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Effects of dietary manipulation on compensatory growth of juvenile genetically improved farmed tilapia (*Oreochromis niloticus*)

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Abstract A 40-day feeding trial was conducted to investigate whether feeding a low-protein diet (25%) once daily for either 10 (L10H30) or 20 (L20H20) days then re-feeding a high-protein diet (35%) thrice daily elicit compensatory growth (CG) in genetically improved farmed tilapia (GIFT), *Oreochromis niloticus* (11.02 ± 0.05 g). Fish on the control treatment were fed 35% protein diet over 40 days (H40). Fish were stocked into nine 100-L tanks (30 fish per tank) with 3 replicate tanks for each group. Growth performance, feed utilization, proximate composition of body compartment, serum biochemical parameters, and hepatopancreatic histology and expressions of some genes related to inflammatory cytokine were evaluated every 10 days. Growth of L10H30 fish were similar to the control, whereas the weight of L20H20 fish were lower ($P < 0.05$) at day 20, but this significant difference disappeared at the end of the experiment. During 20–30 days, specific growth rate and feed intake were significantly higher ($P < 0.05$) and feed efficiency was lower ($P < 0.05$) in L20H20 fish than those in H40 fish. Dietary manipulations did not affect ($P > 0.05$) viscerosomatic and hepatosomatic indices, condition factors, serum biochemical parameters, and hepatopancreatic histology. Significant differences ($P < 0.05$) in proximate composition were observed only in viscera and muscle between L20H20 fish and H40 fish at day 20. The mRNA expressions of heat shock protein 70 kDa, tumor necrosis factor-α and interleukin (IL)-1β were higher ($P < 0.05$) in L10H30 and L20H20 fish at day 10, while IL-1β mRNA expression was lower ($P < 0.05$) in L20H20 fish at day 30 than those in H40 fish. Our results indicated that L20H20 fish elicited a complete CG and induced reversible physiological variations in juvenile GIFT.

Keywords Dietary manipulation · Compensatory growth · *Oreochromis niloticus* · Body components · Blood biochemical profiles · Liver structure · Cytokine

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Introduction

Compensatory growth (CG) is defined as a phase of accelerated growth during an adequate refeeding following a period of undernutrition. This response is interested in aquaculture, because it could bring a number of advantages including improvement of feed utilization, labor cost, water quality, and flexible feeding management (Ali et al. 2003; Blanquet and Oliva-Teles 2010; Sevgili et al. 2012; Mohanta et al. 2016). Among methods to provoke CG in fish, like various feed restriction and refeeding protocols, feeding different nutrient

density diets is one of the options used most (Ali et al. 2003; Jobling 2010 and references therein).

Tilapia is a warm-water omnivorous fish of worldwide commercial importance. Various feed deprivations and re-feeding protocols have been used to express the phenomenon of CG in tilapia; it seems that tilapia (initial body weight, 1–23 g) fasting period should not exceed 7 days, whereby fish growth could be compensated (Wang et al. 2000; Byamungu et al. 2001; Wang et al. 2005; Abdel–Tawwab et al. 2006; Wang et al. 2009; Gao et al. 2015; Ali et al. 2016). For example, hybrid tilapia, *Oreochromis mossambicus* × *O. niloticus* (Wang et al. 2000), and Nile tilapia, *O. niloticus* (L.) (Abdel–Tawwab et al. 2006) deprived of feed for 7 days could achieve a full CG at the end of re-alimentation, whereas those deprived for 14–28 days were significantly lower than those on continuous feeding at the end of re-alimentation. In addition, *O. niloticus* that underwent a cyclical feed deprivation and re-feeding failed to show recovery of body weight (Wang et al. 2009; Gao et al. 2015).

Recently, we demonstrated that genetically improved farmed tilapia (GIFT, *Oreochromis niloticus*) (initial body weight 17 g), fed a diet containing 25% protein once daily showed similar body weight to those fed a diet containing 35% protein thrice daily during the initial 2 weeks but lower body weight after 4 weeks (Liu et al. 2016). Thus, we wanted to investigate whether feeding 25% protein diet once daily for more than 7 days then re-feeding 35% protein diet thrice daily elicits a CG in juvenile GIFT. However, feeding a low protein diet or restricted feeding could induce a negative influence on fish health status. For instance, feeding a low-protein diet to red spotted grouper (*Epinephelus akaara*) might result in an abnormal liver function (Wang et al. 2016), and restricted feeding of blunt snout bream (*Megalobrama amblycephala*) could cause oxidative stress, and consequently led to depressed immunity and reduced resistance to *Aeromonas hydrophila* infection (Li et al. 2014). Therefore, in the present study, to evaluate the effects of this dietary manipulation on CG response and health status in GIFT, we investigated the changes of growth performance, feed efficiency, proximate composition, serum biochemical parameters, and hepatopancreatic histology and mRNA expressions of heat shock proteins 70 kDa (HSP70), tumor necrosis factor (TNF)-α and interleukin (IL)-1β.

