

CORRECTION

Correction: Effects of food availability on metabolism, behaviour, growth and their relationships in a triploid carp (doi: 10.1242/jeb.167783)

Sheng Liu and Shi-Jian Fu

There was an error published in *J. Exp. Biol.* (2017) **220**, 4711-4719 (doi: 10.1242/jeb.167783).

A mistake was made by the authors in the calculation of relative standard metabolic rate (rSMR) values. The corrected Results section, Fig. 4 and Table 5 follow. There are no changes to the conclusions of the paper.

The relationships among growth performance, SMR and behaviour

Relative SMR showed only a weak correlation with boldness in the twice-fed group and with exploration in the once-fed group at the end of the experiment (Table S3).

At the end of the experiment, SMR was nearly positively correlated with FR in the once-fed group (Fig. 4A); however, there was no significant correlation between SMR and any growth variable in the twice-fed group.

None of the behavioural variables showed a significant correlation with any growth performance variable in the twice-fed group at the end of the experiment (Table 5). However, both activity and boldness were positively correlated with FR and negatively correlated with FE and/or SGR in the once-fed group (Fig. 4B–F), although the correlations of both activity and boldness with FR (or FE) were not significant after Bonferroni correction.

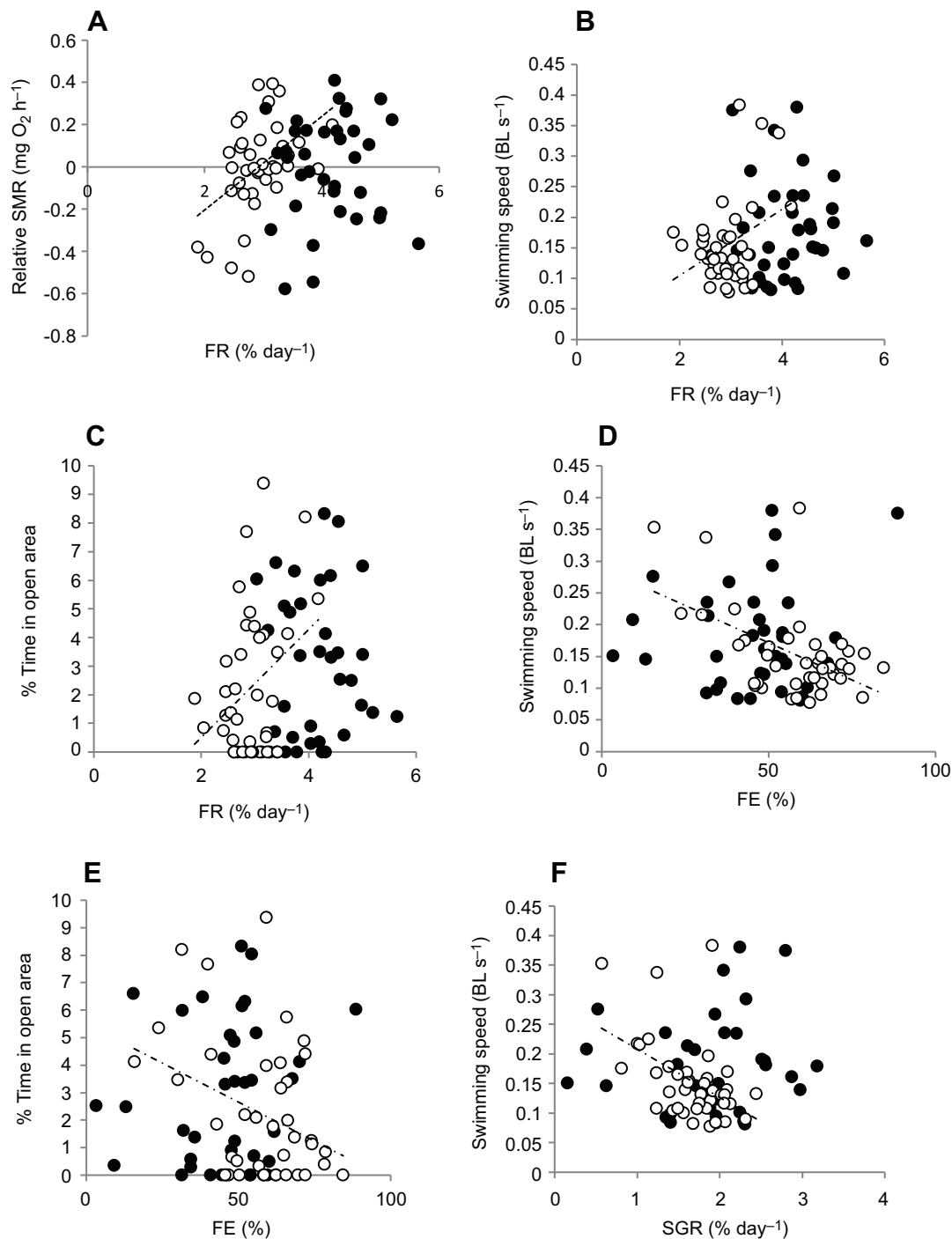


Fig. 4. The relationship between relative standard metabolic rate and growth performance in the final measurement, and the relationships between the personality traits at the final time point and growth performance. The black symbols represent the twice-fed group, and white symbols represent the once-fed group. (A) The relationship between feeding rate (FR) and relative standard metabolic rate (SMR) in the once-fed group ($y_{\text{once-fed}}=0.221x-0.646$, $N=40$, $r=-0.461$, $P=0.003$). (B) The relationship between FR and activity ($y_{\text{once-fed}}=0.054x-0.003$, $N=40$, $r=0.349$, $P=0.027$). (C) The relationship between FR and boldness ($y_{\text{once-fed}}=1.886x-3.263$, $N=40$, $r=0.336$, $P=0.034$). (D) The relationship between feeding efficiency (FE) and activity ($y_{\text{once-fed}}=-0.002+0.288$, $N=40$, $r=-0.518$, $P=0.001$). (E) The relationship between FE and boldness ($y_{\text{once-fed}}=-0.056x+5.4491$, $N=40$, $r=-0.346$, $P=0.029$). (F) The relationship between SGR and activity ($y_{\text{once-fed}}=-0.081x+0.289$, $N=40$, $r=-0.247$, $P=0.002$).

