

Compensatory growth, proximate composition and amino acid contents after experiencing cycles of feed deprivation and re-feeding in young yellow catfish (*Pelteobagrus fulvidraco* R.)

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Abstract

The compensatory growth, proximate composition and amino acid contents changes of young yellow catfish (*Pelteobagrus fulvidraco* R.) (1.63-1.69 g) had been investigated using a 45-day cyclic feed deprivation and re-feeding experiment. The control group (S₀) was fed daily with live tubificid worms (*Limnodrilus hoffmeisteri*), while the S_{1/4}, S_{1/2}, and S_{1/1} groups cyclically experienced one-day of feed deprivation followed by four, two or one day(s) of feeding, respectively. Over- or full-compensatory growth was achieved in the cyclic deprivation/re-feeding groups through increased feeding rate (*FR*) and feed conversion efficiency (*FCE*). However, the fish behaved different courses of growth compensation, the compensatory growth responses of fish subjected to a weaker intensity of feed deprivation (i.e., S_{1/4}) compared with more intense deprivation (i.e., S_{1/1}) was achieved in these groups mainly by a gradual increases in *FR* or by maintaining a high *FCE*, respectively. The cyclic deprivation/re-feeding schedules did not affect the proximate composition of the fish body, however, the amino acid parameters were inversely related to the specific growth rate, the fish showing growth over-compensation contained significantly lower contents of total amino acids, essential and non-essential amino acids.

Keywords: Amino acid, Compensatory growth, Over compensation, Feed conversion efficiency, Feeding rate, Proximate composition, Yellow catfish

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Introduction

Compensatory growth is commonly described as a phase of unusually accelerated growth in vertebrates (including mammals, birds and fish) following a period of malnutrition (e.g., reduced feeding) or some unfavorable environmental conditions (Ali *et al.*, 2003; Li *et al.*, 2009). In fish, partial or total feed deprivation may induce growth compensation to different extents (partial, full- or over-compensation) by hyperphagia, increases in feed conversion efficiencies or behavioral adjustments (e.g., reduced locomotion) (Ali *et al.*, 2003). The degree of growth compensation in fish is highly variable depending on the species and feeding protocols used, including the duration and intensity of feeding regimens (Oh and Noh, 2007; Oh *et al.*, 2008). Therefore, it is necessary to characterize appropriate feeding regimens that achieve compensatory growth for a specific fish species before practical application to aquaculture, as appropriate exploitation of compensatory growth can result in enhanced growth and feed utilization that ultimately would lead to reductions in feed costs. In addition, the application of this phenomenon could improve husbandry efficiency, water quality and reduce labour costs (Eroldoğan *et al.*, 2006a).

Different experimental designs have been used to investigate compensatory growth. The first type of design is a single phase of food deprivation/re-

feeding (Bélangier *et al.*, 2002; Wang *et al.*, 2004; Tian and Qin, 2004; Oh *et al.*, 2008), which focuses on the impact of starvation time on compensatory growth, or investigates the time course of changes in fish growth rate. Second and more commonly, there is cyclic starvation/re-feeding, which has been applied to induce compensatory growth in several species (Quinton and Blake, 1990; Feng and Qin, 2006; Heide *et al.*, 2006). In this approach, the capacity for compensatory growth is weakened gradually during the re-feeding period of the cycle, but can be reactivated in the next cycle of starvation/re-feeding. Thus, this approach is effective for constantly enhancing the potential for compensatory growth, which increases the duration of compensatory growth, and thus the animals attain improved growth (Hayward *et al.*, 1997; Feng and Qin, 2006). In cyclic regimens, the growth compensatory effect is related to the time interval between starvation and re-feeding, and the ratio of starvation to re-feeding (Quinton and Blake, 1990; Feng and Qin, 2006; Heide *et al.*, 2006). However, prolonged starvation, which is the most extreme form of malnutrition, can cause serious impairment of physiological functions in fish (e.g., metabolic decline and oxidative stress), especially during juvenile stages (Tripathi and Verma, 2003; Morales *et al.*, 2004). Thus, in this present study the length of feed deprivation is shorter than that of re-

feeding, which may be more realistic for seedling cultivation.