Materials and methods

Experimental diets and feeding regimes

Two purified diets were formulated to contain 25 or 35% crude protein (Table 1). The experimental diets were produced according to the methods described in our previous study (Liu et al. 2010). Briefly, all dry ingredients were ground and passed through a 120-μm sieve. The ingredients were then weighed and mixed thoroughly and supplemented with oil and then water. The wet mash was cold-pelleted with a custom-made laboratory pellet mill (diameter, 2 mm). The resultant pellets were air-dried and stored at − 20 °C until used.

The feeding regimes used in the experiment were as follows:

Treatment group 1 (L10H30), initially feeding a diet containing 25% protein once daily for 10 days

Table 1 Composition of the experimental diets (%)

Ingredients	Protein level	
	25	35
Casein	24.50	35.00
Gelatin	6.50	8.50
Dextrin	46.00	30.00
Soy oil	6.02	6.00
Choline chloride	0.20	0.20
Vitamin premix[a]	1.00	1.00
Mineral premix[a]	2.00	2.00
Monocalcium phosphate	2.00	2.00
Microcrystalline cellulose	11.78	15.3
Proximate analysis (% dry matter)		
Crude protein	25.2	35.2
Crude lipid	6.8	6.8
Crude ash	4.5	4.5
Crude fiber	13.0	16.8
NFE	50.5	36.7
Total energy[b] (kJ g^{-1})	17.3	17.3

NFE nitrogen-free extract, calculated as 100 − (crude protein + crude lipid + ash + crude fiber)

[a] The vitamin premix and mineral premix were formulated according to the formula of Shiau and Yu (1999)

[b] Total energy was calculated on the basis of the gross content as 23.6 kJ g^{-1} for crude protein, 39.5 kJ g^{-1} for lipid, and 17.2 kJ g^{-1} for NFE (NRC 2011)

+ re-feeding a diet containing 35% protein thrice daily for 30 days

Treatment group 2 (L20H20), initially feeding a diet containing 25% protein once daily for 20 days + re-feeding a diet containing 35% protein thrice daily for 20 days

Control group (H40), continuously feeding a diet containing 35% protein thrice daily for 40 days.

The fish were fed to apparent satiation at each feeding. Each feeding lasted for 15 min to ensure no uneaten diet could be detected on the tank bottom. Fish were fed once daily at 16:30 during restriction period or thrice daily at 08:30, 12:30, and 16:30 during re-feeding.

Experimental fish and feeding trial

This study was conducted at the experimental center of the Yangtze River Fisheries Research Institute, Wuhan City, Hubei Province, China. Tilapia were obtained from the Hubei Tilapia Breeding Proving Ground (Yingshan, Hubei Province, China) and conditioned for 2 weeks by feeding a commercial diet (containing 35.3% protein and 4.5% lipid, Hubei Tongle Feed Co. LTD., Jingzhou, China) once daily at 16:30 to apparent satiation.

At the start of the experiment, 270 healthy male fish were deprived of diet for 24 h and randomly distributed into 9 tanks (30 fish per tank) in a recirculating aquaculture system. The initial fish body weight was 11.02 ± 0.05 g (mean ± SE) and length was 6.56 ± 0.08 cm (mean ± SE). Three tanks were randomly assigned to each treatment. In addition, the viscera (except hepatopancreas), hepatopancreas, and eviscerated body were taken from five fish, and muscle (beneath the dorsal fin but above the lateral line) was taken from another five fish to determine the initial proximate composition of body compartment.

The culture system >consisted of individual polypropylene tanks, each containing approximately 100 L of water as part of a closed recirculated system with a common water reservoir. The water was circulated (20 L min^{-1}) through separate biofilters to remove impurities and reduce NH_3 concentration. During experimental period, water temperature, pH, and dissolved oxygen concentration were 29–32 °C, 6.9–7.3, and > 5 mg L^{-1}, respectively.

Sample collection

The fish were batch-weighted and counted every 10 days (prior to sampling) to assess survival, mean body weight, specific growth rate (SGR), feed intake (FI), feed efficiency (FE), and protein efficiency ratio (PER). Thereafter, 5 fish from each tank were randomly selected and anesthetized with tricaine methane sulfonate (0.2 g L^{-1} MS–222; GREENHX Biological Technology Co. Ltd., Beijing, China). Then, fish body weight and body length were measured to calculate the condition factor (*K*). After that, 0.2 ml blood was collected from the caudal vein of each fish with a 1-ml plastic syringe. The blood obtained from fish of the same tank was pooled and centrifuged immediately at 1000×*g* for 10 min, and the supernatant was collected for determination of serum biochemical parameters. After blood sampling, the weights of the hepatopancreas and viscera (except hepatopancreas) from 2 fish were measured to calculate the hepatosomatic index (HSI) and viscerosomatic index (VSI), then small pieces of the hepatopancreas from the same location of each fish were dissected and fixed immediately in 4% polyformaldehyde. Subsequently, the muscles obtained from beneath the dorsal fin but above the lateral line were dissected and pooled and frozen at − 20 °C for subsequent proximate composition analysis. From another three fish, one part of the hepatopancreas (about 0.1 g) from the same location of each fish was immediately frozen in liquid nitrogen and maintained at − 80 °C for further analyses. Thereafter, the viscera (except hepatopancreas) and hepatopancreas were also dissected. Finally, the viscera, whole eviscerated bodies, and hepatopancreas of fish from the same tank were pooled, and stored at − 20 °C for proximate composition analysis. The remaining fish were fed according to the feeding regime.