Table 5. The relationship between the final measurement of relative standard metabolic rate, personality and growth performance of the fish

		Twice-fed group			Once-fed group		
		FR (N=36)	FE (N=36)	SGR (N=36)	FR (N=40)	FE (N=40)	SGR (N=40)
Relative SMR	<i>r</i>	0.026	-0.054	-0.057	0.461	-0.307	-0.062
	<i>P</i> -value	0.879	0.752	0.739	0.003*	0.054	0.704
	<i>N</i>	36	36	36	40	40	40
Activity	<i>r</i>	0.004	0.109	0.103	0.349	-0.518	-0.479
	<i>P</i> -value	0.979	0.525	0.549	0.027*	0.001*	0.002*
	<i>N</i>	36	36	36	40	40	40
Exploration	<i>r</i>	-0.103	0.031	-0.048	-0.059	0.172	0.204
	<i>P</i> -value	0.549	0.858	0.783	0.719	0.288	0.206
	<i>N</i>	36	36	36	40	40	40
Boldness	<i>r</i>	0.006	0.158	0.189	0.336	-0.346	-0.247
	<i>P</i> -value	0.974	0.358	0.269	0.034*	0.029*	0.124

FR, feeding rate; FE, feeding efficiency; SGR, specific growth rate; SMR, standard metabolic rate. Activity was measured as swimming speed; exploration was measured as minimum distance to the novel object; boldness was measured as percentage of time spent in the open area. *Not significantly different after Bonferroni correction ($P=0.0167$).

The authors apologise for any inconvenience this may have caused.

RESEARCH ARTICLE

Effects of food availability on metabolism, behaviour, growth and their relationships in a triploid carp

Sheng Liu and Shi-Jian Fu*

ABSTRACT

Metabolism, behaviour and growth are highly flexible in fish species, and inter-individual variation in these traits is evolutionarily and ecologically significant. It has long been suggested that these traits co-vary, although their relationships are debated. In the present study, we investigated whether metabolism, behaviour, growth and the potential relationships among them vary with food availability in sterile triploid carp. In this experimental animal model, we investigated the standard metabolic rate (SMR), growth performance and personality traits (i.e. activity, exploration and boldness) of juvenile individuals before and after 25 days of rearing in which fish were fed either once or twice a day to satiation. Inter-individual differences in SMR in each group showed high repeatability across the experimental period, and twice-fed fish showed higher SMRs than once-fed fish after 25 days of rearing. Compared with the once-fed group, the twice-fed group showed higher feeding rates (FRs) and lower feeding efficiencies (FEs) but similar specific growth rates (SGRs). None of the personality traits was affected by food availability. Furthermore, both boldness and exploration were highly repeatable throughout the experiment in the group fed twice a day, whereas only exploration showed repeatability in the group fed once a day. In the once-fed group, SMR and the personality traits were positively correlated with FR and negatively correlated with FE and/or SGR; however, these relationships did not exist in the twice-fed group due to the surplus of food. These results suggest that food availability significantly affects physiological, behavioural and ecological processes in these fish by altering the trade-off between metabolism and growth.

KEY WORDS: Flexibility, Fitness, Inter-individual variation, Standard metabolic rate, Growth performance, Personality

INTRODUCTION

Metabolism is the process by which energy and materials are exchanged between organisms and their environment (Van Leeuwen et al., 2012; Auer et al., 2015b). Metabolic rates are typically thought to have important impacts on fitness, and inter-individual variation in metabolic rate is thought to be repeatable over time (Norin and Malte, 2011). Somatic growth is one of the most fundamental biological processes required for survival and thus has important fitness consequences, and growth rate is frequently used as an indicator of the capacity to acquire food resources (Arnott et al., 2006; Stephen et al., 2006; Pang et al.,

2016a). It has long been suggested that maintenance metabolism (i.e. the standard metabolic rate, SMR) is closely related to growth performance in fish species; however, the observed relationship between these factors differs among studies (Cutts et al., 2002; Norin and Malte, 2011; Reid et al., 2011). For example, many studies have demonstrated that fast-growing fish have a higher SMR than slow-growing fish because the biochemical processes involved in growth (e.g. protein synthesis) are highly energy intensive and are the main components of SMR (Maxime et al., 1989; Auer et al., 2015b). However, some researchers argue that SMR may be negatively correlated with growth because increased maintenance energy expenditure means less energy available for body mass deposition (Wieser and Forstner, 1986; Rosenfeld et al., 2014).

The personality of an animal is defined as the 'suites of correlated behaviours across situations', i.e. repeatable individual differences in behaviours such as activity, exploration and boldness (Réale et al., 2010; Mazué and Godin, 2015). Many animals exhibit personality types, and bolder individuals are typically more explorative and active (Martins and Bhat, 2014). It has been found that behavioural repertoires in some fish species are inter-coordinated with metabolism, with individuals having high energy demands exhibiting increased foraging and exploration behaviours (Coppens et al., 2010; Cote et al., 2010; Atwell et al., 2012). Such behavioural and physiological co-variation has led to the hypothesis that personality types reflect the variation in metabolic rate (Atwell et al., 2012), i.e. high-SMR individuals typically show proactive personalities, whereas low-SMR individuals show reactive personalities (Lahti et al., 2002; Réale et al., 2010). Unlike the relationship between SMR and growth (or personality), the relationship between personality and growth rate has drawn little scientific attention (Øverli et al., 2006; Schjolden et al., 2006). One study of a cichlid fish (*Neolamprologus pulcher*) found that individuals with a proactive personality type (high activity, exploration and boldness) showed faster growth rates than individuals with a reactive personality type (Heg et al., 2011). In contrast, a study of brown trout (*Salmo trutta*) found that shy individuals had higher growth rates than bolder conspecifics (Adriaenssens and Johnsson, 2011). These findings suggest that the relationships among metabolism, behaviour and growth might be species specific. Further investigation might provide insights into this issue, as no studies have yet tested the relationships among all three components in a fish species in a single experiment. Thus, the first aim of the present study was to test whether SMR and behavioural traits are repeatable, and if so, whether SMR, personality and growth are correlated with each other in a fish species.

Fish often live in variable environments in which conditions such as food availability change profoundly, and are significantly correlated with growth, SMR and/or behavioural traits (Killen et al., 2011; Priyadarshana et al., 2006; Auer et al., 2016b). Typically, fish show high food consumption and thus faster growth rates when food availability is high (Dibattista et al., 2006; Auer

Laboratory of Evolutionary Physiology and Behavior, Chongqing Key Laboratory of Animal Biology, Chongqing Normal University, Chongqing 401331, China.

