

# Effects of water temperature and initial weight on growth, digestion and energy budget of yellow catfish *Pelteobagrus fulvidraco* (Richardson, 1846)

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## Summary

The effects of water temperature and body weight on feeding, growth, and energy budget were inevitable in the yellow catfish *Pelteobagrus fulvidraco* (Richardson, 1846), an important fish cultivated in China. This study explores the interaction of water temperature and body weight on both energy utilization strategy and energy conversion efficiency to promote further healthy culture of yellow catfish. Fish with body weights of 6 g (Group S), 16 g (Group M) and 35 g (Group B) were reared in 15 circular glass steel cylinders 80 cm in diameter × 70 cm in height (180 L) at water temperatures of 21, 24, 27, 30 and 33°C (3 replicates for each temperature) for 42 days to investigate effects of water temperature and body weight on the feeding, growth, digestion and energy budget in yellow catfish. Results showed that the levels of dry matter, protein and energy in the body were significantly affected by water temperature ( $p < .05$ ). Feeding, growth, feed conversion efficiency, digestion and energy allocation parameters were significantly related to both water temperature and body weight ( $p < .05$ ). Yellow catfish had higher maximal food consumption ( $C_{\max}$ ), food intake rate, specific growth rate, food conversion efficiency, apparent digestibility coefficient, and growth energy allocation ( $G$ ) at 24–30°C, and optimal growth at a water temperature of 27°C. Two-factor analysis of variance revealed that there was reciprocation of both water temperature and body weight on the above parameters. At the optimal temperature of 27°C, the value of energy for growth ( $G$ ) was the highest, and the value of energy for feces ( $F$ ) produced was the lowest. Yellow catfish with various body weights had energy budget equations of  $100 A = 63.70 R + 36.30 G$  in Group S,  $100 A = 62.54 R + 37.46 G$  in Group M, and  $100 A = 67.47 R + 32.53 G$  in Group B if the equations were described as percentage of the proportion of the assimilation energy. Therefore, the optimal temperature was 27°C according to its feeding, growth and digestion.

## 1 | INTRODUCTION

Feeding is the only energy investment that directly affects allocation and utilization of energy in energy budgets for fishes. Many ecological factors, especially water temperature, affect growth and other metabolic processes by influencing feeding (Chippis, Einfalt, & Wahl, 2000; Wang & Qiu, 2000; Xie, 1989). The apparent digestibility of fish

increases with increases in temperature within a suitable temperature range (Wang & Qiu, 2002; Xie & Sun, 1993). However, Qiu (2004) reported that digestibility decreased with an increase in temperature in *Spinibarbus denticulatus*. Digestibility decreased in a U-shaped change curve with temperature increases in juvenile half-smooth tongue sole *Cynoglossus semilaevis* (Fang, Tian, Dong, & Zang, 2010). Some research has suggested that digestibility might not be affected by temperature

(Beamish, 1972). In estimation of an energy budget, an important factor is water temperature, which affects feeding, basal metabolism, growth, excretion and defecation (Yuan, 2005). Cui, Chen, and Wang (1995) showed that the metabolic rate of fish increased with increases in temperature within a certain range, beyond which the metabolic rate decreased with further temperature increases. That growth energy (G) proportion in food energy (C) resulted in a bell shaped curve with respect to water temperature in red fin puffer *Fugu rubripes* (Jia, Sun, & Tang, 2008). In addition, growth energy percentage and energy utilization decreased in response to higher energy demand at water temperatures that were too high or low (Peres & Oliva-Teles, 1999).

Body weight is an important intrinsic factor affecting the growth of fish (Han, 2005). The power function equation between the maximal food consumption ( $C_{\max}$ ) and body weight ( $W$ ) is described as  $C_{\max} = aW^b$  in most species of fish (Cui, 1989). In general, specific growth rate (SGR) and food conversion efficiency (FCE) of fish decrease with increases in body weight (Peng, Wang, Ye, & Zhang, 2008; Ye & Zhang, 2002). Peng et al. (2008) and Zhou, Wu, and Zhang (2008) found that the proportion of fish growth energy (G) decreased gradually with the increases in body weight. There is a lack of consensus on interaction effects of water temperature and body weight on energy budgets in fish (Han, 2005; Imsland, Sunde, Folkvord, & Stefansson, 1996; Liu, 1998; Pedersen & Jobling, 1989; Zhou, 2002).

In the present study, effects of water temperature and body weight on the feeding, growth, and energy budget were investigated in yellow catfish, *Pelteobagrus fulvidraco* (Richardson), an important fish cultivated in China. This study explores the interaction of water temperature and body weight on both energy utilization strategy and energy conversion efficiency to promote further healthy culture of yellow catfish.

## 2 | MATERIALS AND METHODS

### 2.1 | Materials

All *P. fulvidraco* used in this experiment were purchased from the breeding base of Freshwater Fisheries Research Center, Chinese Academy of Fishery Sciences, Bihai Agricultural Technology Demonstration Park of Hubei Province, Wuhan. Yellow catfish juveniles with different initial body weights were acclimated for 2 weeks in 15 indoor tanks (2.1 m × 1.6 m × 1.1 m) at a density of 500 individuals per tank for small (4.78 ± 0.11 g), 200 per tank for middle (12.41 ± 0.29 g), and 100 individuals per tank for large (32.63 ± 0.57 g) individuals. During acclimation, water in the tanks was continually aerated except during feeding periods. The dissolved oxygen and water temperature inside all tanks were measured at 10:00 daily with 6.9 ± 0.5 mg/L ( $n = 210$ ) dissolved oxygen and a 21.8 ± 1.1°C ( $n = 210$ ) water temperature for 2 weeks. Tanks were exposed to natural light with 12L:12D. Fish were fed twice a day at 07:00 and 18:00.

Cr<sub>2</sub>O<sub>3</sub> was added as an inertia indicator in the experimental diet at a dose of 1% for determination of digestibility. Diet ingredients and nutrient contents are given in Table 1. Formed into pellets of 1 and 2 mm diameters, the diets were oven-dried at 60°C and maintained at 4°C before use.