Analytical methods

The moisture, crude protein, crude lipid, ash, and crude fiber contents of samples were determined according to GB/T 5009.3–2003 (Determination of moisture in foods), GB/T 5009.5–2003 (Determination of protein in foods), GB/T 5009.6–2003 (determination of fat in foods), GB/T 5009.4–2003 (determination of ash in foods), and GB/T 6434–2006 (feeding stuff–determination of crude fiber content–method with intermediate filtration) (the National Standard of the People's

Republic of China). Briefly, moisture was determined after desiccation at 105 °C for 4 h, crude protein was determined using the automated Kjeldahl method (K–360; Nitrogen Analyzer, BÜCHI instrument, Flawil, Switzerland, N × 6.25), crude lipid was determined using petroleum ether extraction with the Soxhlet procedure, ash was determined by incineration at 550 °C for 12 h, and crude fiber measured by drying and ashing after extraction with 0.13 mol L^{-1} H_2SO_4 and 0.23 mol L^{-1} NaOH.

The serum glutamic oxaloacetic transaminase (AST, MDH–UV method), glutamic pyruvic transaminase (ALT, LDH–UV method), glucose (GLU, hexokinase method), total cholesterol (TCHO, CHOD–PAP method), triglyceride (TG, GPO–PAP method), and total protein (TP, Biuret method) were determined using Sysmex kits (Sysmex Wuxi Co. LTD., Wuxi, China) with the Sysmex-800 automatic biochemical analyzer (Sysmex Infosystems, Kobe, Japan).

The hepatopancreas fragments fixed immediately in 4% polyformaldehyde for 24 h were treated in accordance with standard histological techniques to obtain semi-serial sections (5 μm thickness) and stained using hematoxylin and eosin (Rui et al. 1980). OLYMPUS CX41 microscope with OLYMPUS DP73 digital camera was used for image capturing. Their microphotographs were obtained at a magnification of × 20. Image Pro Plus software 6.0 (Media Cybernetics, Inc., Bethesda, MD, USA), which can automatically distinguish regions stained with different colors, was used to calculate the area ratio of the cell nucleus, cytoplasm, and vacuoles. We randomly examined 4 microscope fields for each sample, and the results from individual observation were then combined for overall results.

Quantitative real-time RT–PCR

Primers used for TNF-α, IL-1β, and HSP70 were designed with PerlPrimer software (perlprimer.sourceforge.net) and synthesized by TaKaRa Bioengineering Co., Ltd. (Dalian, China) (Table 2). Total RNA was extracted from the hepatopancreas tissues of each tank with TRIzol reagent (Invitrogen, Carlsbad, CA). The extracted RNA was finally eluted in an appropriate amount of water treated with 0.1% diethyl pyrocarbonate (Sigma-Aldrich, St. Louis, MO, USA). For each sample, RNA integrity was confirmed using agarose gel electrophoresis by staining with ethidium bromide and visualizing under UV light. The amount of RNA was determined, and its purity (OD_{260}/OD_{280} between 1.8 and 2.2) was verified using an ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The cDNA was synthesized using random primers and a High-Capacity cDNA Reverse Transcription Kit (Applied Biosystems, Foster City, CA, USA). The β-actin gene was selected as the internal reference. Quantitative real-time PCR was performed using the 7500 Real-Time PCR System (Applied Biosystems, USA) with a program of 50 °C for 2 min, 95 °C for 10 min, and 40 cycles of 95 °C for 15 s and 60 °C for 1 min. For each sample, template copy numbers were internally normalized with their respective input control. In all the experiments, real-time PCR was performed at least in triplicate. The data were expressed as the relative expression of the reference gene by using the $2^{-\Delta\Delta Ct}$ method described in our previous study (Yang et al. 2013).