*Author for correspondence (shijianfu9@cqu.edu.cn)

 S.-J.F., 0000-0001-7665-9037

Received 5 August 2017; Accepted 24 October 2017

et al., 2015b). Furthermore, flexibility in metabolic rate is one of the primary traits underlying organismal performance, and there is evidence of a positive relationship between metabolism and food availability in fish species (Rosenfeld and Taylor, 2009; Reid et al., 2011). In addition, behavioural traits vary with food availability; however, the relationship varies among studies. For example, a study in *Pseudorasbora parva* and *Rasbora daniconius* found that individuals performed more foraging behaviours (and were more active and aggressive) when food resources were lacking (Priyadarshana et al., 2006), whereas a study of rainbow trout (*Oncorhynchus mykiss*) found that individuals performed more risk-taking behaviours under conditions of food abundance (Biro et al., 2006). These physiological and behavioural responses to food availability and their ecological consequences are vital adaptations of fish in the natural environment. Metabolism, growth and behaviour can each vary with food availability, as can the relationships among them. For example, the relationship between growth rate and SMR can change from being positively to negatively correlated with a decrease in food availability due to intensified competition for energy between maintenance metabolism and growth under food limitation (Auer et al., 2015a). Similarly, the relationship between behavioural traits and SMR (or growth performance) can vary with food availability by shifting the direction of the trade-off between the costs and benefits of increased energy expenditure and feeding opportunity (Finstad et al., 2007). For example, the correlation between risk-taking behaviour and routine metabolic rate was intensified under decreased food availability in juvenile European seabass (*Dicentrarchus labrax*) (Killen et al., 2011). The interconnections among energy metabolism, behaviour and growth as well as their adjustment via adaptation to fluctuations in food availability might be among the forces driving the diversity in metabolism and personality in nature. Thus, the second aim of the present study was to test whether SMR, growth performance and behavioural traits in a fish species change with food availability and if so, whether their potential interconnections also change.

MATERIALS AND METHODS

Experimental animals and acclimation

To achieve the aims of this study, we selected infertile triploid carp (allotetraploid hybrids of red crucian and common carp males and females) (Liu et al., 2001) as an experimental model to avoid the effects of reproductive development on metabolism and its relationship with growth or behaviour. Furthermore, the relatively fast growth rate of this fish model (i.e. 30% higher than that of the common carp) facilitated hypotheses testing in the present study (Liu et al., 2001). We examined differences in body size, SMR and behavioural traits between fish fed once a day to apparent satiation and fish fed twice a day to apparent satiation at both the beginning and at the end of a 25-day experiment. Fish were fed individually to enable the measurement of food intake and avoid the influence of social hierarchy on inter-individual differences in feeding.

Experimental carp were purchased from a local fish hatchery (mean body mass±s.e.m., 3.15±0.06 g; $N=80$). Prior to the experiment, the fish were housed for 2 weeks in a 250 l holding tank at a water temperature of 25±0.5°C. Throughout the pre-acclimation period, the fish were fed with a commercial fish food to satiation once daily (at 08:00 h), and the uneaten food and faeces were collected with a siphon 1 h after feeding. The water was constantly aerated to ensure that the dissolved oxygen level was maintained to at least 90% of saturation. The photoperiod was 12 h:12 h light:dark.

This study was approved by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (permit number Zhao-20151024-01) and 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.

Experimental protocol

After 2 weeks of pre-acclimation, the body size of each fish was measured; SMR was then measured by continuous-flow respirometry after 48 h of fasting. Each fish was lightly anaesthetized in neutralized tricaine methane sulphonate (MS-222, 50 mg l⁻¹) for 2 min before performing the body size measurement. Subsequently, the behavioural traits (activity, exploration and boldness) of each fish were determined twice on consecutive days using a hand-built (non-commercial) behavioural open instrument (details of the SMR and behavioural trait measurements are given below). Most behavioural traits showed high consistency between the two measurements (Table S1); therefore, the mean values were used for statistical analysis.

Fish were cultured individually in 80 separate compartments (length×width×height: 17×10×15 cm) for 25 days in a cycling tank system fitted with mechanical and biological filters and ultraviolet sterilizers. Individual fish were randomly divided into two groups (40 individuals per group): one group fed to satiation twice daily, defined as the ‘twice-fed’ group; and the other fed to satiation once daily, defined as the ‘once-fed’ group. The twice-fed group was fed at 08:00 and 18:00 h, and the once-fed group was fed at 18:00 h. Uneaten food and faeces were collected after 1 h, and the food consumption of individual fish at each time point was calculated from the number and mean weight of the pellets (5.60±0.03 mg; a screen mesh was used to acquire pellets of the same size).

After 25 days of rearing, the SMR, body size and all behavioural traits of each fish from both groups were measured again as at the beginning of the experiment.

Measurement of oxygen consumption (\dot{M}_{O_2})

SMR was determined as the rate of oxygen uptake (\dot{M}_{O_2}) at 25°C by continuous-flow respirometry (see details in Fu et al., 2005). Fish were fasted for 24 h to evacuate their guts prior to their placement into individual chambers (volume of 300 ml) and then acclimated for another 24 h; \dot{M}_{O_2} was then measured 15 times at 1 h intervals. The following formula was used to calculate the \dot{M}_{O_2} (mg h⁻¹) of individual fish:

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

where ΔO_2 is the difference in oxygen concentration (mg l⁻¹) between the experimental chamber and the control chamber (chamber without fish), and v is the water flow rate in the experimental chamber (l h⁻¹). The dissolved oxygen concentration was measured at the outlet of the chamber with an oximeter (HQ40d, Hach Company, Loveland, CO, USA), and the flow rate of the water through the respirometry chamber was measured by collecting the water outflow from each chamber.

Measurements of behavioural traits

A 92 l aquarium (75×35×45 cm) lined with white plastic sheeting on the inside was used as the experimental arena to measure all behavioural traits (Fig. 1). To minimize disturbance from the observers during the experiments, the tank was surrounded with an opaque canvas, and it was divided into two compartments by a removable opaque plastic partition (ensuring an undisturbed

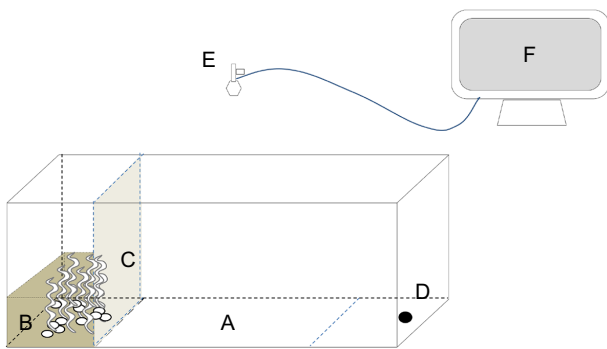


Fig. 1. Design of the experimental aquarium used in the study. (A) Open area (length×width×height: 55×35×45 cm); (B) hidden area (length×width×height: 20×35×45 cm); (C) removable opaque PVC divider; (D) black, round, plastic object; (E) camera; (F) monitor.

acclimatization period), which was used to separate the open area (length×width×height: 55×35×45 cm) from a hidden area with shelter (length×width×height: 20×35×45 cm). The water depth was maintained at 10 cm during the experiment. A black, round, plastic object was added to the open area to measure exploration and removed to measure activity (Jones and Godin, 2010; Alain et al., 2015). A hidden area contained an artificial plant and gravel to create shelter. The behaviours of the test fish were recorded using a webcam (Pro 9000 webcam, Logitech) connected to a remote monitor, and the experimental tank was illuminated by fluorescent lights.