The yellow catfish *P. fulvidraco*, is an economically and nutritionally important freshwater species that is distributed and cultured in Southeast Asian countries, especially in China (Cao *et al.*, 2009; Liu *et al.*, 2010). To the best of our knowledge, the effects of cycles of fixed lengths of feed deprivation followed by different lengths of feeding *ad libitum* have yet to be investigated during the seedling stages of *P. fulvidraco* cultivation. In addition, in different cyclic starvation/re-feeding regimens, although the effects on body composition have been investigated for some species (Zhu *et al.*, 2004; Heide *et al.*, 2006; Mattila *et al.*, 2009), little information has been reported regarding changes in the amino acid contents of the fish body.

The purpose of this present study was to investigate the capacity of young yellow catfish for growth compensation during cyclic feeding regimens with different periods of re-feeding, and to examine the effects on body composition and amino acid contents. Furthermore, the contributions of hyperphagia and/or feed conversion efficiency to any compensatory responses were evaluated.

Materials and methods

Fish and experimental conditions

Young fish of 1.63-1.69 g were obtained from Fisheries Research Institute of Jingzhou, Hubei, China. The fish were transferred to the laboratory

and randomly assigned to 12 aerated fiberglass tanks (70 cm×55 cm×36 cm) of the circulating water system in natural light conditions. Prior to the experiment, the fish were reared for 2 weeks and fed daily to apparent satiation. During the acclimation and the experiment, the live tubificid worms (*L. hoffmeisteri*) was used as the diet for the fish. During the experiment, aeration maintained the dissolved oxygen above 6.2 mg/L and the ammonia nitrogen below 0.09 mg/L, the pH ranged from 6.7 to 7.4. Water temperature was controlled at 25.0±1.0°C by air conditioning.

Experimental design and procedures

At the start of the experiment, the 12 tanks were divided into 4 groups and 3 tanks were assigned to each treatment, each tank contained 30 fish. Specifically, The S_{1/4}, S_{1/2}, and S_{1/1} group cyclically experienced one-day of feed deprivation followed by four, two or one day(s) of re-feeding at *ad libitum* ration, respectively, and the control group (S₀) was fed daily to satiation.

Before the experiment, all fish were deprived of food for one day and weighed. During the feeding days, a certain amount of live tubificid worms was weighed and then fed to the fish, any uneaten feed was siphoned off from the tanks at the next morning. The experiment lasted for 45 days (except for the S_{1/1} group, which lasted for 44 days). The total time of actual feeding in the S₀, S_{1/4}, S_{1/2} and S_{1/1} groups were 45 d, 36 d, 30 d and 22 d, respectively. To calculate feed intake in each tank for

each day, the uneaten food was blotted dry, weighed and calibrated according to the leaching rate of the live tubificid worms. Three samples of food were put into three fish-free tanks, re-collected after 24 h, dried and weighed, and then the leaching rate was determined.

At 15th day, 30th day and the end of the experiment, all tanks of fish were individually weighed and the mean weights of fish were calculated. To determine the initial body composition of fish at the start of the experiment, a batch of 30 fish were dried to constant weight at 70°C. It was performed in triplicate and mean values were calculated. At the end of the experiment, all fish in each tank were deprived of food for one day, weighed, and then dried to constant weight at 70°C to determine dry weight, body composition and amino acid contents.

Chemical analyses

Dry matter was determined for fish and diet samples (in triplicate) by drying to constant weight at 105°C. Nitrogen content was analyzed for the fish and the diet using an elemental analyzer (Perkin Elmer 2400, Perkin-Elmer Corporation, Connecticut, U.S.A.), while crude protein content was calculated from nitrogen content by multiplying by 6.25. Crude lipid was determined for fish by ether extraction using a Soxtec System (Soxtec system HT6, Tecator, Hoganas, Sweden), and energy for fish and diet using a bomb calorimeter (Phillipson microbomb calorimeter, Gentry Instruments Inc.,

Aiken, U.S.A.) according to the method of Luo *et al.* (2005). The contents of amino acids were determined on the two sub-samples from each group of fish in the triplicate groups after acid hydrolysis using an automatic amino acid analyzer (Hitachi835-50, Tokyo, Japan) equipped with a custom ion exchange resin column (Hitachi no. 2619). Due to that it could not be detected after acid hydrolysis, tryptophan was not estimated.