Calculation and statistical analysis

The following calculations were performed during 10-day intervals:

$$\text{SGR}\ (\%\ \text{day}^{-1}) = 100 \times [\ln(\text{final mean weight}) - \ln(\text{initial mean weight})]/10\ \text{days}$$

$$\text{FI}\ (\%\ \text{body weight day}^{-1}) = 100 \times \text{total feed intake} / [10\ \text{days} \times (\text{final fish weight} + \text{dead fish weight} + \text{initial fish weight}) / 2]$$

Table 2 Primers used for real-time PCR

Gene name	Forward primer (5′ to 3′)	Reverse primer (5′ to 3′)	Amplicon size (bp)	Accession number
TNF-α	GAGTGATCTGCGGGAATACTGAC	CGTCCACAGCGTGTCTCCTT	231	NM_001279533.1
IL-1β	TCTCAGCGATGGGTGTAGGG	CTCAGTTCACCAGCAGGGATG	177	XM_019365842.1
HSP70	CTTCAACGACTCCCAGCGACAG	AGATGCCGTCTTCAATGGTCAG	203	NM_001311332.1
β-actin	ACGAAACCACCTACAACAGCAT	TCCAGACGGAGTATTTACGCTC	198	XM_003443127.4

FE = (final fish weight + dead fish weight − initial fish weight) / dry feed intake

PER = (final fish weight + dead fish weight − initial fish weight) / (dry feed intake × dietary protein level)

Survival (%) = 100 × final fish number/initial fish number

K (g cm^{-3}) = 100 × body weight/(body length)^3

HSI (%) = 100 × hepatopancreas weight/body weight

VSI (%) = 100 × viscera weight/body weight

Data were analyzed using SPSS 22.0 (IBM Corporation, Somers, NY, USA). The data are presented as mean ± SE of three replicates. Data normality and homogeneity of variances were analyzed. Where data were homogeneous, a one-way ANOVA using Tukey's honestly significant difference (HSD) procedure was used. Arcsine- or logarithm-transformation were applied on non-homogeneous data, and the Kruskal–Wallis non-parametric test was further used when the data were still non-homogeneous. Statistical significance was set at $P < 0.05$.

Results

Growth performance and feed utilization

At the end of the feeding trial, there was no significant difference ($P > 0.05$) in mean body weight among each group (Table 3). Compared to fish in H40 group, fish in L10H30 group had similar ($P > 0.05$) mean body weight, SGR, FE, and survival at the same sampling times but had higher ($P < 0.05$) PER during 0–10 days and lower ($P < 0.05$) FI during 20–30 days. However, fish in L20H20 group had lower ($P < 0.05$) mean body weight, SGR, and FI during 10–20 days, whereas higher ($P < 0.05$) SGR and FI and lower ($P < 0.05$) FE and PER during 20–30 days.

HSI, VSI, and K

No statistically significant differences ($P > 0.05$) in HSI, VSI, and K were observed among the treatments at the sampling points (Table 4).

Proximate composition of body compartments

Feeding fish with low protein diet for 10 or 20 days did not significantly ($P > 0.05$) change crude protein, lipid, and moisture contents of whole eviscerated body and hepatopancreas compared with the control over the study period (Tables 5 and 6).

At day 20, there were lower ($P < 0.05$) crude lipid and higher ($P < 0.05$) moisture contents of viscera in L20H20 fish than those in H40 fish (Table 7). Crude

Table 3 Growth performance and feed utilization of juvenile GIFT under different dietary manipulation

Days	L10H30	L20H20	H40
Mean body weight (g)			
10	15.38 ± 0.43	15.71 ± 0.35	16.61 ± 0.44
20	26.17 ± 0.46b	20.72 ± 0.71a	26.74 ± 0.09b
30	37.54 ± 0.49	32.68 ± 1.81	36.95 ± 0.25
40	51.51 ± 2.23	49.25 ± 4.76	52.92 ± 3.68
SGR (% day^{-1})			
10	3.35 ± 0.33	3.60 ± 0.14	4.00 ± 0.34
20	5.32 ± 0.27b	2.76 ± 0.23a	4.77 ± 0.24b
30	3.61 ± 0.27a	4.54 ± 0.23b	3.24 ± 0.04a
40	3.15 ± 0.33	4.04 ± 0.39	3.55 ± 0.61
FE			
10	0.94 ± 0.05	1.09 ± 0.06	0.86 ± 0.03
20	0.79 ± 0.03	0.72 ± 0.11	0.84 ± 0.03
30	0.83 ± 0.03b	0.54 ± 0.06a	0.78 ± 0.02b
40	0.74 ± 0.06	0.76 ± 0.06	0.84 ± 0.04
PER			
10	3.31 ± 0.19b	3.82 ± 0.22b	2.16 ± 0.11a
20	1.99 ± 0.09	2.57 ± 0.40	2.12 ± 0.08
30	2.41 ± 0.06c	1.42 ± 0.12a	1.96 ± 0.06b
40	1.88 ± 0.15	1.93 ± 0.16	2.13 ± 0.11
FI (% body weight day^{-1})			
10	3.41 ± 0.10a	3.09 ± 0.09a	4.53 ± 0.01b
20	6.47 ± 0.11b	3.25 ± 0.81a	5.66 ± 0.04ab
30	3.46 ± 0.17a	7.72 ± 0.27c	4.42 ± 0.14b
40	3.83 ± 0.17a	5.18 ± 0.17b	3.87 ± 0.07a
Survival (%)			
10	97.78 ± 2.22	92.22 ± 2.94	97.78 ± 2.22
20	100.00	95.36 ± 3.03	100.00
30	95.88 ± 0.11	98.41 ± 1.58	100.00
40	98.24 ± 1.75	97.78 ± 2.22	100.00