Activity

Fish were individually transferred to a holding chamber in the middle of the open area of the aquarium. After the chamber was gently pulled up from the bottom, the fish was allowed to acclimate to the surrounding environment for 1 h (the fish could not access the hidden area due to the partition between the open and hidden areas). The movements of the fish were then recorded by webcam for 10 min (at 15 frames per second) (Heg et al., 2011).

Exploration

After measuring activity, the novel item (i.e. the black, round, plastic object) was carefully transferred to the open area. The movements of the fish were then recorded for another 20 min to measure exploration (Adriaenssens and Johnsson, 2011; Mazué et al., 2015).

Boldness

After measuring exploration and removing the opaque partition and novel object, the fish was driven into the hidden area, and its movement in the tank was recorded for 30 min to measure boldness (Alain et al., 2015; Mazué et al., 2015). On the following day, all three behavioural traits were measured again.

Videos were converted from .wmv to .avi format using Format Factory (<http://format-factory.softonic.cn>) and imported into an automated tracking programme. The videos of activity and exploration were analysed with EthoVision XT 9 (Noldus, Wageningen, The Netherlands), and boldness was analysed by idTracker (version 2.1) [see Pérez-Escudero et al. (2014) for a full description of the tracking software]. These programmes automatically tracked the position of the experimental fish in each frame and converted the x - and y -coordinates from pixels to centimetres. The parameter used to measure activity was the

spontaneous swimming speed [v , body lengths (BL) s^{-1}], which was calculated as follows:

$$v(t) = \sqrt{(x(t) - x(t-1))^2 + (y(t) - y(t-1))^2} / (d \times BL), \quad (2)$$

where $x(t)$ and $x(t-1)$ and $y(t)$ and $y(t-1)$ are the x - and y -coordinates of the measured fish at time t and the time of the previous frame ($t-1$), and d is the length of the time interval. BL is the body length of experimental fish.

The variable used to measure exploration was the minimum distance (D) to the novel object, which was calculated as follows:

$$D = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}, \quad (3)$$

where x_i and y_i and x_j and y_j are the x - and y -coordinates of individual fish (i) and the novel object (j).

The variable used to measure boldness was the percentage of time spent in the open area, which was calculated from the fish's position in each frame.

The mean values of the two measurements of each variable per fish were used for the final data analysis.

Measurement of growth performance

At the beginning and end of the 25-day rearing period, body mass (to the nearest 0.01 g) and body length (to the nearest 0.1 cm) were measured for each fish individually following mild anaesthesia with neutralized MS-222 (50 mg l^{-1}). The body mass and food intake data over the 25-day rearing period were used to calculate the growth performance variables feeding rate (FR, % day^{-1}), feeding efficiency (FE, %) and growth rate, quantified as the specific growth rate (SGR, % day^{-1}), as follows:

$$FR = 100 \times I / [(M_1 + M_2) / 2] / T, \quad (4)$$

$$FE = 100 \times (M_2 - M_1) / I, \quad (5)$$

$$SGR = 100 \times [\ln(M_2) - \ln(M_1)] / T, \quad (6)$$

where M_1 and M_2 represent the body mass (g) of the fish at the beginning and end, respectively, of the experimental period (25 days); I (g) represents the total food intake; and T denotes the duration (25 days).

Data analysis

The program SPSS 17 was used for data analysis. P values less than 0.05 were considered statistically significant, and all the data are presented as the means±s.e.m. The effect of feeding treatment on growth performance was tested by independent t -test, and the effects of measurement time point (beginning versus end) and feeding treatment on SMR (body size was used as covariate) and the behavioural variables were tested by a mixed linear model, including fish identity (ID) as a random effect. Where significant differences were found, differences between the two groups at the beginning or end of the experiment were evaluated by t -test, whereas differences between the two periods were tested by paired-sample t -test. Repeatability was tested by calculating the intra-class correlation coefficient (ICC; Lessells and Boag, 1987). The relationships between each of the behavioural variables and growth performance, metabolism and behaviour were tested by Pearson's correlation analysis. The effect of food availability on FE, FR, SGR and their interaction was tested by general linear model specifying food availability as treatment effect and either FE or FR as covariate. The relative SMR, i.e. the residual SMR after calculating the expected

Table 1. The effects of feeding treatment (twice-fed versus once-fed) and measurement time (initial versus final) on the standard metabolic rate and personality of the experimental fish

	SMR			Activity			Exploration			Boldness		
	d.f.	F	Significance	d.f.	F	Significance	d.f.	F	Significance	d.f.	F	Significance
Mass	147.0	43.35	$P<0.001$									
Time	137.9	18.25	$P<0.001$	74	28.24	<0.001	74	22.02	<0.001	74	7.590	0.007
Group	71.95	7.004	$P=0.010$	74	0.009	0.924	74	0.846	0.361	74	3.244	0.076
Time×group	72.79	15.67	$P<0.001$	74	4.845	0.031	74	0.085	0.771	74	0.002	0.962

Activity was measured as spontaneous swimming speed; exploration was measured as minimum distance to the novel object; boldness was measured as percentage of time spent in the open area. SMR, standard metabolic rate; d.f., degrees of freedom.

values for a fish with a given body mass, was used for Pearson correlation analysis of metabolism and any other variables.

RESULTS

SMR

Both feeding treatment and measurement time point significantly affected SMR (Table 1, Fig. 2A). There was no significant difference in SMR between the two treatment groups at the beginning of the experiment. However, after 25 days of rearing, the SMR of the twice-fed group had increased significantly, whereas that of the once-fed group showed no significant change. Thus, the SMR of the once-fed group was significantly lower than that of the twice-fed group at the end of the experiment. Furthermore, SMR showed high repeatability throughout the experimental period in both groups (Table 2).

Individual personality

The behavioural variables were not significantly affected by feeding treatment but were significantly affected by measurement time point (Table 1). Fish showed significantly higher activity levels (as indicated by higher swimming speeds; Fig. 2B), greater exploration (as indicated by shorter minimum distances to the novel object; Fig. 2C), and greater boldness (as indicated by higher percentage time spent in the open area) after 25 days of rearing than at the beginning of the experiment (Fig. 2D). Furthermore, the swimming speed of the twice-fed group increased more than that of the once-fed group.