Calculation and statistical analyses

Wet weight specific growth rates (SGR_w), mean feeding rates (FR), actual feeding rates ($Act.FR$) and feed conversion efficiencies (FCE) were calculated as follows: $SGR_w = 100(\ln W_t - \ln W_o)/t$, where W_t and W_o were fish body wet weight (g) at the start and end of the experimental period respectively, and t was the intervening period in days; $FR = 200I_{Td}/t \times (W_t + W_o)$, where I_{Td} was the amount of food consumption (dry weight) during the experimental period; $Act.FR = 200I_{Td}/T \times (W_t + W_o)$, where T was actual days of feeding; $FCE = 100(W_t - W_o)/I_{Td}$.

Statistical analyses were performed using Statistica Version 5.0 in Windows. All data were expressed as means \pm standard deviation (SD), and were compared by one-way analysis of variance. Multiple comparisons (Duncan's procedure) were performed to evaluate the significance of any differences between different feeding regimens or between different stages of

the experiment.

Results

Growth

At the start of the experiment, there were no significant differences in the wet weights of fish in each of the groups ($p>0.05$). At 15th day, the mean wet weights of fish in the three cyclic deprivation/re-feeding groups were lower than the control, and this difference was significant for the $S_{1/2}$ and $S_{1/1}$ groups when compared to the S_0 ($p<0.05$). At 30th day, the mean wet

weight of fish in each cyclic deprivation/re-feeding group was not different from that of the control ($p>0.05$), which indicated that full growth compensation had occurred by this time. At the end of the experiment, there was no significant difference in mean wet weight between the $S_{1/1}$ and S_0 control groups ($p>0.05$), but the $S_{1/4}$ and $S_{1/2}$ groups had significantly greater mean wet weights compared with the control ($p<0.05$) indicating that the $S_{1/4}$ and $S_{1/2}$ groups showed over-compensatory growth (Table 1).

Table 1: Initial and final wet body weights and SGR_W of yellow catfish experiencing different feeding regimens (means \pm SD).

Parameter	Time or periods	Feeding regimen ^a			
		S_0	$S_{1/4}$	$S_{1/2}$	$S_{1/1}$
Wet body weight	initial	1.63 \pm 0.03	1.67 \pm 0.03	1.67 \pm 0.05	1.69 \pm 0.05
	15 d	2.13 \pm 0.03 ^a	2.07 \pm 0.08 ^{ab}	1.92 \pm 0.09 ^b	1.96 \pm 0.08 ^b
	30 d	2.50 \pm 0.09	2.64 \pm 0.11	2.51 \pm 0.08	2.48 \pm 0.18
	45 d	2.66 \pm 0.03 ^a	3.02 \pm 0.12 ^b	2.94 \pm 0.12 ^b	2.86 \pm 0.23 ^a
	0–15 d	1.65 \pm 0.12 ^{X a}	1.41 \pm 0.24 ^{X a}	0.92 \pm 0.12 ^b	0.89 \pm 0.15 ^b
SGR_W	16–30 d	0.69 \pm 0.15 ^Y	0.94 \pm 0.10 ^Y	1.04 \pm 0.17	0.86 \pm 0.13
	31–45 d	0.57 \pm 0.09 ^{Y a}	0.87 \pm 0.13 ^{Y b}	1.04 \pm 0.19 ^b	1.03 \pm 0.14 ^b
	0–45 d	0.97 \pm 0.05	1.07 \pm 0.17	1.01 \pm 0.15	0.93 \pm 0.05

^aLetters after each value indicates the results of pair-wise comparisons. Different superscript uppercase letters (X, Y) indicate significant differences between different experimental stages ($p<0.05$), different lower-case letters (a, b) indicate significant differences between groups experiencing different feeding regimens ($p<0.05$).

During the first stage (0–15 days) of the experiment, the SGR_W of the control group was significantly greater than the $S_{1/2}$ and $S_{1/1}$ groups ($p<0.05$), and slightly higher than the $S_{1/4}$ group ($p>0.05$). During the second stage (16–30 days), the SGR_W did not differ among fish of the four experimental groups ($p>0.05$). During the third stage (31–45 days), the SGR_W of fish in the control was significantly lower than that in the treatment groups ($p<0.05$),

but there were no significant difference in SGR_W between each of treatment groups. However, during the entire experiment, there were no significant differences in SGR_W between each of the four groups ($p>0.05$). In addition, as the experiment progressed, fish of the S_0 and $S_{1/4}$ groups exhibited significant reductions in SGR_W ($p<0.05$), but there was no significant difference in SGR_W between the $S_{1/2}$ and $S_{1/1}$ groups ($p>0.05$) during the different stages of

the experiment (Table 1).