Values are mean ± SE of three tanks per treatment group. Different lowercase letters in the same line indicate significant differences ($P < 0.05$)

Table 4 HSI, VSI, and *K* of juvenile GIFT under different dietary manipulation

Day	L10H30	L20H20	H40
HSI (%)			
10	3.43 ± 0.18	4.14 ± 0.87	2.96 ± 0.40
20	2.92 ± 0.42	2.64 ± 0.29	3.15 ± 0.44
30	2.75 ± 0.48	3.11 ± 0.19	3.04 ± 0.18
40	2.96 ± 0.10	3.30 ± 0.26	3.21 ± 0.28
VSI (%)			
10	9.46 ± 0.93	8.71 ± 0.35	8.07 ± 0.56
20	7.04 ± 0.98	8.67 ± 0.46	7.52 ± 0.63
30	7.18 ± 0.84	7.32 ± 0.46	6.75 ± 1.03
40	7.04 ± 0.74	8.99 ± 1.17	7.22 ± 0.87
K (g cm^{-3})			
10	3.94 ± 0.22	3.53 ± 0.15	3.44 ± 0.12
20	3.93 ± 0.25	3.63 ± 0.06	3.55 ± 0.33
30	3.25 ± 0.14	3.30 ± 0.47	3.33 ± 0.05
40	3.31 ± 0.20	3.69 ± 0.18	3.52 ± 0.15

Values are mean ± SE of three tanks per treatment group

protein and lipid contents of muscles in L20H20 fish were lower ($P < 0.05$) than those in H40 fish (Table 8).

Table 5 Proximate composition of whole eviscerated body of juvenile GIFT under different dietary manipulation (%, wet basis)

Day	L10H30	L20H20	H40
Crude protein			
Initial		14.08	
10	14.28 ± 0.77	15.74 ± 0.20	14.92 ± 0.11
20	15.63 ± 0.63	15.92 ± 0.82	15.02 ± 0.28
30	16.36 ± 0.82	16.11 ± 0.13	16.00 ± 0.53
40	18.10 ± 0.22	17.59 ± 0.60	16.28 ± 0.34
Crude lipid			
Initial		3.75	
10	4.75 ± 0.26	4.21 ± 0.05	4.99 ± 0.34
20	7.43 ± 0.38	5.72 ± 0.79	6.42 ± 0.71
30	8.67 ± 0.53	7.21 ± 0.34	7.87 ± 0.54
40	8.71 ± 0.39	9.26 ± 0.57	8.71 ± 0.23
Moisture			
Initial		73.70	
10	73.94 ± 0.32	74.49 ± 0.35	72.93 ± 1.81
20	71.80 ± 0.47	73.65 ± 0.91	71.51 ± 0.74
30	68.73 ± 0.51	71.53 ± 0.39	70.49 ± 0.89
40	68.22 ± 1.36	68.54 ± 0.74	68.86 ± 0.48

Values are mean ± SE of three tanks per treatment group

Table 6 Proximate composition of hepatopancreas of juvenile GIFT under different dietary manipulation (%, wet basis)

Day	L10H30	L20H20	H40
Crude protein			
Initial		12.93	
10	9.43 ± 0.93	8.40 ± 0.49	11.57 ± 1.02
20	13.38 ± 0.12	10.75 ± 0.80	13.71 ± 1.58
30	13.98 ± 0.71b	11.22 ± 0.69a	11.55 ± 0.30ab
40	12.77 ± 0.97	11.00 ± 0.48	13.36 ± 0.47
Crude lipid			
Initial		9.20	
10	8.29 ± 0.27	10.75 ± 0.64	10.58 ± 0.73
20	12.65 ± 1.65	9.73 ± 0.81	12.60 ± 1.25
30	10.06 ± 0.77	10.66 ± 0.31	8.04 ± 1.69
40	10.03 ± 0.83	11.26 ± 0.79	9.36 ± 0.79
Moisture			
Initial		66.45	
10	66.59 ± 0.90	65.09 ± 0.98	66.75 ± 0.95
20	66.07 ± 1.54	66.65 ± 0.71	66.28 ± 1.41
30	68.73 ± 0.45	67.00 ± 0.76	70.27 ± 1.85
40	67.83 ± 1.67	68.41 ± 1.21	66.61 ± 1.05

Values are mean ± SE of three tanks per treatment group. Different lowercase letters in the same line indicate significant differences ($P < 0.05$)

Serum biochemical parameters

No significant differences ($P > 0.05$) in serum biochemical parameters were observed in the same time among the groups over the experiment (Table 9).

Hepatopancreatic histology

The histological examinations of the hepatopancreas revealed no obvious structural differences and infiltration of inflammatory cells attributable to experimental treatments. Moreover, no significant differences ($P > 0.05$) in the area ratio of the cell nucleus, cytoplasm, and vacuoles were observed (Table 10).