Activity showed no repeatability in either the twice-fed or once-fed group, whereas boldness showed repeatability in both groups (Table 2). Exploration showed repeatability in the twice-fed group but not in the once-fed group.

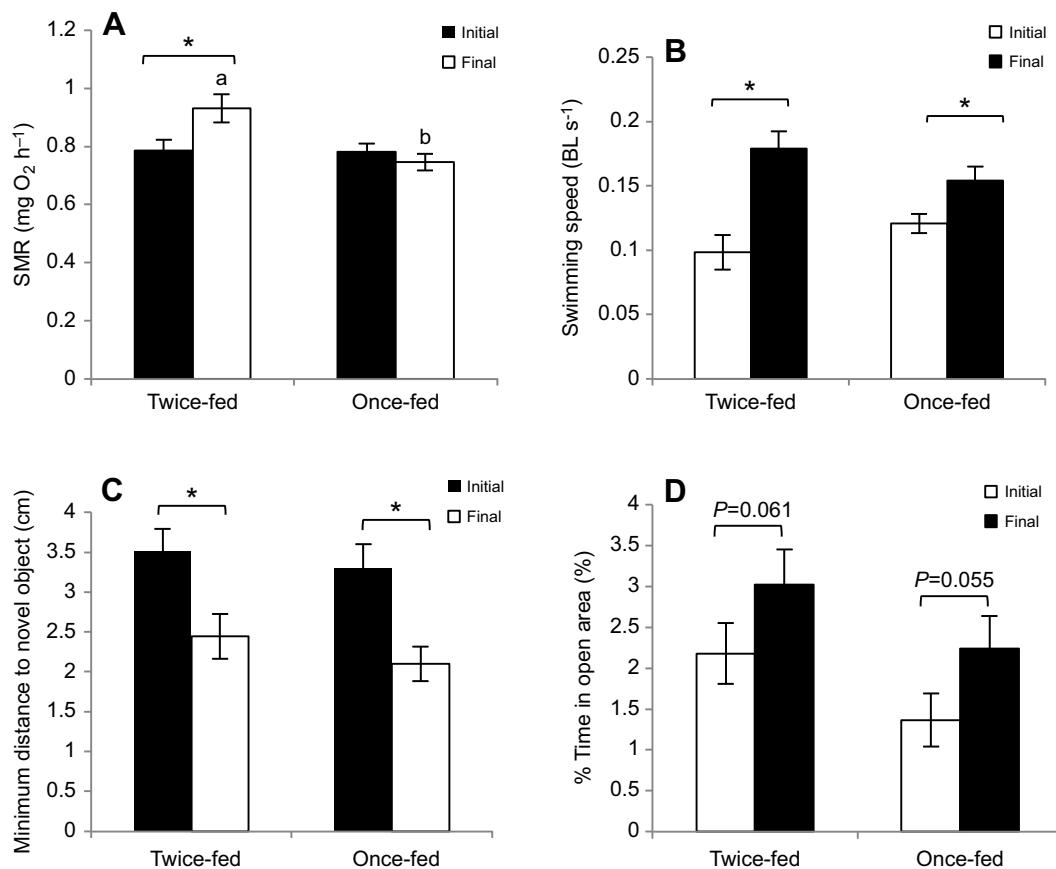


Fig. 2. The effects of feeding treatment (twice-fed versus once-fed) and measurement time (initial versus final) on standard metabolic rate and the personality of experimental fish (triploid carp). Values are means ± s.e.m., $N_{\text{twice-fed}}=36$, $N_{\text{once-fed}}=40$. (A) Standard metabolic rate (SMR); (B) activity: spontaneous swimming speed (BL, body lengths); (C) exploration: minimum distance to a novel object; (D) boldness: percentage of time spent in the open area. The black bars represent the initial measurement, and white bars represent the final measurement. *Significant difference between the initial and final measurements ($P<0.05$).

Table 2. Intra-class correlation coefficients of the initial and final measurements indicating the repeatability of the measurements of standard metabolic rate and the personality traits of activity, exploration and boldness

	Twice-fed group			Once-fed group		
	N	r	P-value	N	r	P-value
SMR	36	0.733	<0.001	40	0.588	<0.001
Activity	36	0.188	0.133	40	-0.002	0.504
Exploration	36	0.629	0.002	40	-0.099	0.616
Boldness	36	0.641	0.002	40	0.621	0.002

Activity was measured as swimming speed; exploration was measured as minimum distance to the novel object; boldness was measured as percentage of time spent in the open area.

SMR, standard metabolic rate.

There were significant correlations between any two of the three behavioural variables (i.e. activity, exploration and boldness) in both groups at both the beginning and end of the experiment (Table S2, Fig. S1).

Growth performance

Body mass did not differ significantly between the two groups of common carp at the beginning of the experiment (Tables 3 and 4). Compared with those in the once-fed group, the fish in the twice-fed group showed significantly higher FR but lower FE. Therefore, there was no significant difference in SGR between the two groups. FR was negatively correlated with FE in both groups (Fig. 3A, Tables 3 and 4). SGR was positively correlated with FE in both groups (Fig. 3B) but showed no significant correlation with FR in either group.

The relationships among growth performance, SMR and behaviour

Relative SMR showed only a weak correlation with boldness in the twice-fed group and with exploration in the once-fed group at the end of the experiment (Table S3).

At the end of the experiment, SMR was nearly positively correlated with FR and was negatively correlated with FE in the once-fed group (Fig. 4A); however, there was no significant correlation between SMR and any growth variable in the twice-fed group.

None of the behavioural variables showed a significant correlation with any growth performance variable in the twice-fed

Table 3. Statistical results of paired-sample *t*-test: the effects of feeding treatment (twice-fed versus once-fed) on the growth performance of the experimental fish, and the effects of feeding treatment (twice-fed versus once-fed) and feeding rate on the feeding efficiency and specific growth rate of the experimental fish

Variable	Twice-fed group	Once-fed group	Significance
N	36	40	
Initial body mass (g)	3.00±0.07	3.19±0.08	$t=-1.713$ $P=0.091$
Final body mass (g)	4.90±0.20	4.86±0.15	$t=-0.158$ $P=0.875$
FR (% day ⁻¹)	4.12±0.10	2.92±0.07	$t=9.529$ $P<0.001$
FE (%)	45.41±2.87	57.34±2.44	$t=-3.187$ $P=0.002$
SGR (% day ⁻¹)	1.88±0.12	1.66±0.06	$t=1.706$ $P=0.102$

Values are means±s.e.m.