The experimental water circulating system consisted of 15 fiberglass tank systems with 45 tanks (80 cm ø × 70 cm height, filled with 180 L water). Tap water and water temperatures in the tanks were maintained by a heat-controlling rod (Atman HT-300W). During the experiment, water in the tanks was continually aerated except at feeding time; 1/3 of the water was exchanged daily. Experimental tanks were in natural light, and dissolved oxygen, pH and water temperature inside all tanks were measured at 10:00 every day. Water quality parameters during the experiment are given in Table 2. Water flow rate through the tanks was controlled by a switch at 50 L/min.

### 2.2 | Experimental protocol

After acclimation, healthy juveniles with initial body weights of 6 g (small, S), 16 g (middle, M) and 36 g (large, L) were fasted for 1 day, then reared randomly in 45 tanks at a rate of 45 individuals per tank for S (group S), 17 individuals per tank for M (group M) and 8 individuals per tank for L (group L) for 42 days. Water temperatures were 21, 24, 27, 30, and 33°C. Each treatment was in triplicate. Water

**TABLE 1** Ingredients (% wet weight) and proximate composition (% dry matter) of the experimental diet

Ingredients	Contents (%)
Peru fishmeal	35.00
Fish oil	1.00
α-starch	5.00
Soybean meal <sup>a</sup>	36.00
Wheat flour	17.00
Soybean oil	1.00
Immune polysaccharide	0.10
Mineral premix <sup>b</sup>	3.40
Vitamin premix <sup>c</sup>	0.30
Vitamin C	0.10
Choline chloride	0.10
Chromic oxide	1.00
Proximate composition (% dry matter)	
Dry matter	94.38
Crude protein	39.88
Crude fat	4.49
Ash	7.12
Gross energy (kJ/g)	16.70

<sup>a</sup>Soybean meal as a by-product was obtained from soaked-oil soybean without squeezing.

<sup>b</sup>Mineral premix (mg/kg diet): NaCl, 500; MgSO<sub>4</sub>·7H<sub>2</sub>O, 7,500; NaH<sub>2</sub>PO<sub>4</sub>·2H<sub>2</sub>O, 12,500; KH<sub>2</sub>PO<sub>4</sub>, 16,000; Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>·H<sub>2</sub>O, 100,000; FeSO<sub>4</sub>, 1,250; C<sub>6</sub>H<sub>10</sub>CaO<sub>6</sub>·5H<sub>2</sub>O, 1,750; ZnSO<sub>4</sub>·7H<sub>2</sub>O, 176.5; MnSO<sub>4</sub>·4H<sub>2</sub>O, 81; CuSO<sub>4</sub>·5H<sub>2</sub>O, 15.5; CoSO<sub>4</sub>·6H<sub>2</sub>O, 0.5; KI, 1.5; starch, 22.5.

<sup>c</sup>Vitamin premix (mg/kg diet): thiamin, 20; riboflavin, 20; pyridoxine, 20; cyanocobalamin, 2; folic acid, 5; calcium pantothenate, 50; inositol, 100; niacin, 100; biotin, 5; starch, 3,226; ascorbic acid, 111; Vit. A, 110; Vit. D<sub>3</sub>, 20; Vit. E (DL-α-tocopherol acetate), 100; Vit. K<sub>3</sub> (menadione sodium bisulfite), 10.

Temperature (°C)	21	24	27	30	33
Actual temperature (°C)	21.1 ± 0.5	23.6 ± 0.6	27.1 ± 0.3	30.5 ± 0.4	33.0 ± 0.7
Dissolved oxygen (mg/L)	6.47 ± 0.61	6.45 ± 0.49	6.35 ± 0.44	6.41 ± 0.37	6.32 ± 0.49
pH	7.36 ± 0.06	7.28 ± 0.07	7.39 ± 0.06	7.26 ± 0.10	7.42 ± 0.08

**TABLE 2** Water quality parameters in the experiment at five experimental water temperatures

temperature in the tanks gradually increased to the required temperature using a control-heating rod (Atman HT-300W) at a rate of less than 2°C per day. After water warming, the fish were acclimatized for 5 days, fasted for 1 day under the experimental conditions prior to the formal start of the experiment.

During the experiment, fish were fed to satiation twice a day at 7:00 and 18:00; the feeding amount was recorded daily. After 40 min feeding, food remains were siphoned off, dried, and weighed. Food residue recovery was calibrated by placing a certain amount of food in water for 1 hr, oven-dried to a constant weight and then weighed. Apparent feed intake of the fish was estimated by the food residue recovery, whereby the feces were siphoned off 2 h after feeding and dried at 70°C for use.

At the end of the experiment, the experimental fish were fasted for 1 day, and then weighed individually. Four, three, and two samples were randomly obtained from tanks in groups S, M, and L, respectively, and weighed and oven-dried to constant weights for body composition analysis.

## 2.3 | Determination of the samples

At the end of the experiment, the contents of dry matter, protein, fat, ash, and energy in the fish and diet, protein and energy content in the feces, and Cr<sub>2</sub>O<sub>3</sub> content in feed and feces were measured. Dry matter was determined by drying to a constant weight at 105°C in an oven (constant temperature DHG-9140A type electric heating drying box manufactured by Shanghai Yiheng Instruments Co., Ltd). Crude protein content was measured with an automatic analyzer (Kjeltec™ 2300—based on Tecator™ Technology). Crude fat content was determined using ethyl ether extraction, and ash content was measured by burning at 550°C for 6 hr to constant weight in a muffle furnace (SX-4-10 box type resistant furnace manufactured by Tianjin Taisite Instrument Co., Ltd.). Energy was measured using a Phillipson microbomb calorimeter (Gentry Instruments Inc., Aiken, OH, USA). Cr<sub>2</sub>O<sub>3</sub> contents of feed and feces were determined by TAS-986 atomic absorption spectrophotometer (Beijing Puxi General Instrument Co., Ltd) via the content of Cr.