Hepatopancreatic TNF-α, IL-1β, and HSP70 mRNA expression levels

The changes in relative mRNA expression levels of TNF-α, IL-1β, and HSP70 during the experiment are summarized in Fig. 1. At day 10, the expressions of hepatopancreatic TNF-α, IL-1β, and HSP70 mRNA

Table 7 Proximate composition of viscera of juvenile GIFT under different dietary manipulation (%, wet basis)

Day	L10H30	L20H20	H40
Crude protein			
Initial		9.73	
10	9.26 ± 0.98	9.46 ± 0.23	9.39 ± 0.74
20	11.20 ± 1.54	10.20 ± 0.99	10.18 ± 0.79
30	8.83 ± 0.96	8.84 ± 3.26	8.68 ± 0.91
40	11.01 ± 0.72	10.93 ± 0.97	11.92 ± 2.17
Crude lipid			
Initial		5.33	
10	5.11 ± 0.94	7.24 ± 1.25	5.97 ± 0.79
20	14.15 ± 0.88b	8.08 ± 0.46a	15.94 ± 0.88b
30	14.39 ± 1.53	10.12 ± 3.60	16.05 ± 3.36
40	24.08 ± 1.45	20.30 ± 2.35	24.13 ± 2.54
Moisture			
Initial		79.37	
10	76.77 ± 0.05	75.93 ± 0.53	76.03 ± 1.17
20	71.32 ± 0.25ab	74.58 ± 0.62b	69.51 ± 1.14a
30	71.13 ± 1.50	71.93 ± 0.34	67.10 ± 2.67
40	61.34 ± 0.91	65.99 ± 2.62	62.05 ± 2.89

Values are mean ± SE of three tanks per treatment group. Different lowercase letters in the same line indicate significant differences ($P < 0.05$)

were higher ($P < 0.05$) in fish on L10H30 and L20H20 than in those on H40. However, no significant differences ($P > 0.05$) in TNF-α, IL-1β, and HSP70 mRNA expression levels were observed among the groups at the end of the experiment. Furthermore, the IL-1β mRNA expression was lower ($P < 0.05$) in L20H20 fish than in H40 fish at day 30, while no obvious changes ($P > 0.05$) were found at day 20 and 40.

Discussion

Previous studies reported a 30–35% dietary protein requirement at daily feeding more than once, for supporting maximum growth of Nile tilapia, *O. niloticus* (initial body weight 3–183 g) (Siddiqui et al. 1988; Hafedh 1999; Riche et al. 2004; Abdel-Tawwab et al. 2010; Sun et al. 2011; Chen et al. 2014a; Kpundeh et al. 2015). Thus, feeding 25% protein diet once daily to juvenile GIFT is insufficient for maximum growth and hence at day 10, a decreasing trend in mean body weight in L10H30 and L20H20 groups versus the control group in our study. However, all fish weight showed an increase compared to the initial weight, which indicated that feeding once daily with 25% protein diet surpassed the maintenance energy and nutrient requirements for juvenile GIFT and can support positive growth. Furthermore, in longer durations, dietary manipulation (20 days) induce significantly lower growth than the control fish in the present study, which is consistent with the results of rainbow trout (*Oncorhynchus mykiss*) (Sevgili et al., 2012).

Feeding history before re-alimentation was thought to be a major factor in eliciting CG response. For example, Indian major carp (*Labeo rohita*) (initial body weight 3.75 g) did not show a full CG after fasting for > 21 days (Yengkokpam et al. 2014), but full CG occurred in the fish (initial body weight, 4.29 g) after a moderate feed restriction (50–75% of satiation) for 42 days (Srijila et al. 2014). Similar results were reported in Asian sea bass (*Lates calcarifer*) (Tian and Qin 2003, 2004) and Atlantic Salmon (*Salmo salar*) (Johansen et al. 2001). In the present study, GIFT fed 25% protein diet once daily for 20 days were able to

Table 8 Proximate composition of muscle of juvenile GIFT under different dietary manipulation (%, wet basis)

Day	L10H30	L20H20	H40
Crude protein			
Initial		15.46	
10	15.85 ± 0.06	16.68 ± 0.67	17.42 ± 0.14
20	17.92 ± 0.13a	17.48 ± 0.20a	19.19 ± 0.11b
30	17.76 ± 0.49	17.79 ± 0.40	19.04 ± 0.23
40	19.38 ± 0.34	19.00 ± 0.72	19.21 ± 0.37
Crude lipid			
Initial		0.79	
10	0.65 ± 0.07	0.68 ± 0.21	0.84 ± 0.11
20	0.89 ± 0.10ab	0.66 ± 0.06a	0.99 ± 0.06b
30	0.95 ± 0.13	0.88 ± 0.23	0.95 ± 0.10
40	1.58 ± 0.23	1.56 ± 0.16	1.55 ± 0.06
Moisture			
Initial		76.40	
10	79.16 ± 0.12	78.91 ± 0.23	78.19 ± 0.29
20	78.49 ± 0.22	78.49 ± 0.02	77.85 ± 0.19
30	77.93 ± 0.22	77.99 ± 0.27	77.69 ± 0.28
40	77.08 ± 0.27	77.26 ± 0.11	76.98 ± 0.38