FR, feeding rate; FE, feeding efficiency; SGR, specific growth rate.

Table 4. Statistical results of general linear model: the effects of feeding treatment (twice-fed versus once-fed) on the growth performance of the experimental fish, and the effects of feeding treatment (twice-fed versus once-fed) and feeding rate on the feeding efficiency and specific growth rate of the experimental fish

Dependent variable	Independent variable	F	P-value
FE	Group	1.923	0.170
	FR	19.890	<0.001
	Group×FR	2.563	0.114
SGR	Group	0.256	0.614
	FE	251.139	<0.001
SGR	Group×FE	12.426	0.001
	Group	0.376	0.542
	FR	0.012	0.914
	Group×FR	0.749	0.390

FR, feeding rate; FE, feeding efficiency; SGR, specific growth rate.

group at the end of the experiment (Table 5). However, both activity and boldness were positively correlated with FR and negatively correlated with FE and/or SGR in the once-fed group (Fig. 4B–F), although the correlations of both activity and boldness with FR (or FR) were not significant after Bonferroni correction.

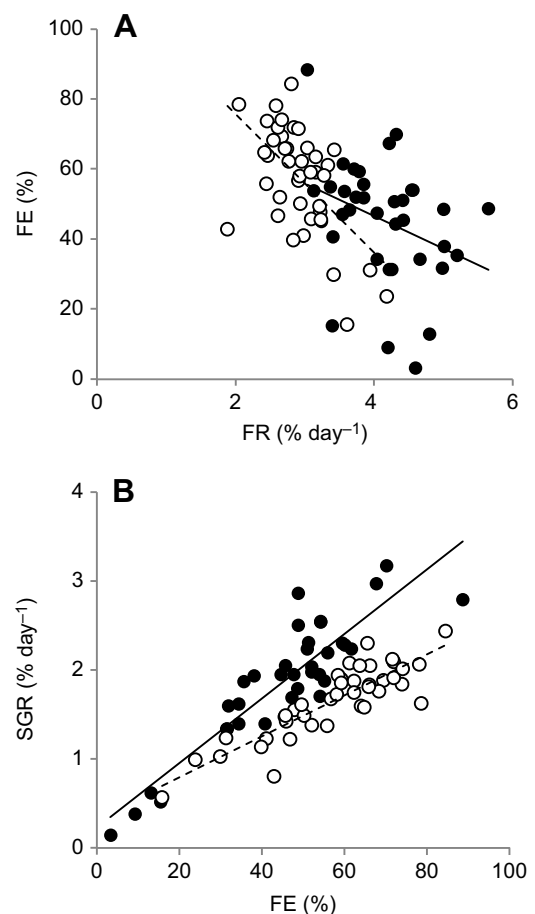


Fig. 3. The relationships among growth performance variables. The black symbols represent the twice-fed group, and white symbols represent the once-fed group. (A) The relationship between feeding rate (FR) and feeding efficiency (FE) ($y_{\text{twice-fed}}=-9.322x+83.84$, $N=36$, $r=-0.340$, $P=0.042$; $y_{\text{once-fed}}=-19.7x+114.9$, $N=40$, $r=-0.576$, $P<0.001$). (B) The relationship between FE and specific growth rate (SGR) ($y_{\text{twice-fed}}=0.036x+0.231$, $N=36$, $r=0.896$, $P<0.001$; $y_{\text{once-fed}}=0.023x+0.335$, $N=40$, $r=0.870$, $P<0.001$).