## 2.4 | Measurement index and calculation formula

### 2.4.1 | Feeding and growth index

Ingestion rate (IR), specific growth rate in wet weight (SGR<sub>w</sub>), specific growth rate in dry weight (SGR<sub>d</sub>), specific growth rate in protein (SGR<sub>p</sub>), specific growth rate in energy (SGR<sub>e</sub>), feed conversion efficiency in

wet weight (FCE<sub>w</sub>), feed conversion efficiency in dry weight (FCE<sub>d</sub>), feed conversion efficiency in protein (FCE<sub>p</sub>), and feed conversion efficiency in energy (FCE<sub>e</sub>) were calculated according to the equations:

$$IR(\%/day) = FI \times 100 / \{[(W_t + W_0) / 2] \times t\}$$

$$SGR_w(\%/day) = 100 \times (\ln W_t - \ln W_0) / t$$

$$SGR_d(\%/day) = 100 \times [\ln (W_t \times CD_t) - \ln (W_0 \times CD_0)] / t$$

$$SGR_p(\%/day) = 100 \times [\ln (W_t \times CP_t) - \ln (W_0 \times CP_0)] / t$$

$$SGR_e(\%/day) = 100 \times [\ln (W_t \times CE_t) - \ln (W_0 \times CE_0)] / t$$

$$FCE_w(\%) = 100 \times (W_t - W_0) / FI$$

$$FCE_d(\%) = 100 \times (W_t \times CD_t - W_0 \times CD_0) / (FI \times CD)$$

$$FCE_p(\%) = 100 \times (W_t \times CP_t - W_0 \times CP_0) / (FI \times CP)$$

$$FCE_e(\%) = 100 \times (W_t \times CE_t - W_0 \times CE_0) / (FI \times CE)$$

where  $W_t$  and  $W_0$  are the final and initial wet body weight (g),  $CD_t$  and  $CD_0$  are the dry matter contents in final and initial body weight (%),  $CP_t$  and  $CP_0$  are the protein contents in final and initial body weight (%),  $CE_t$  and  $CE_0$  (kJ/g) are the energy contents in final and initial body weight (kJ/g),  $FI$  is the food consumption per fish (g),  $CD$  is the dry matter in feed (%),  $CP$  is the protein content in feed (%),  $CE$  is the energy level in feed (kJ/g), and  $t$  is the duration of the experiment (day).

### 2.4.2 | Digestibility index

Nitrogenous excretion ( $u$ , mg g<sup>-1</sup> day<sup>-1</sup>), faecal production ( $f$ , mg g<sup>-1</sup> day<sup>-1</sup>), apparent digestibility coefficient in dry matter (ADC<sub>d</sub>, %), apparent digestibility coefficient in crude protein (ADC<sub>p</sub>, %), and apparent digestibility coefficient in gross energy (ADC<sub>e</sub>, %) were estimated according to the equations:

$$u = UN / \{[(W_t + W_0) / 2] \times t\}$$

$$f = FF / \{[(W_t + W_0) / 2] \times t\}$$

$$ADC_d = 100 \times (1 - C_1 / C_2)$$

$$ADC_p = 100 \times (1 - C_1 P_2 / C_2 P_1)$$

$$ADC_e = 100 \times (1 - C_1 E_2 / C_2 E_1)$$

**TABLE 3** Body composition (%) and energy content (kJ/g wet weight) of juvenile yellow catfish *Pelteobagrus fulvidraco* with different body weights at five experimental water temperatures

Temperature (°C)	Size	Dry matter (%)	Protein (%)	Lipid (%)	Ash (%)	Energy (kJ/g)
33	S	24.74 ± 0.13ab	15.09 ± 0.18Ba	5.37 ± 0.33	3.88 ± 0.04	5.38 ± 0.05a
33	M	25.44 ± 0.53a	15.79 ± 0.14ABa	6.07 ± 0.39	3.88 ± 0.05	5.71 ± 0.14
33	B	25.48 ± 0.69	16.18 ± 0.27A	6.48 ± 0.66	3.85 ± 0.03	5.74 ± 0.19
30	S	24.55 ± 0.26a	15.67 ± 0.12Bab	5.47 ± 0.09B	3.82 ± 0.03	5.34 ± 0.01a
30	M	25.60 ± 0.74a	16.01 ± 0.47Aa	6.52 ± 0.57AB	3.58 ± 0.05	5.70 ± 0.16
30	B	25.35 ± 0.63	16.33 ± 0.35A	7.10 ± 0.44A	3.41 ± 0.06	5.82 ± 0.14
27	S	25.88 ± 0.25c	16.53 ± 0.32c	6.04 ± 0.16B	3.57 ± 0.07	5.82 ± 0.06b
27	M	26.17 ± 0.24b	16.92 ± 0.16b	6.31 ± 0.33B	3.46 ± 0.06	5.87 ± 0.09
27	B	26.30 ± 0.21	17.32 ± 0.31	7.39 ± 0.28A	3.40 ± 0.10	6.14 ± 0.08
24	S	25.47 ± 0.38bc	16.13 ± 0.33Bbc	5.44 ± 0.20B	3.74 ± 0.05	5.95 ± 0.16b
24	M	25.91 ± 0.43ab	16.88 ± 0.11ABb	5.81 ± 0.51B	3.57 ± 0.06	5.86 ± 0.09
24	B	26.06 ± 0.37	17.12 ± 0.40A	7.40 ± 0.31A	3.41 ± 0.05	5.97 ± 0.06
21	S	26.18 ± 0.15c	15.20 ± 0.26Ba	5.28 ± 0.30	3.98 ± 0.13	6.09 ± 0.07b
21	M	26.36 ± 0.30c	16.15 ± 0.14Aab	6.19 ± 0.27	3.86 ± 0.10	5.93 ± 0.04
21	B	26.27 ± 0.26	16.50 ± 0.36A	6.30 ± 0.33	3.78 ± 0.10	5.89 ± 0.10
Two-way ANOVA						
Temperature		*	*	ns	ns	*
Size		ns	*	*	ns	ns
Interaction		ns	ns	ns	ns	ns

Values (mean ± SE,  $n = 3$ ) with different uppercase letters within the same column are significantly different at .05 probability levels within various body weight groups ( $p < .05$ ); values (mean ± SE,  $n = 3$ ) with different letters within the same column are significantly different at the .05 probability level within different temperature groups ( $p < .05$ ); values (mean ± SE,  $n = 3$ ) with same letters within the same column are not significantly different ( $p > .05$ ), and sequential. \*Significantly different ( $p < .05$ ); ns = significantly different, and sequential.

where  $C_1$  and  $C_2$  are the  $Cr_2O_3$  contents in feed and feces (%),  $P_1$  and  $P_2$  (%) are the protein contents in feed and feces (%),  $E_1$  and  $E_2$  are the energy contents in feed and feces (kJ/g), UN is the nitrogen excretion per fish (mg) and FF is the dry weight of feces produced per fish (mg).