Feed utilization

As shown in Table 2, the fish of the three treatment groups exhibited significantly lower mean *FR* values compared with the fish of the control during each of stages ($p < 0.05$), the *Act.FR* of the treatment groups were significantly greater than that of the control in the first (0–15 days) and the second (16–30 days) stages of the experiment ($p < 0.05$). The mean *FR* of the treatment groups decreased significantly with elongation of the feed

deprivation period ($p < 0.05$). During the entire experiment, the mean *FR* of the control was significantly greater compared to the other groups ($p < 0.05$), but the inverse was the case for the *Act.FR* values ($p < 0.05$). As the experiment progressed, the mean *FR* and *Act.FR* increased significantly in the S_0 and $S_{1/4}$ groups ($p < 0.05$), but there were no significant differences between each of the experimental stages for the mean *FR* and *Act.FR* values in the $S_{1/1}$ or $S_{1/2}$ groups ($p > 0.05$).

Table 2: Mean *FR*, *Act.FR* and *FCE* in yellow catfish experiencing different feeding regimens (mean \pm SD).

Parameter	Periods	Feeding regimen ^a			
		S_0	$S_{1/4}$	$S_{1/2}$	$S_{1/1}$
Mean <i>FR</i> (%/d)	0-15 d	2.94 \pm 0.12 ^{X a}	2.49 \pm 0.07 ^{X b}	2.18 \pm 0.11 ^c	1.87 \pm 0.13 ^d
	16-30d	3.04 \pm 0.09 ^{X a}	2.68 \pm 0.03 ^{Y b}	2.22 \pm 0.05 ^c	1.83 \pm 0.08 ^d
	31-45d	3.29 \pm 0.07 ^{Y a}	2.92 \pm 0.07 ^{Z b}	2.18 \pm 0.03 ^c	1.83 \pm 0.09 ^d
	0-45 d	3.06 \pm 0.06 ^a	2.70 \pm 0.04 ^b	2.21 \pm 0.07 ^c	1.85 \pm 0.07 ^d
<i>Act.FR</i> (%/d)	0-15 d	2.94 \pm 0.12 ^{X a}	3.11 \pm 0.09 ^{X a}	3.27 \pm 0.17 ^{ab}	3.50 \pm 0.11 ^b
	16-30d	3.04 \pm 0.09 ^{X a}	3.33 \pm 0.13 ^{Y b}	3.40 \pm 0.08 ^b	3.51 \pm 0.14 ^b
	31-45d	3.29 \pm 0.07 ^{Y a}	3.65 \pm 0.09 ^{Z b}	3.28 \pm 0.05 ^a	3.43 \pm 0.57 ^{ab}
	0-45 d	3.06 \pm 0.06 ^a	3.36 \pm 0.13 ^b	3.31 \pm 0.11 ^b	3.48 \pm 0.16 ^b
<i>FCE</i> (%)	0-15 d	58.96 \pm 4.01 ^{X a}	56.72 \pm 3.66 ^{Xa}	45.97 \pm 3.44 ^{X b}	51.67 \pm 6.77 ^{ab}
	16-30d	43.14 \pm 1.27 ^{Y a}	52.80 \pm 5.67 ^{X b}	60.04 \pm 1.95 ^{Y c}	52.68 \pm 4.40 ^b
	31-45d	31.03 \pm 5.53 ^{Z a}	37.33 \pm 0.81 ^{Y b}	47.50 \pm 2.47 ^{X c}	55.13 \pm 4.75 ^d
	0-45 d	44.40 \pm 2.32 ^a	49.00 \pm 1.50 ^b	51.18 \pm 1.52 ^b	53.20 \pm 2.44 ^b

^aLetters after each value indicates the results of pair-wise comparisons. Different superscript uppercase letters (X, Y) indicate significant differences between different experimental stages ($p < 0.05$), different lower-case letters (a, b) indicate significant differences between groups experiencing different feeding regimens ($p < 0.05$).