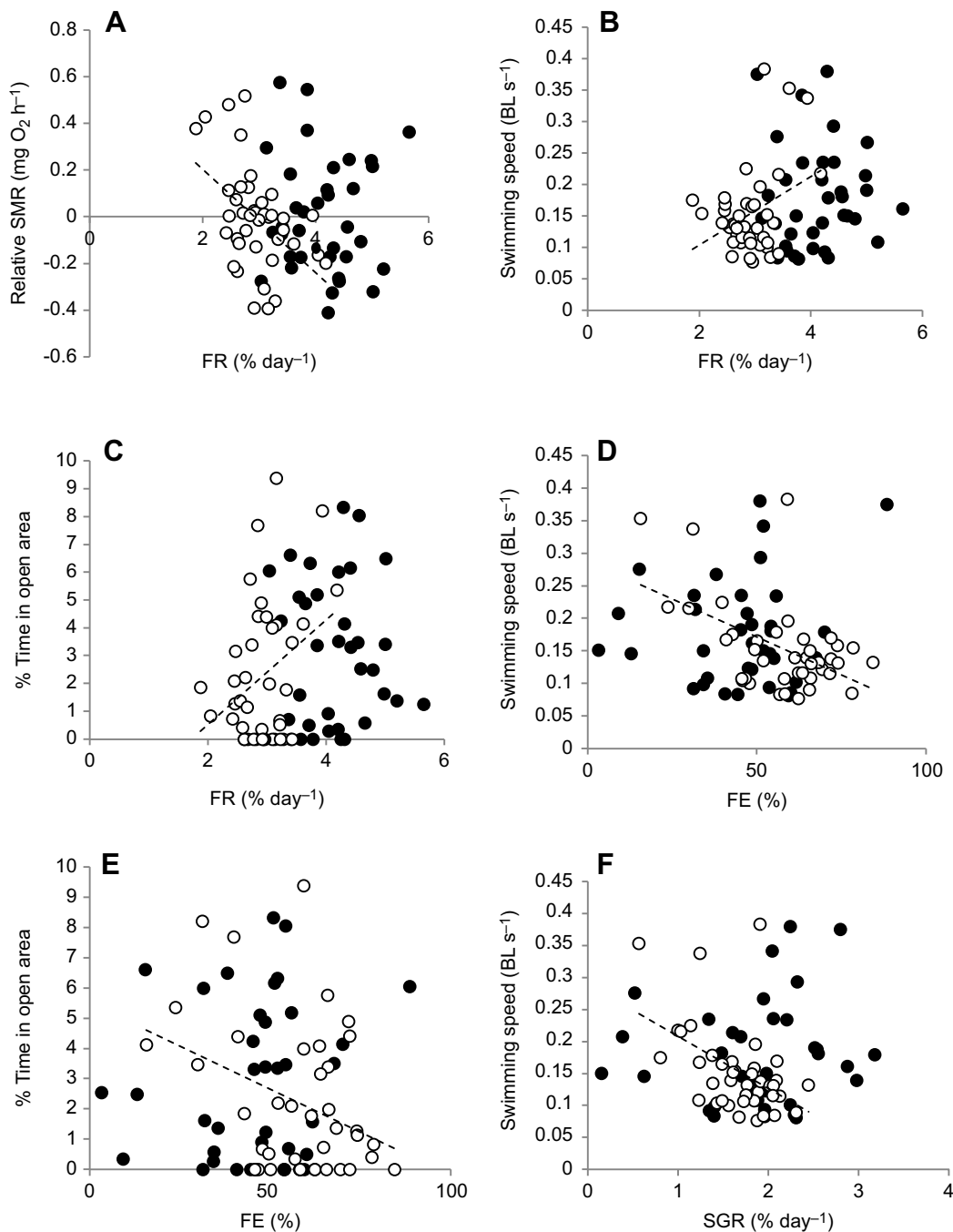


Fig. 4. The relationship between relative standard metabolic rate and growth performance in the final measurement, and the relationships between the personality traits at the final time point and growth performance. The black symbols represent the twice-fed group, and white symbols represent the once-fed group. (A) The relationship between FR and relative standard metabolic rate in the once-fed group ($y_{\text{once-fed}} = -0.221x + 0.646$, $N=40$, $r = -0.461$, $P=0.003$). (B) The relationship between FR and activity ($y_{\text{once-fed}} = 0.054x - 0.003$, $N=40$, $r = 0.349$, $P=0.027$). (C) The relationship between FR and boldness ($y_{\text{once-fed}} = 1.886x - 3.263$, $N=40$, $r = 0.336$, $P=0.034$). (D) The relationship between FE and activity ($y_{\text{once-fed}} = -0.002 + 0.288$, $N=40$, $r = -0.518$, $P=0.001$). (E) The relationship between FE and boldness ($y_{\text{once-fed}} = -0.056x + 5.4491$, $n=40$, $r = -0.346$, $P=0.029$). (F) The relationship between SGR and activity ($y_{\text{once-fed}} = -0.081x + 0.289$, $N=40$, $r = -0.247$, $P=0.002$).

DISCUSSION

Effect of food availability on SMR and SMR repeatability

In the present study, the SMR values increased by 18% and decreased by 4% in the twice-fed and once-fed groups, respectively, after 25 days of rearing, and SMR showed high repeatability across the experiment. Notable and consistent intra-species differences in SMR have been documented for many fish species (Cutts et al.,

2002; Seibel, 2007; Norin and Malte, 2011), which might be the underlying energetic basis for differentiation in physiological performance and/or behavioural traits (Biro and Stamps, 2010). Previous studies in fish have found that fasting or restricted feeding can weaken the repeatability of SMR (O'Connor et al., 2000; Norin and Malte, 2011); however, SMR repeatability was not affected by food availability in the present study, possibly because

Table 5. The relationship between the final measurement of relative standard metabolic rate, personality and growth performance of the fish

		Twice-fed group			Once-fed group		
		FR (N=36)	FE (N=36)	SGR (N=36)	FR (N=40)	FE (N=40)	SGR (N=40)
Relative SMR	<i>r</i>	−0.026	0.054	0.057	−0.461	0.307	0.062
	<i>P</i> -value	0.879	0.752	0.739	0.003	0.054	0.704
	<i>N</i>	36	36	36	40	40	40
Activity	<i>r</i>	0.004	0.109	0.103	0.349	−0.518	−0.479
	<i>P</i> -value	0.979	0.525	0.549	0.027*	0.001	0.002
	<i>N</i>	36	36	36	40	40	40
Exploration	<i>r</i>	−0.103	0.031	−0.048	−0.056	0.172	0.204
	<i>P</i> -value	0.549	0.858	0.783	0.719	0.288	0.206
	<i>N</i>	36	36	36	40	40	40
Boldness	<i>r</i>	0.006	0.158	0.189	0.336	−0.346	−0.247
	<i>P</i> -value	0.974	0.358	0.269	0.034*	0.029*	0.124

FR, feeding rate; FE, feeding efficiency; SGR, specific growth rate; SMR, standard metabolic rate. Activity was measured as swimming speed; exploration was measured as minimum distance to the novel object; boldness was measured as percentage of time spent in the open area. *Not significantly different after Bonferroni correction ($P=0.0167$).

the difference in food availability (twice-fed versus once-fed to satiation per day) was much lower than that in previous studies (i.e. fasting versus restricted feeding).

Only the fish in the twice-fed group increased their SMR over the experiment, having a higher final SMR than fish in the once-fed group after 25 days of rearing. Although the fish in the once-fed group showed no increase in SMR, as measured by oxygen consumption per fish, body mass in this group increased by more than 50%. These results suggest that had we used SMR per unit body weight as our measure, the fish in this group would have shown a decrease in this variable over the experiment. A significant decrease in SMR over the course of an experiment has been reported frequently for cyprinid fish species (Fu et al., 2012; Pang et al., 2016b). Such decreases are potentially due to an insufficient acclimation period before performing the experimental measurements and/or metabolic down-regulation due to generally unchanging experimental conditions (the so-called ‘captive effect’; Fu et al., 2005). Nevertheless, our results clearly demonstrated that SMR varied in response to food availability. The evolutionary adjustment of energy metabolism to food availability is consistent with our expectations, and similar results have been reported in several other fish species. For example, studies in brown trout (*S. trutta*) have found that fish reared under higher food availability showed higher SMR than those reared under lower food availability (Auer et al., 2015b, 2016a).

Effect of food treatment on behavioural traits and repeatability

As in most other fish species (Adriaenssens and Johnsson, 2013; Mazué et al., 2015), all three personality traits showed profound inter-individual variation in the triploid carp studied here. Such variation is assumed to be evolutionarily and ecologically significant for population fitness (Careau and Garland, 2012; Závorka et al., 2015). Inter-individual differences in behavioural traits are assumed to be somewhat stable throughout time or across contexts, whereas the values of behavioural traits themselves might vary according to environmental factors, including food availability (Chapman et al., 2010; Biro and Stamps, 2010; Nati et al., 2016). However, in the present study, none of the behavioural trait variables significantly differed between the two food availability treatments, which contrasts with observations in brown trout showing increased activity with higher food availability (Näslund and Johnsson, 2016). The reason for this discrepancy might be that the difference between food availability treatments was insufficient to elicit a change in personality, as mentioned previously; alternatively, this discrepancy might reflect

relatively reactive personalities of triploid carp. For example, in previous studies, diploid common carp of similar body size and subjected to similar acclimation temperatures spent 900% more time moving (Fu et al., 2012) and showed 500% higher swimming speeds (Cui, 2016) compared with the triploid carp in the present study.