Values are mean ± SE of three tanks per treatment group. Different lowercase letters in the same line indicate significant differences ($P < 0.05$)

Table 9 Serum biochemical parameters of juvenile GIFT under different dietary manipulation

Day	L10H30	L20H20	H40
ALT (U L^{-1})			
10	74.67 ± 16.22	60.00 ± 15.14	37.33 ± 7.42
20	30.67 ± 1.33	30.67 ± 5.33	28.00 ± 2.31
30	26.67 ± 5.81	57.33 ± 17.64	33.33 ± 1.33
40	24.00 ± 4.62	42.67 ± 6.67	34.67 ± 13.13
AST (U L^{-1})			
10	147.33 ± 30.03	178.67 ± 19.64	121.33 ± 13.33
20	102.67 ± 7.06	126.67 ± 13.53	101.33 ± 21.46
30	88.67 ± 18.81	125.33 ± 23.70	121.33 ± 43.47
40	72.00 ± 2.31	114.67 ± 10.41	80.00 ± 19.73
GLU (mmol L^{-1})			
10	4.55 ± 1.31	6.11 ± 0.56	5.81 ± 0.19
20	4.65 ± 0.11	5.23 ± 0.52	6.04 ± 0.23
30	3.93 ± 0.39	5.04 ± 0.74	4.73 ± 0.60
40	4.21 ± 0.15	5.45 ± 0.07	5.53 ± 0.28
TCHO (mmol L^{-1})			
10	3.41 ± 0.26	3.05 ± 0.38	3.60 ± 0.21
20	3.68 ± 0.12	3.40 ± 0.27	3.61 ± 0.23
30	4.00 ± 0.45	5.39 ± 0.90	4.28 ± 0.22
40	4.84 ± 0.92	5.43 ± 0.75	5.96 ± 1.25
TGK (mmol L^{-1})			
10	3.74 ± 0.46	4.09 ± 0.58	3.64 ± 0.31
20	4.40 ± 0.50	4.19 ± 0.42	4.01 ± 0.70
30	4.44 ± 1.70	4.24 ± 0.08	5.09 ± 0.72
40	5.51 ± 0.80	6.65 ± 1.35	6.03 ± 1.50
TP (g L^{-1})			
10	17.33 ± 1.76	10.33 ± 3.53	12.00 ± 2.31
20	14.67 ± 3.52	12.00 ± 2.31	12.00 ± 2.31
30	22.67 ± 3.52	29.33 ± 4.00	24.00 ± 2.31
40	20.00 ± 4.00	2.679 ± 6.52	28.00 ± 2.31

Values are mean ± SE of three tanks per treatment group

catch up with the control fish after 10 days feeding with 35% protein diet thrice daily (Table 3). These findings can suggest that co-restriction of diet and protein in juvenile GIFT showed a better compensatory capacity than *O. mossambicus* × *O. niloticus* (Wang et al. 2000) or *O. niloticus* (L.) (Abdel–Tawwab et al. 2006). When tilapia also consumes natural feeds in practical culture conditions, our results further suggest that these dietary manipulation can be applied in the culture of GIFT. Since Wang et al. (2004) found that *O. mossambicus* × *O. niloticus* fed 0.5–3.0% rations for 28 days did not achieve a weight catch up during re-alimentation, the long-term effects of dietary co-restriction of diet and protein in GIFT should be investigated further.

The main reason for CG response are reported as an enhanced FI (hyperphagia) or/and improved feed and nutrient utilization efficiency during refeeding period (Gaylord and Gatlin III 2000; Ali et al. 2003; Mohanta et al. 2016). In the present study, complete CG observed in the L20H20 group was due to increased FI (Table 3), which is consistent with the findings of *O. mossambicus* × *O. niloticus* (Wang et al. 2000).

An increase in HSI, VSI, and *K* generally indicates improvement of nutritional status (Jobling et al. 1994; Saraiva et al. 2016). In general, *K* (Jobling et al. 1994; Gaylord and Gatlin III 2000; Pang et al. 2016), HSI (Gaylord and Gatlin III 2000; Cho 2005; Cho et al. 2006), and VSI (Caruso et al. 2012; Sevgili et al. 2013) decrease during starvation and recover after re-alimentation. In our study, however, no significant differences in these parameters were observed, which could be due to the fact that dietary restrictions in terms of protein, feeding level, and duration were moderate.