In the first and second stages of the experiment, there were no obvious changes in *FCE* with increasing duration of feed deprivation. However, in the third stage, the *FCE* was significantly greater in the groups with the longer periods of feed deprivation ($p < 0.05$). During the entire experiment, the *FCE* values of the three treatment

groups were significantly greater than the control group ($p < 0.05$). The *FCE* between the treatment groups did not differ significantly but exhibited an increasing trend with the longer periods of feed deprivation. As the experiment progressed, the *FCE* decreased significantly in the S_0 and $S_{1/4}$ groups ($p < 0.05$). In the $S_{1/2}$ group the *FCE*

increased during the early experimental stages but then decreased, while in the $S_{1/1}$ group the *FCE* did not change significantly during any experimental stages ($p>0.05$) (Table 2).

Proximate composition and amino acid contents

At the end of the experiment, there were no significant differences in dry matter, lipid, protein concentrations or energy values among the fish of the four groups ($p>0.05$) (Table 3). However, the concentrations of 15 amino acids were significantly lower in

the $S_{1/4}$ and $S_{1/2}$ groups compared with the $S_{1/1}$ and control groups ($p<0.05$), and only valine and cysteine concentrations did not differ between the groups ($p>0.05$). Moreover, the concentrations of total essential amino acids (EAA), total non-essential amino acids (NEAA) and total amino acids (AA) were greater in the $S_{1/4}$ and $S_{1/2}$ groups than those in the $S_{1/1}$ and control groups ($p<0.05$). No significant differences in any of the amino acid parameters were detected between the $S_{1/4}$ and $S_{1/2}$ groups, or between the $S_{1/1}$ and control groups (Table 4).

Table 3: Body composition and energy per unit wet weight of yellow catfish experiencing different feeding regimens (mean \pm SD).

Feeding regimen	Dry matter (%)	Protein (%)	Lipid (%)	Energy (J/mg)
Initial	14.62 \pm 0.98	8.76 \pm 0.42	2.39 \pm 0.18	3.24 \pm 0.30
S_0	26.60 \pm 2.39	17.17 \pm 1.48	5.85 \pm 0.88	6.15 \pm 0.58
$S_{1/4}$	26.13 \pm 0.89	16.37 \pm 0.64	5.86 \pm 0.10	6.08 \pm 0.35
$S_{1/2}$	25.85 \pm 1.79	16.73 \pm 1.05	5.99 \pm 0.83	6.22 \pm 0.57
$S_{1/1}$	27.04 \pm 1.16	17.02 \pm 0.75	6.17 \pm 0.61	6.34 \pm 0.15

Table 4: Amino acid content per unit wet weight of yellow catfish experiencing different feeding regimens (mean \pm S.D.)

Amino acid	Feeding regimen ^a			
	S_0	$S_{1/4}$	$S_{1/2}$	$S_{1/1}$
Thr	0.70 \pm 0.01ab	0.68 \pm 0.01b	0.66 \pm 0.00c	0.70 \pm 0.00a
Val	0.85 \pm 0.03	0.84 \pm 0.02	0.82 \pm 0.04	0.85 \pm 0.03
Met	0.44 \pm 0.01a	0.41 \pm 0.01b	0.41 \pm 0.01b	0.43 \pm 0.01a
Ile	0.76 \pm 0.01a	0.73 \pm 0.01b	0.72 \pm 0.02b	0.75 \pm 0.02ab
Leu	1.37 \pm 0.02a	1.33 \pm 0.01b	1.30 \pm 0.02b	1.36 \pm 0.01a
Phe	0.73 \pm 0.01a	0.70 \pm 0.01b	0.70 \pm 0.01b	0.72 \pm 0.01a
Lys	1.39 \pm 0.02a	1.34 \pm 0.02b	1.31 \pm 0.02b	1.37 \pm 0.02a
His	0.40 \pm 0.00	0.39 \pm 0.01	0.38 \pm 0.01	0.40 \pm 0.01
Arg	1.08 \pm 0.01a	1.03 \pm 0.01b	1.01 \pm 0.02b	1.06 \pm 0.01a
Σ EAA	7.72 \pm 0.08a	7.45 \pm 0.09b	7.32 \pm 0.14b	7.65 \pm 0.10a
Asp	1.49 \pm 0.02a	1.40 \pm 0.01b	1.43 \pm 0.02b	1.47 \pm 0.01a
Ser	1.06 \pm 0.01a	0.99 \pm 0.01b	1.01 \pm 0.02b	1.04 \pm 0.01a
Glu	2.45 \pm 0.04a	2.33 \pm 0.04b	2.37 \pm 0.03b	2.45 \pm 0.02a
Gly	1.26 \pm 0.02a	1.17 \pm 0.02b	1.20 \pm 0.02b	1.25 \pm 0.01a
Ala	1.13 \pm 0.02a	1.08 \pm 0.03b	1.10 \pm 0.01b	1.14 \pm 0.02a
Cys	0.11 \pm 0.02	0.11 \pm 0.01	0.12 \pm 0.00	0.12 \pm 0.01
Tyr	0.55 \pm 0.01a	0.52 \pm 0.00b	0.53 \pm 0.01b	0.54 \pm 0.00a
Pro	0.80 \pm 0.01a	0.73 \pm 0.01b	0.76 \pm 0.03ab	0.78 \pm 0.02a
Σ NEAA	8.86 \pm 0.12a	8.34 \pm 0.09b	8.51 \pm 0.10b	8.78 \pm 0.06a
Σ AA	16.58 \pm 0.24a	15.97 \pm 0.16b	15.66 \pm 0.23b	16.44 \pm 0.13a