## 2.5 | Energy budget

Energy budgets were calculated using the method described by Zhou et al. (2008), and were established according to the equation:  $C = F + U + R + G$  or  $A = R + G$ , where  $A$  is assimilated energy,  $C$  is energy consumed from food assimilation (kJ per ind/day),  $G$  is energy for growth,  $F$  is energy of feces produced,  $R$  is energy lost through respiration, and  $U$  is energy loss through ammonia excretion. The  $C$ ,  $F$ ,  $U$ ,  $R$  and  $G$  were estimated according to the equations:

$$C = FI \times CE$$

$$F = C \times (1 - ADC_e / 100)$$

$$U = [(NI - NF - NR) \times 17 / 14] \times 24.83$$

$$G = W_t \times CE_t - W_0 \times CE_0$$

$$R = C - F - U - G$$

where FI is food ingestion (g/day), CE is energy content of feed (kJ/g), NI, NF and NR are nitrogen infeed, feces and retention in fish (kJ), and CE<sub>t</sub> (kJ/g) and CE<sub>0</sub> (kJ/g) are the energy of final and initial body weight of the fish.

## 2.6 | Statistical analysis

All data were collated by Microsoft Excel 2003 and analyzed using the statistical software package SPSS (Version 6.0). One-way of variance (ANOVA) was used to analyze the effects of yellow catfish size and water temperature, and two-way analysis of variance followed by Duncan's multiple range tests were used to analyze differences in indices. Differences were considered significant or highly significant at probability levels of  $p < .05$  and  $p < .01$ , respectively. Figures were made with Origin 8 software.

## 3 | RESULTS

### 3.1 | Body composition and energy content

The influences of body weight and water temperature on body composition and energy content in *P. fulvidraco* are shown in Table 3.

Variance analysis showed significant effects of water temperature on dry matter and energy content of the fish ( $p < .05$ ), with maximal matter and energy content at 21 and 27°C. Water temperature and body weight had significant effects on whole body protein content ( $p < .05$ ), with maximal protein content at 27 and 24°C. The interaction between water temperature and body weight showed no significant effect on protein content of the fish ( $p > .05$ ). The multiple comparisons revealed that there were significant differences in fat contents of the fish with different body weights among the treatment groups ( $p < .05$ ), except for fish at 33 and 21°C. There were significant effects of water temperature and interactions of both body weight and water temperature on fat contents ( $p < .05$ ). The interaction effects between water temperature and body weight, and effects of water temperature and body weight on ash content in the fish were not significant ( $p > .05$ ).

### 3.2 | Food ingestion, growth and digestive parameters

The maximal food ingestion rate ( $C_{max}$ ), food ingestion rate (IR), SGR, FCE and apparent digestibility (ADC) in the yellow catfish in various groups are shown in Table 4. There were significant effects of water temperature and body weight as well as interactions between the parameters in the yellow catfish in the present experiment ( $p < .05$ ) (Table 5). The relationship between  $C_{max}$  and water temperature was described as a bell shaped curve at different water temperatures;  $C_{max}$  was found to increase with the increases in body weight within groups of various weights. The relationship between the  $C_{max}$  and body weight in the fish was expressed by the equation  $\ln C_{max} = a + b \ln W$  within water temperature replicates in the experiment (Figure 1). The same situation was observed with the effect of water temperature on IR, but not with the effect of body weight on IR. Two-factor analysis of variance showed that there were significant interaction effects of both water temperature and body weight on IR in the fish ( $p < .05$ ).

There were similar change tendencies in  $SGR_w$ ,  $SGR_d$ ,  $SGR_p$  and  $SGR_e$  in the yellow catfish within similar experimental water temperature and body weights, and their relationship with water temperature showed a bell shaped curve, with maximal values at 27°C. However, the SGR related negatively to body weight. Two-factor analysis of variance revealed that the water temperature and body weight had significant effects on SGR ( $p < .05$ ), and significant interactions of both water temperature and body weight on  $SGR_w$ ,  $SGR_d$  and  $SGR_p$  were observed in yellow catfish ( $p < .05$ ). There was a significant effect of water temperature on FCE in the fish ( $p < .05$ ), significantly lower at 21°C than that at other water temperatures ( $p < .05$ ). There was a significant effect of body weight on FCE in the fish ( $p < .05$ ). A significant interaction between temperature and body weight on FCE (except for  $FCE_e$ ) was found in the yellow catfish ( $p < .05$ ).

Water temperature and body weight affected ADC in yellow catfish significantly ( $p < .05$ ), and there was a significant interaction effect between water temperature and body weight on ADC ( $p < .05$ ). There

was no significant effect of water temperature and body weight on  $ADC_p$  and  $ADC_d$  in the fish ( $p > .05$ ).

### 3.3 | Energy budget

The bioenergetics parameters in *P. fulvidraco* are shown in Table 6. The proportion of energy for growth (G) in energy consumed from food assimilation (C) were described in a bell shaped curve with respect to water temperature negatively correlated to body weight, with the order of proportion arranged as: 27°C > 24°C > 30°C > 33°C > 21°C. Two-factor analysis of variance showed that both water temperature and body weight had significant effects on the proportion of G in C ( $p < .05$ ), without a significant interaction effect of both on the proportion of G in C ( $p > .05$ ). Both water temperature and body weight had a significant effect on proportion of energy of feces produced (F) in C ( $p < .05$ ), but showed the opposite trend with respect to the proportion of G in C. Water temperature had a significant effect on the proportion of energy lost through ammonia excretion (U) in C ( $p < .05$ ), while body weight did not significantly affect the proportion of U in C ( $p > .05$ ). However, there was a significant interaction between temperature and body weight on the proportion of U in C in the fish ( $p < .05$ ). The same tendency was observed in the proportion of energy lost through respiration (R) in C. There was a significant effect of water temperature and body weight on the proportion of assimilated energy (A) in C when the energy budget was expressed as the proportion of A in C ( $p < .05$ ). The yellow catfish in group M had the highest proportion of A in C, significantly higher than the animals in group L ( $p < .05$ ), but were not significantly different from the fish in group S ( $p > .05$ ). The proportion of A in R was opposite to the proportion of A in G.