Interestingly, all three behavioural traits changed significantly after 2 weeks of treatment; specifically, fish showed higher activity, exploration and boldness at the end of the experiment than at the beginning. These findings suggest that the fish might not have been well acclimated at the beginning of the experiment and that the associated stress response might have inhibited all three personality traits. Addressing whether the behavioural traits of experimental fish show repeatability and whether these traits are affected by food availability were among the main goals of the present study. Boldness, measured as the percentage of time spent in the open area, showed high repeatability in both treatment groups. This result suggests that boldness is highly conserved in the experimental fish and is consistent with the results of studies of guppies (*Poecilia reticulata*) (Chapman et al., 2010) and mosquitofish (*Gambusia affinis*) (Cote et al., 2010). However, activity, measured as the spontaneous swimming speed, showed no repeatability in either group despite high consistency between the two consecutive measurements. This result contrasts with a previous study that demonstrated consistency in activity across time in mosquitofish (Cote et al., 2010), brown trout (Adriaenssens and Johnsson, 2013) and European seabass (Killen et al., 2011). The reason for this difference might be due to incomplete acclimation at the beginning of the experiment, as mentioned previously, or the unique characteristics of the fish used in the present study (i.e. triploid carp), which showed low movement but high growth potential. Exploration, as indicated by the minimum distance to a novel object, showed repeatability in the twice-fed group but not in the once-fed group. This result is not unexpected; exploration showed strong inter-individual variation, and the two consecutive measurements showed either no consistency or a weak correlation. Therefore, this variable might not be an ideal indicator of exploration in triploid carp.

Effect of food availability on growth performance

In our study, the FR of fish in the twice-fed group was 39% higher than that of the once-fed group, which was in line with our expectations. However, compared with those in the once-fed group, the fish in the twice-fed group apparently had no advantage in terms of SGR (an 11%, non-significant increase) due to the lower FE (29%) of fish in the twice-fed group. A similar result was found for

juvenile Brazilian sardines (*Sardinella brasiliensis*), demonstrating that higher FR causes lower FE (Han et al., 2004; Baloi et al., 2017).

Interestingly, SGR was positively correlated with FE in both groups but was not related to FR. This might be due to narrow variation in FR due to the individual rearing of the fish and the offering of food for only a 30-min period. Thus, FR was mainly limited by the size of the oesophagus (cyprinid fish species have no stomach) or appetite. However, FE was negatively correlated with FR, which suggested that decreased digestibility might also have contributed to the decreased FE in fish with high FR in the present study. Previous studies of juvenile red snapper (*Lutjanus argentimaculatus*) (Ghulam and Pirzadaja, 2009), juvenile cichlid fish (*Simochromis pleurospilus*) (Kotrschal et al., 2014), and juvenile Brazilian sardines (Baloi et al., 2017) have found that fish reared with high FR typically have a higher gastric evacuation rate but a lower digestibility coefficient.

The relationships among growth performance, SMR and personality

SMR and personality

Generally, a life-history trade-off hypothesis predicts a positive correlation between behavioural syndromes (i.e. activity, exploration and boldness) and metabolic rate (Le Galliard et al., 2013); however, environment stressors, such as low food availability, can alter the relationships between physiology and behaviour (Killen et al., 2013). For example, in a study of European seabass, no relationship between metabolic rate and boldness was found except under food deprivation conditions (Killen et al., 2011). Our study found that relative SMR showed only weak correlations with boldness and exploration in both the once- and twice-fed groups of experimental fish (juvenile triploid carp). A possible explanation for this finding is that the correlation between metabolism and behaviour might be difficult to detect when there is adequate food (in either the twice-fed or once-fed group) (Killen et al., 2011, 2013). The satiation treatment in most previous studies is equivalent to that of the once-fed group in this study (Sun et al., 2006).

SMR and growth performance

It has long been suggested that metabolism is closely related to growth performance (Le Galliard et al., 2013). In the present study, SMR appeared to be negatively correlated with FE but positively correlated with FR in the once-fed group. This suggests that the increased maintenance metabolism of higher SMR individuals resulted in a lower ratio of ingested energy to tissue deposition due to energy competition between metabolism and growth. However, the negative effect of the higher maintenance metabolic expenditure on growth was compensated for by a higher FR in higher SMR individuals; thus, no correlation was found between final SMR and SGR in the once-fed group. Furthermore, no relationship was found between SMR and any growth variable in the twice-fed group. This finding is not unexpected, as FR in the twice-fed group was more limited by gastrointestinal structure and as competition between maintenance metabolism and growth might cease to exist when individuals are reared with unlimited food resources. Thus, our study clearly demonstrated that the relationship between growth performance and SMR is flexible and can change with food availability. These findings agree with the results of other studies (Reid et al., 2011; Auer et al., 2015b).

Growth performance and personality

It has been suggested that personality might be positively correlated with growth in fish species (Stamps, 2007; Biro and Stamps, 2008;

Cole and Quinn, 2014) due to the higher competitive ability as well as food handling and processing capacity of fish with proactive personalities. However, in the present study, both activity and boldness were uncorrelated with FR in the once-fed group after Bonferroni correction, and both were negatively correlated with FE in the once-fed group. The results from a similar study showed that shy trout grow faster (Adriaenssens and Johnsson, 2011) than bold trout. The reason for these results might be that the experimental fish were reared individually such that the competitive ability of proactive individuals gave them no food resource advantage. Furthermore, compared with proactive individuals, individuals with less active personalities might generally spend less energy on routine activities, leaving more energy for growth. The results of this study upheld the prediction that less active individuals adopt a low gain/low cost strategy, allowing them to maintain a more constant SGR. Furthermore, the growth benefit may be inflated under experimental conditions of limited food resources and no competition among conspecifics (Závorka et al., 2015). There was no relationship between the growth variables and behavioural traits in the twice-fed group, potentially due to the high availability of food resources that lessened the metabolic competition between growth and other behavioural traits (Ragland and Carter, 2004; Johnsson and Bohlinz, 2006; Careau et al., 2008). Nevertheless, our study clearly demonstrated that the relationship between personality and growth performance is complicated and varies with food availability and rearing regime.

Acknowledgements

We thank Dr Neil Metcalfe for insightful comments and constructive suggestions regarding the statistical analyses and writing, which greatly improved the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.-J.F.; Methodology: S.L.; Formal analysis: S.L.; Resources: S.-J.F.; Data curation: S.L., S.-J.F.; Writing - original draft: S.L.; Writing - review & editing: S.-J.F.; Project administration: S.-J.F.; Funding acquisition: S.-J.F.

Funding

This study was funded by a grant from the National Science Foundation of China (NSFC 31670418).

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.167783.supplemental>

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