^aLower-case letters after each value indicates the results of pair-wise comparisons. Different letters (a, b) indicate significant differences between groups experiencing different feeding regimens ($p<0.05$).

Discussion

Yellow catfish is a small-sized fish and displays a relatively slow growth (Li *et al.*, 2006; Ye *et al.*, 2006; Cao *et al.*, 2009). Naturally, 1-year-old and 2-year-old yellow catfish can only grow to 25~50 g and 50~120 g, respectively (Li, 2010). During the whole period of this study, SGRs of 4 groups ranged from 0.93 to 1.07 (Table 1). In the similar rearing conditions, the SGRs of yellow catfish with initial weights of 3.2 g and 5.1 g were 0.9~1.95 and 0.71~0.98 respectively (Chen *et al.*, 2010; Tang *et al.*, 2011). Moreover, for the darkbarbel catfish, *Pelteobagrus vachelli*, another species of *Pelteobagrus* with faster growth than the yellow catfish (Gan *et al.*, 2008), the SGR (1.0 g of initial weight) was still 1.12~1.27 (Yang *et al.*, 2011). So, the growth in this study was within the normal range of the species.

At the end of the experiment, the cyclic feeding groups exhibited over ($S_{1/4}$ and $S_{1/2}$) or full ($S_{1/1}$) growth compensation compared to the control. Despite not statistically significant, the $S_{1/1}$ group showed greater weight gain than the control indicating that over growth compensation was approached in this group. Similarly, in cyclic deprivation/re-feeding practices, full and over growth compensation has been obtained in some other species, such as fingerling of channel catfish *Ictalurus punctatus* (Chatakondi and Yant, 2001), young or juvenile three-spined stickleback *Gasterosteus aculeatus* (Wu *et al.*, 2002; Wu *et al.*, 2003) and juvenile *Lepomis* hybrids (Hayward *et*

al., 1997). Additionally, rainbow trout *Oncorhynchus mykiss* juveniles that experienced two or four days of fasting, followed by re-feeding until the relative feed intake differed by less than 10% of the fed controls, obtained full growth compensation (Nikki *et al.*, 2004). However, Only partial growth compensation has been found in most of previous studies (Zhu *et al.*, 2004; Eroldoğan *et al.*, 2006a; Heide *et al.*, 2006; Turano *et al.*, 2007; Mattila *et al.*, 2009; Wang *et al.*, 2009; Blanquet and Oliva-Teles, 2010). So, the extent of compensatory growth obtained may be mainly correlative with the specific intermittent feeding schedules and the whole experimental durations. With the progression of this experiment, the deprived fish gradually exhibited full- or over- growth compensation in the later stages, which was indicated by the improved body masses and higher *SGR* compared to the controls. So, sufficient cultural period and cycles of deprivation/re-feeding, by which deprived fish can continuously undergo growth compensation, are necessary for the fish to converge on the growth trajectory of the controls (Heide *et al.*, 2006).