Therefore, water temperature had a significant influence on various components in the energy budgets of yellow catfish ( $p < .05$ ). The energy budget equations are described in the yellow catfish of various body weights exposed to different water temperatures by a combination of different energy budget equations in the fish with various body weights exposed to the same temperature (Table 7).

The energy budget equations in the yellow catfish with the same body weights exposed to different water temperatures are described by the combination of different energy budget equations in the fish of the same body weight exposed to various temperatures when the energy budget equation was expressed as proportion of A:

$$\text{In the group S: } 100A = 63.70R + 36.30G$$

$$\text{In the group M: } 100A = 62.54R + 37.46G$$

$$\text{In the group B: } 100A = 67.47R + 32.53G$$

## 4 | DISCUSSION

In fish, food ingestion is positive related to water temperature when food is not limited; that is, food intake will increase as the water

**TABLE 4** Maximum food ingestion ( $C_{max}$ , g per fish/day), food ingestion rate (FI, % per day), initial body weight (IBW, g), final body weight (FBW, g), specific growth rate in wet weight ( $SGR_w$ , % per day), specific growth rate in dry weight ( $SGR_d$ , % per day), specific growth rate in protein ( $SGR_p$ , % per day), specific growth rate in energy ( $SGR_e$ , % per day), feed conversion efficiency in wet weight ( $FCE_w$ , %), feed conversion efficiency in dry weight ( $FCE_d$ , %), feed conversion efficiency in protein ( $FCE_p$ , %), feed conversion efficiency in energy ( $FCE_e$ , %), apparent digestibility coefficient in dry matter ( $ADC_d$ , %), apparent digestibility coefficient in protein ( $ADC_p$ , %), apparent digestibility coefficients in energy ( $ADC_e$ , %) of juvenile yellow catfish *Pelteobagrus fulvidraco* with different body weights at five experimental water temperatures

Temperature (°C)	Size	$C_{max}$	FI	IBW	FBW	$SGR_w$
33	S	0.24 ± 0.00Cb	2.62 ± 0.08A	6.03 ± 0.13C	12.67 ± 0.52Cb	1.76 ± 0.13Ab
33	M	0.58 ± 0.01Bb	2.30 ± 0.08ABa	16.24 ± 0.27B	34.40 ± 0.95Bb	1.79 ± 0.05Ab
33	B	1.07 ± 0.04Ab	2.16 ± 0.12Bab	36.33 ± 0.27A	63.07 ± 1.43Ab	1.31 ± 0.07Bb
30	S	0.27 ± 0.00Cc	2.51 ± 0.07	5.95 ± 0.10C	15.71 ± 0.34Cc	2.31 ± 0.01Accd
30	M	0.68 ± 0.01Bd	2.53 ± 0.03b	16.27 ± 0.33B	37.23 ± 0.55Bc	1.97 ± 0.06Bbc
30	B	1.27 ± 0.08Ac	2.41 ± 0.15bc	35.41 ± 0.60A	70.28 ± 1.02Ac	1.63 ± 0.02Cc
27	S	0.30 ± 0.00Cd	2.55 ± 0.06	6.03 ± 0.23C	17.74 ± 0.43Cd	2.57 ± 0.11Ad
27	M	0.78 ± 0.01Be	2.73 ± 0.04c	16.33 ± 0.30B	40.77 ± 1.07Bd	2.18 ± 0.07Bc
27	B	1.46 ± 0.07Ac	2.60 ± 0.13c	35.67 ± 0.65A	76.39 ± 0.57Ad	1.81 ± 0.03Cd
24	S	0.26 ± 0.00Cc	2.47 ± 0.00	6.07 ± 0.17C	15.37 ± 0.33Cc	2.21 ± 0.09Ac
24	M	0.64 ± 0.01Bc	2.38 ± 0.05ab	16.10 ± 0.12B	37.84 ± 0.68Bc	2.03 ± 0.06Ac
24	B	1.33 ± 0.06Abc	2.45 ± 0.13bc	36.06 ± 0.29A	72.06 ± 0.18Ac	1.65 ± 0.01Bc
21	S	0.21 ± 0.00Ca	2.72 ± 0.12A	5.92 ± 0.14C	9.41 ± 0.36Ca	1.10 ± 0.04Aa
21	M	0.51 ± 0.02Ba	2.39 ± 0.03Bab	16.04 ± 0.21B	26.96 ± 0.86Ba	1.24 ± 0.07Aa
21	B	0.81 ± 0.02Aa	1.92 ± 0.07Ca	35.73 ± 0.49A	48.85 ± 0.85Aa	0.74 ± 0.02Ba
Temperature (°C)	Size	$SGR_d$	$SGR_p$	$SGR_e$	$FCE_w$	$FCE_d$
33	S	1.84 ± 0.14Ab	1.76 ± 0.11Ab	1.83 ± 0.16Ab	64.65 ± 6.52b	17.42 ± 1.73b
33	M	1.87 ± 0.06Ab	1.90 ± 0.05Ab	1.88 ± 0.07Ab	74.44 ± 4.40b	20.68 ± 1.13b
33	B	1.37 ± 0.07Bb	1.39 ± 0.11Bb	1.35 ± 0.07Bb	59.94 ± 6.39b	16.67 ± 1.48b
30	S	2.37 ± 0.03Ac	2.40 ± 0.03Ac	2.36 ± 0.02Ac	85.71 ± 2.72Ac	22.61 ± 0.84c
30	M	2.07 ± 0.08Bbc	2.11 ± 0.06Bc	2.06 ± 0.07Bbc	73.76 ± 3.00Bb	20.67 ± 1.30b
30	B	1.68 ± 0.04Cc	1.73 ± 0.05Cc	1.70 ± 0.05Cc	65.80 ± 3.78Bb	18.12 ± 1.85b
27	S	2.75 ± 0.12Ad	2.78 ± 0.06Ad	2.82 ± 0.13Ad	92.02 ± 4.63Ac	26.17 ± 1.18Ac
27	M	2.33 ± 0.09Bd	2.45 ± 0.08Bd	2.34 ± 0.09Bd	74.81 ± 3.20Bb	21.62 ± 1.08Bb
27	B	1.95 ± 0.04Cd	2.05 ± 0.03Cd	2.02 ± 0.03Bd	66.72 ± 2.71Bb	19.50 ± 0.97Bb
24	S	2.36 ± 0.08Ab	2.37 ± 0.09Ac	2.52 ± 0.09Accd	83.73 ± 3.04Ac	23.46 ± 0.65Ac
24	M	2.16 ± 0.03Bcd	2.30 ± 0.07Accd	2.19 ± 0.03Bcd	80.72 ± 3.79Ab	23.01 ± 0.44Ab
24	B	1.76 ± 0.04Cc	1.86 ± 0.04Bcd	1.78 ± 0.01Cc	64.88 ± 2.81Bb	18.77 ± 1.14Bb
21	S	1.31 ± 0.03Aa	1.11 ± 0.06Ba	1.46 ± 0.04Aa	40.04 ± 3.10Ba	12.67 ± 0.76a
21	M	1.41 ± 0.09Aa	1.40 ± 0.05Aa	1.42 ± 0.09Aa	50.58 ± 3.06Aa	15.57 ± 1.10a
21	B	0.88 ± 0.04Ba	0.87 ± 0.07Ca	0.85 ± 0.05Ba	38.53 ± 1.92Ba	12.32 ± 0.86a
Temperature (°C)	Size	$FCE_p$	$FCE_e$	$ADC_d$	$ADC_p$	$ADC_e$
33	S	24.38 ± 2.01b	21.40 ± 2.47a	69.46 ± 0.77Ab	85.24 ± 0.27Aab	76.90 ± 0.89Aab
33	M	30.69 ± 1.87b	26.30 ± 1.48b	65.88 ± 0.85Ba	82.01 ± 0.35Ba	74.54 ± 0.65ABb
33	B	25.48 ± 3.65ab	20.93 ± 1.76b	63.05 ± 1.07Ba	79.40 ± 0.48Cb	72.12 ± 0.86Bb
30	S	34.41 ± 1.20c	27.72 ± 0.93b	72.77 ± 0.23Ac	87.24 ± 0.54Abc	80.73 ± 0.17Ac
30	M	30.95 ± 1.45b	25.91 ± 1.42b	69.24 ± 0.52Bb	83.66 ± 0.23Bcd	78.44 ± 0.32Bd
30	B	28.14 ± 2.57b	23.66 ± 1.96b	66.67 ± 0.84Cb	83.11 ± 0.47Bc	76.51 ± 0.40Ccd
27	S	39.78 ± 1.13Ad	33.72 ± 1.92Ac	73.93 ± 0.59Ac	88.04 ± 0.37Ac	82.10 ± 0.40Ac
27	M	34.05 ± 1.46ABbc	27.41 ± 1.37Bb	70.24 ± 0.35Bb	84.74 ± 0.55Bd	79.84 ± 0.27Bd
27	B	31.48 ± 2.20Bb	26.36 ± 1.66Bb	67.68 ± 0.42Cb	82.60 ± 0.44Cc	77.93 ± 0.27Cd

