correlated with each other and are ecologically important in active fish species. Thus, in the present study, we aimed to test whether feeding affects the performance of steady and unsteady swimming and whether such effects may be related to postprandial behavioral changes. We selected a small, frequently foraging fish, the rose bitterling (*Rhodeus ocellatus*), as an experimental model. Rose bitterlings prefer

still bodies of water such as ponds and lakes but also occupy rivers with slow flow. These fish usually swim and forage in areas with high predation stress. To achieve our goal, we first measured the postprandial metabolic response as indicated by oxygen consumption rate (MO₂) after a satiating meal to characterize the digestive process of this fish. Then, we measured the latency and degree of regained appetite after a satiating meal to qualitatively determine its foraging mode. Lastly, we measured the spontaneous physical activities, Ucrit and fast-start response of fish during fasting and digesting (3 h after feeding, when postprandial metabolism peaks).

2. Materials and methods

2.1. Experimental animals and acclimation

Juvenile rose bitterlings (*Rhodeus ocellatus*) ($N = 206$, see Table 1 for body size) were obtained from a local pond and kept in tanks containing 25 ± 1 °C de-chlorinated, fully aerated tap water for 2 weeks before the experiment. The photoperiod was maintained at 14 L:10 D, and the dissolved oxygen level was kept above 90% saturation. One-tenth of the water in the tank was replaced daily with freshwater.

Throughout the experimental period, the fish were fed once daily (at 09:00 am) to satiation with a commercial frozen sludge worm (*Tubifex tubifex*). The uneaten food and feces were removed with a siphon 30 min after feeding.

2.2. Experimental design

Experiment I (Feeding metabolism test). After 2 d of fasting, 15 individuals were selected for measurement of the postprandial metabolic response after a satiating meal of sludge worm.

Experiment II (Resumption of appetite test) Sixty individuals were selected and offered a satiating meal (sludge worm). Then, five groups of 12 individuals were randomly selected after 1, 2, 3, 4 and 48 h, and another meal was offered. Then, whether and how much each individual ate was recorded.

Experiment III (Spontaneous swimming test) Thirty-three fish after 2 d of fasting and 38 digesting fish (2–3 h after feeding, when postprandial metabolic rate peaked according to experiment I) were selected for observation of spontaneous swimming activities.

Experiment IV (Fast-start escape response test). Twenty fasting and 20 digesting individuals were selected for measurement of the fast-start escape response.

Experiment V (Ucrit test). Ten fasting (48 h postfeeding) and 10 digesting individuals were selected for measurement of Ucrit.

2.3. Experimental facilities and measurements

2.3.1. Measurement of postprandial metabolic response

To investigate the postprandial MO₂ responses in rose bitterling, after 24 h of fasting, 15 fish were individually moved to a continuous-flow respirometer with a water temperature of 25 ± 0.5 °C (see structure in Fu et al., 2005) and acclimated for another 24 h. Then, MO₂ was measured 7 times at 1 h intervals to determine the prefeeding MO₂. Then, each fish was fed a satiating meal of sludge worm (approximately 1.4% of body mass). Afterward, the MO₂ was measured at 1 h

Table 1
The body size of experimental fish used in the present study (Mean \pm S.E.).

Feeding metabolism resumption of appetite	Spontaneous activity		Critical swimming speed		Fast-start escape response			
	Fasting	Digesting	Fasting	Digesting	Fasting	Digesting		
n	15	60	38	33	10	10	20	20
Body weight (g)	1.36 \pm 0.07	1.29 \pm 0.02	1.33 \pm 0.05	1.33 \pm 0.05	1.22 \pm 0.04	1.24 \pm 0.05	1.24 \pm 0.08	1.13 \pm 0.03
Body length (cm)	3.95 \pm 0.05	3.95 \pm 0.02	3.98 \pm 0.05	3.98 \pm 0.05	3.98 \pm 0.05	3.94 \pm 0.06	3.95 \pm 0.08	3.81 \pm 0.03

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