The elicitation and achievement of full- and over-compensation in this present study may be due to the young stage of life, short-term (one day) of feed deprivation, and sufficient re-feeding periods, which could allow the final body weight of the deprived young yellow catfish to catch up with that of the control. Hayward and Wang (2001)

concluded that younger fish may demonstrate a more vigorous and resilient compensatory growth response than the older fish. Indeed, our previous study revealed that yellow catfish larvae exhibited full- or over-compensation growth in different cyclic schedules of deprivation/re-feeding (Yao *et al.*, 2009). In order to induce a compensatory growth response caused by sufficient nutritional stress, compared to the bigger fish, just through less prolonged durations of food deprivation could smaller fish achieve a desirable growth compensation (Foss *et al.*, 2009), since that smaller fish may be weaker in resistance against long-term starvation stress (Tripathi and Verma, 2003; Morales *et al.*, 2004). On the other hand, some researchers have suggested that the reason for that fish do not always achieve full-compensation is that re-feeding periods are insufficient to regain lost weight completely (Zhu *et al.*, 2004; Heide *et al.*, 2006; Foss *et al.*, 2009). The experiments have revealed that weight gains of juvenile turbot *Scophthalmus maximus* (Blanquet and Oliva-Teles, 2010) in a cyclic 1-day feed deprivation/6-days re-feeding regimen, and juvenile whitefish *Coregonus lavaretus* in a cyclic 2-days deprivation/5-days re-feeding regimen (Känkänen and Pirhonen, 2009), were not significantly less than those of the controls. From the above researches, it seems that appropriate period of feed deprivation and sufficient duration of re-feeding are very important for young fish to display full- or over- growth

compensation.

Hyperphagia, improved *FCE*, or sometimes a combination of both processes underlie the compensatory growth responses in fish (Eroldoğan *et al.*, 2006a; Heide *et al.*, 2006; Wang *et al.*, 2009). In this study, the higher *Act.FR* and *FCE* of the cyclic feeding groups indicated that full- or over-growth compensation was achieved in deprived fish through both hyperphagia and improved *FCE*. Other fish species fed with cyclic schedules of feed deprivation and re-feeding also show compensatory growth that is due to both hyperphagia and increased *FCE*, including hybrid sunfish (Hayward *et al.*, 1997), channel catfish (Chatakondi and Yant, 2001), three-spined stickleback (Wu *et al.*, 2003), Pacific salmon *Oncorhynchus* spp. (Feng and Qin, 2006) and the Atlantic halibut *Hippoglossus hippoglossus* (Heide *et al.*, 2006). Thus, the combination of increased *FR* and *FCE* may be an important mechanism underlying compensatory growth in fish.

Few studies have investigated the temporal dynamics of appetite and *FCE* during the course of intermittent feeding schedules, although a similar experimental schedule (6 weeks of cyclic feeding regimens) has been done with whitefish, *C. lavaretus* (Känkänen and Pirhonen, 2009). In this present study, during the initial experimental stage, the $S_{1/4}$ group had lower *Act.FR* and higher *FCE* than the $S_{1/2}$ or $S_{1/1}$ groups, but with the progression of the experiment the *Act.FR* increased and the *FCE* decreased in the $S_{1/4}$ group,

respectively. The change trends of *FR* and *FCE* in $S_{1/4}$ group were similar to those in the control group, but opposite to those in the $S_{1/1}$ group, in which the fish was subjected to more intense feed deprivation. Therefore, the processes and tendencies of growth compensation had been adequately reflected in the 45 days of experimental period. As the experiment progressed, the compensatory growth responses in $S_{1/4}$ and $S_{1/1}$ groups may have been achieved

through gradual improvements of *FR* and consistent high *FCE*, respectively. Thus, it can be inferred that improvement in *FCE* is the main contributory factor for compensatory growth in response to relatively intense cyclic food deprivation. This suggestion is supported to some extent by the data from channel catfish fingerlings (Chatakondi and Yant, 2001) and gilthead seabream juveniles (Eroldoğan *et al.*, 2006b).

Table 5: Coefficients of the regression equation relating AA, EAA and NEAA concentrations to specific growth rate of wet weight in young yellow catfish^a.

Y	N^b	a	b	R²	P
Σ AA	12	18.21	-1.94	0.46	$p=0.016<0.05$
Σ EAA	12	8.44	-0.90	0.37	$p=0.034<0.05$
Σ NEAA	12	9.77	-1.05	0.40	$p=0.028<0.05$

^aRegression equations were expressed as $Y=a+bW$, where W was the specific growth rate of wet body weight of fish;

^b N was the number of fish samples.