(Continues)



TABLE 4 (Continued)

Temperature (°C)	Size	FCE <sub>p</sub>	FCE <sub>e</sub>	ADC <sub>d</sub>	ADC <sub>p</sub>	ADC <sub>e</sub>
24	S	35.25 ± 1.32Accd	32.18 ± 1.36Abc	72.41 ± 0.77Ac	86.51 ± 0.42Ab	78.48 ± 0.87Ab
24	M	36.90 ± 1.76Ac	29.64 ± 0.70Ab	68.53 ± 0.54Bb	83.09 ± 0.29Bbc	76.69 ± 0.23ABc
24	B	30.36 ± 2.63Bb	24.50 ± 1.54Bb	66.05 ± 0.33Cb	82.13 ± 0.21Bc	75.22 ± 0.80Bc
21	S	15.43 ± 1.61a	18.07 ± 1.33a	66.63 ± 0.70Aa	84.58 ± 0.15Aa	76.03 ± 0.89Aa
21	M	22.50 ± 0.99a	19.91 ± 1.36a	64.29 ± 0.49Ba	81.00 ± 0.60Ba	72.66 ± 0.82Ba
21	B	18.18 ± 2.00a	15.18 ± 1.27a	61.30 ± 0.66CAa	77.48 ± 0.40Ca	69.52 ± 0.58Ca

TABLE 5 Two-way ANOVA of ingestion, growth and digestibility parameters in the experiment

Item	Temperature	Size	Interaction
C <sub>max</sub> (g per fish/day)	*	*	*
FR	*	*	*
IBW	ns	*	ns
FBW	*	*	*
SGR <sub>w</sub>	*	*	*
SGR <sub>d</sub>	*	*	*
SGR <sub>p</sub>	*	*	*
SGR <sub>e</sub>	*	*	ns
FCE <sub>w</sub>	*	*	*
FCE <sub>d</sub>	*	*	*
FCE <sub>p</sub>	*	*	*
FCE <sub>e</sub>	*	*	ns
ADC <sub>d</sub>	*	*	ns
ADC <sub>p</sub>	*	*	*
ADC <sub>e</sub>	*	*	ns

temperature rises. When the water temperature is beyond a certain range, however, food ingestion will decrease with an increasing water temperature (Brett & Groves, 1979; Shi, 1991). In the present study, the maximal food ingestion rate ( $C_{\max}$ ) significantly increased with an elevated water temperature within the range of 21–27°C, but significantly decreased with an increase in water temperature within the range of 27–33°C. The changing trend of  $C_{\max}$  in yellow catfish is similar to the observations of the optimal feeding water temperature of 28°C in juvenile three-banded sweet lip (*Plectorhynchus cinctus*) (Wang & Qiu, 2000), and to the optimal feeding water temperature of 25.5°C in *Leiocassis longirostris* with body weight of 400 g (Han, 2005). In the present experiment, relationships between  $C_{\max}$  and body weight are described as a logarithmic function equation  $\ln C_{\max} = a + b \ln W$ , which is consistent with the fact that the relationship between the maximum food consumption and body weight is expressed as a power function  $C_{\max} = aW^b$  in most of the fish summarized by Cui (1989). The value of  $b$  is generally less than 1, indicating that food consumption decreased with increases in body weight. Interestingly,  $b = 1.0134$  was observed in the optimal growth group (group 27°C) in the present experiment, indicating that the food consumption rate increased with the increase in body weight, but below the threshold of significance. However, the regression  $b$  value was below 1 (0.80–0.99) in the yellow catfish in

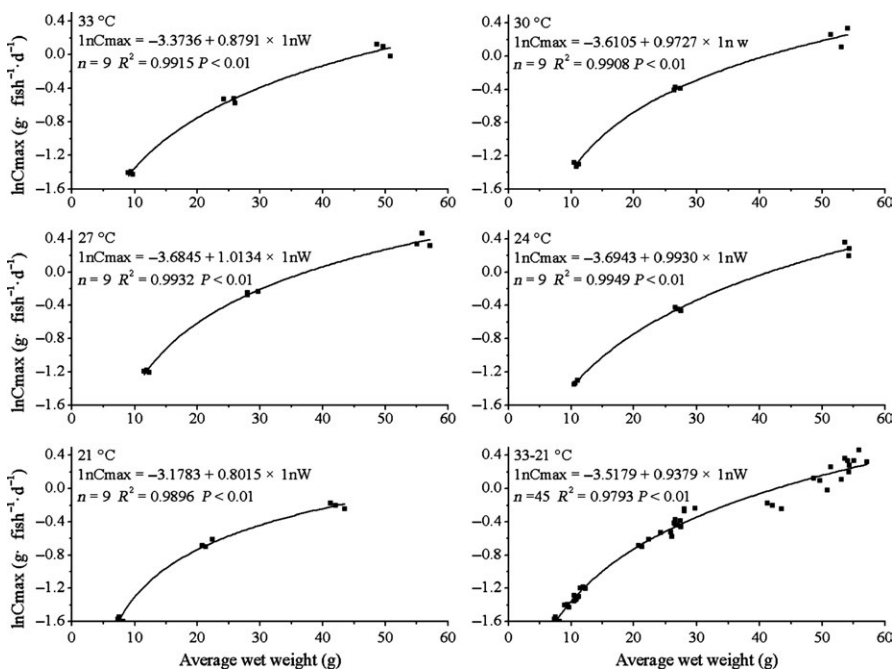


FIGURE 1 Regression relationship between maximum food consumption ( $C_{\max}$ ) and average wet weight of yellow catfish *Pelteobagrus fulvidraco* at different temperatures during the 60 days experiment

**TABLE 6** Energy budgets of juvenile yellow catfish *Pelteobagrus fulvidraco* with different body weights at five experimental water temperatures during the 60 days experiment

Temperature (°C)	Size	C (kJ g <sup>-1</sup> day <sup>-1</sup> )	As a percentage of C (%)				As a percentage of A (%)	
			G	F	U	R	R	G
33	S	0.438 ± 0.013A	21.40 ± 2.47a	23.10 ± 0.89Bbc	6.52 ± 0.20b	48.99 ± 1.73b	69.67 ± 3.13Ac	30.33 ± 3.13Ba
33	M	0.384 ± 0.013ABa	26.30 ± 1.48b	25.46 ± 0.65ABc	5.56 ± 0.26ab	42.68 ± 1.95ab	61.84 ± 2.40Bab	38.16 ± 2.40Ab
33	B	0.361 ± 0.019Bab	20.93 ± 1.76b	27.88 ± 0.86Ac	5.93 ± 0.48	45.25 ± 2.25	68.33 ± 2.87Aa	31.67 ± 2.87Bb
30	S	0.419 ± 0.012	27.72 ± 0.93b	19.27 ± 0.17Ca	5.72 ± 0.15a	47.29 ± 0.90b	63.05 ± 1.22Bb	36.95 ± 1.22Ab
30	M	0.423 ± 0.005b	25.91 ± 1.42b	21.56 ± 0.32Ba	5.91 ± 0.17bc	46.63 ± 1.19b	64.29 ± 1.83Bb	35.71 ± 1.83Aab
30	B	0.402 ± 0.025bc	23.66 ± 1.96bc	23.49 ± 0.40Aab	6.05 ± 0.33	46.81 ± 1.95	66.43 ± 2.78Aa	33.57 ± 2.78Bb
27	S	0.426 ± 0.010	33.72 ± 1.92Ac	17.90 ± 0.40Ca	5.23 ± 0.09a	43.14 ± 1.56a	56.15 ± 2.28Ba	43.85 ± 2.28Ac
27	M	0.455 ± 0.006c	31.20 ± 1.37Bc	20.16 ± 0.27Ba	5.68 ± 0.19b	42.96 ± 1.43b	57.93 ± 1.87Ba	42.07 ± 1.87Ab
27	B	0.435 ± 0.022c	27.48 ± 1.66Bc	22.07 ± 0.27Aa	5.80 ± 0.23	44.66 ± 1.23	61.91 ± 2.09Aa	38.09 ± 2.09Bb
24	S	0.412 ± 0.001	32.18 ± 1.36Abc	21.52 ± 0.87Bb	5.41 ± 0.13a	40.89 ± 0.80a	55.98 ± 1.43Ba	44.02 ± 1.43Ac
24	M	0.398 ± 0.008ab	29.64 ± 0.70Abc	23.31 ± 0.23ABb	5.05 ± 0.19a	41.99 ± 0.67a	58.62 ± 0.93Ba	41.38 ± 0.93Ab
24	B	0.410 ± 0.021bc	24.50 ± 1.54Bbc	24.78 ± 0.80Ab	5.67 ± 0.35	45.06 ± 1.74	64.77 ± 2.30Aa	35.23 ± 2.30Bb
21	S	0.455 ± 0.020A	18.07 ± 1.33a	23.97 ± 0.89Cc	7.46 ± 0.17c	50.50 ± 1.19b	73.67 ± 1.78ABc	26.33 ± 1.78ABa
21	M	0.399 ± 0.006Bab	19.91 ± 1.36a	27.34 ± 0.82Bd	6.33 ± 0.05c	46.42 ± 0.52b	70.03 ± 1.68Bc	29.97 ± 1.68Aa
21	B	0.321 ± 0.011Ca	15.18 ± 1.27a	30.48 ± 0.58Ad	6.53 ± 0.27	47.81 ± 1.33	75.90 ± 2.01Ab	24.10 ± 2.01Ba
<b>Two-way ANOVA</b>								
Temperature		*	*	*		*	*	*
Size		*	*	ns		ns	*	*
Interaction		ns	ns	*		*	ns	ns