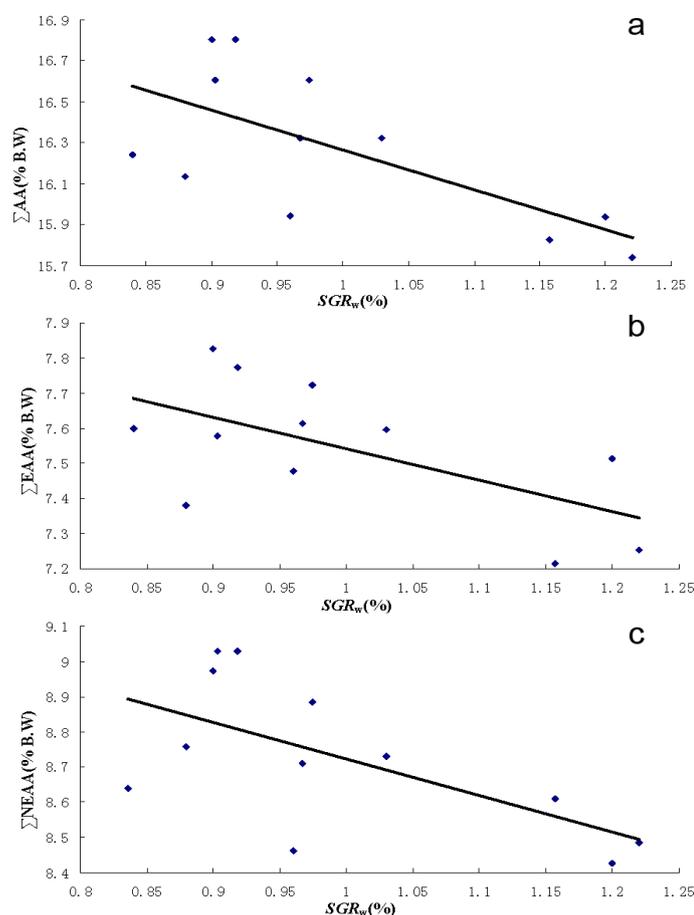


Figure 1: Relationship between (a) AA, (b) EAA and (c) NEAA and SGR_w of yellow catfish in different experimental stages. Each point represents a repeated calculated value of SGR_w .

The proximate compositions of the fish in the cyclic deprivation/re-feeding groups were similar to that in the control at the end of the experiment. For many fish species, Chemical compositions are unaffected by deprivation/re-feeding strategies for many (Zhu *et al.*, 2004; Cho *et al.*, 2006; Heide *et al.*, 2006; Oh *et al.*, 2008; Tian *et al.*, 2010). This indicates that a short-term starvation followed by various lengths of re-feeding does not affect the body composition of the young yellow catfish, and subsequent application of cyclic feeding strategies do not negatively affect overall body

composition of the seed nursery. However, the total AA, EAA and NEAA concentrations of the groups exhibiting over-compensatory growth were lower than those of the group exhibiting full-compensatory growth and the control. Huang *et al.* (2007) showed that different starvation/re-feeding periods did not significantly affect the AA concentrations of yellow catfish juveniles. This discrepancy may be due to the differences in the fish sizes and feeding schedules. In this study, further analysis suggested that the total AA, EAA and NEAA concentrations correlated inversely and

significantly with SGR_W (Table 5, Fig. 1). Thus, the lower amino acid parameters in the $S_{1/4}$ and $S_{1/2}$ groups may be attributed to slightly lower protein retention (Table 3) caused by marginally greater SGR_W during the entire experiment.

In conclusion, over growth compensation was elicited by cyclic feeding schedules that incorporated a short-term period of feed deprivation. Growth compensation was achieved through hyperphagia and improved FCE , but the improvement in FCE played a greater role in the compensatory growth responses of fish subjected to more severe feed deprivation. The results of this present study could be used to design feeding schedules that decrease feed costs and improve growth rates in yellow catfish seedling cultivation practices, although AA concentrations decreased in fish displaying over-compensation. However, there remain some challenges before the over- or full-compensation phenomena can be applied completely in aquaculture, and further studies should explore the long-term physiological effects of cyclic feed deprivation and confirm the economic benefits in field experiments.

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