A = assimilated energy; C = energy consumed from food assimilation, F = energy of feces produced, G = energy for growth, R = energy lost through respiration, U = energy loss through ammonia excretion (excretory energy loss).

other water temperature groups and various body weight groups at various water temperatures. The regression *b* value in the present experiment was larger than that in the three-banded sweet lip (*b* = 0.60–0.64) (Wang & Qiu, 2000) and in *Leiocassis longirostris* (Han, 2005). In the equation of maximum food consumption rate = food intake × average body weight, the higher regression *b* value of yellow catfish may be attributed to the relative slow growth, lower FCE and lower apparent digestibility found in small fish (Han, 2005). In the experiment the optimal temperature for feeding and growth was 24–30°C. In our experiment, however, the test fish in the smallest body weight class showed similar growth to the average weight of the fish fed the maximum food ration. Finally, as in most other fishes (Liu & Sun, 2005; Peng et al., 2008), the food ingestion rate of yellow catfish decreased with increases in body weight.

In the temperature range given in this experiment, the apparent digestibility (ADC) in the yellow catfish showed a bell shaped curve, describing the relationship between the temperature and ADC. On the contrary, digestibility was not affected by temperature (Beamish, 1972). Digestibility decreased with increasing water temperatures in minnow species (*Phoxinus phoxinus*) (Cui & Wootton, 1988) and *Spinibarbus denticulatus* (Qiu, 2004). More interestingly, the digestibility changed as 'U' type with the increase in temperature in juvenile half-smooth tongue-sole (*Cynoglossus semilaevis*) reported by

Fang et al. (2010). These results suggest that there are differences between fish species regarding temperature and digestibility. As FCE is affected by the final body weight and maximum food ingestion, high FCE at a high temperature may result from an increase in maximum food consumption being concealed by rapid growth at high water temperatures. In addition, although the energy consumed from food assimilation (C) was not reduced in the lower water temperature group (21°C group), in this experiment the reduction of FCE derived from the high proportion of *F* in *C*, and low apparent digestibility. In poikilothermal animals, a warming of the temperature – a very important environmental factor in the suitable temperature range, will accelerate the move of food through the digestive tract of animals, and facilitate digestion via improvement in digestive enzyme activity; however, beyond optimum temperatures, digestive enzyme activity of animals will be significantly reduced (Han, 2005). As temperatures rise the evacuation rates increase, which may contribute to lower digestibility. In contrast, high water temperatures may result in rapid digestion by high digestive enzyme activity. Therefore, higher evacuation rates, coupled with higher levels of digestive enzyme activity associated with temperature increases could affect feed conversion efficiency. Low FCE could be due to an increase in feces caused by rapid movement of consumed food through the digestive tract; alternatively, high FCE can be found due to a decrease in feces if the mobility



**TABLE 7** Energy budget equations in juvenile yellow catfish *Pelteobagrus fulvidraco* with various body weights exposed to the same temperature

Temperature (°C)	Energy budget equations
33	100 C = 25.48 F + 6.00 U + 45.64 R + 22.88 G or 100 A = 66.61 R + 33.39 G
30	100 C = 21.44 F + 5.89 U + 46.91 R + 25.76 G or 100 A = 64.59 R + 35.41 G
27	100 C = 20.04 F + 5.57 U + 43.59 R + 30.80 G or 100 A = 58.66 R + 41.34 G
24	100 C = 23.20 F + 5.38 U + 42.65 R + 28.77 G or 100 A = 59.79 R + 40.21 G
21	100 C = 27.26 F + 6.77 U + 48.24 R + 17.72 G or 100 A = 73.20 R + 26.80 G

speed is less than the rate of digestion. Lei & Li (2000) pointed out that variations in water temperature under wild rearing conditions do not cause significant changes in digestibility in most fish and shrimp because of a balance in the relationship between food movement speed and enzyme activity (Lei & Li, 2000).

A comparison of trends found among  $C_{max}$ , ADC, and FCE with water temperature suggests that higher SGRs in yellow catfish are a result of a higher food ingestion, high ADC, and high FCE at appropriate water temperatures. Beyond the optimal water temperature, however, growth energy was reduced with increases in water temperature because active feeding behavior was unable to keep pace with the temperature-induced increase in the basal metabolic rate. In contrast, physiological effects of high temperatures result in the inhibition of normal growth in yellow catfish (Tian, Dong, & Wang, 2004).

In this experiment, the proportion of growth energy (G) in the energy consumed from food assimilation (C) showed a bell shaped curve with water temperature, which is consistent with the results in redfin puffer (*Takifugu rubripes*) reported by Jia et al. (2008). Above the optimum growth temperature range, food ingestion rate, feeding speed and the proportion of energy lost through respiration (R) in energy consumed from food assimilation (C) in yellow catfish increased, and food was not fully digested to form feces, causing a proportional increase in fecal energy (F) and a decrease in percentage of growth energy (G) in C. When water temperature was kept below the optimum growth temperature range, however, food ingestion rate in yellow catfish decreased and the proportion of feces increased due to low digestive enzyme activity and undigested food, even though the food moved slowly through the digestive tract. The combined energy budget, expressed to account for percentage of assimilated energy (A), of yellow catfish with various body weights at different water temperatures is consistent (symmetry) with that in redfin puffer (Jia et al., 2008). The present result supported the hypothesis that the proportion of growth energy gradually decreased with increases in body weight (Peng et al., 2008; Zhou et al., 2008). Numerous authors have suggested that water temperature and body weight exhibit an interaction effect on both growth and feeding in fish (Imsland et al., 1996; Pedersen & Jobling, 1989; Zhou, 2002), similar to the results obtained in this study, whereas the opposite conclusion was

reported in *Leiocassis longirostris* (Han, 2005). These variations may be the results of different fish species and experimental conditions (Han, 2005; Liu, 1998).

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