In some fish, a positive correlation between size and whole-body protein and lipid content has been detected (Shearer 1994; Abdel–Tawwab et al. 2015). Similarly,

Table 10 Area ratio (%) of the hepatocyte nucleus, cytoplasm, and vacuoles of juvenile GIFT under different dietary manipulation

Day	L10H30	L20H20	H40
Nucleus			
10	8.00 ± 3.24	11.46 ± 1.45	8.38 ± 3.24
20	13.62 ± 1.46	12.19 ± 1.33	10.78 ± 2.21
30	10.91 ± 1.38	12.13 ± 1.08	8.87 ± 1.96
40	7.99 ± 1.57	14.69 ± 3.21	7.08 ± 3.25
Cytoplasm			
10	51.82 ± 6.36	54.14 ± 5.59	67.15 ± 8.32
20	65.02 ± 8.32	66.00 ± 1.76	73.68 ± 4.32
30	73.37 ± 4.34	65.28 ± 5.07	66.06 ± 3.13
40	73.10 ± 2.41	62.03 ± 6.43	65.29 ± 7.63
Vacuoles			
10	40.18 ± 3.12	34.40 ± 4.14	24.47 ± 1.55
20	21.36 ± 8.37	21.81 ± 2.11	12.25 ± 3.38
30	16.49 ± 5.15	22.48 ± 6.56	28.37 ± 3.48
40	18.91 ± 3.67	23.28 ± 6.16	27.63 ± 8.23

Values are mean ± SE of three tanks per treatment group

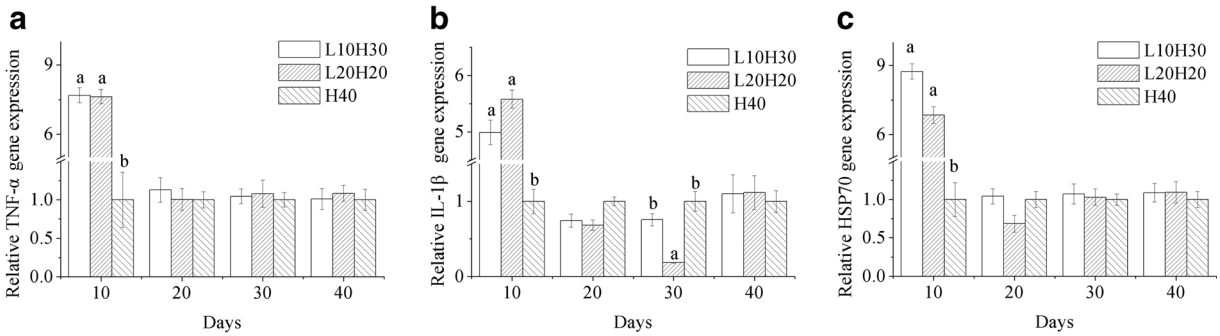

Fig. 1 Effects of the dietary manipulation on TNF-α (a), IL-1β (b), and HSP70 (c) mRNA expression levels in the tilapias hepatopancreas. Results are expressed as mean ± SE ($n = 3$). Means in the same sampling time with different letters are significantly different between groups ($P < 0.05$)

fish in the L10H30, L20H20, and H40 groups showed increased eviscerated whole-body crude protein content and lipid storage during the experimental period. Moreover, at the end of the experiment, viscera lipid content increased by about 20%, demonstrating that visceral fat is an important energy storage depot in *O. niloticus* (Hanley 1991).

In the present study, remarkably lower crude lipid contents of muscle and viscera were found in L20H20 at day 20 compared with the control. Similar results were reported for *S. salar* (Johansen et al. 2001), turbot (*Scophthalmus maximus* L.) (Blanquet and Oliva–Teles 2010), and *L. rohita* (Srijila et al. 2014), which had lower whole-body lipid contents in feed restriction than in control. Since lipid represents the primary energy storage form in fish, the present results were the response of low energy intake by fish fed 25% protein diet once daily.

Fish liver plays an important role in the metabolism and considered as the first organ to be affected by a feed restriction (Power et al. 2000; Gambardella et al. 2012). Prolonged feed restrictions lead to changes in hepatocyte morphology and enhances oxidation and oxidative stress in the liver of some fish species (Storch and Juario 1983; Ostaszewska et al. 2006). In the present study, liver histology was unaffected by the dietary manipulations (Table 10), being inconsistent with the findings of studies related to alterations of the hepatic morphological structure in fish as a result of severe feed restrictions. For example, the hepatic morphology of European Sea Bass (*Dicentrarchus labrax*) was characterized by a large spectrum of vacuolization during starvation (Gambardella et al. 2012). In addition, nuclear area and volume decreased due to diet restriction in sea bream (*Sparus aurata*) (Power et al. 2000) and pacu (*Piaractus mesopotamicus*) (Souza et al. 2001). However, in the present study, variables related to liver functions and metabolism such as serum AST and ALT activities (Limdi and Hyde 2003), and GLU, TCHO, TGK, and TP contents (Enes et al. 2009; Moro et al. 2010), did not differ significantly among the treatments over the study period (Table 6), indicating that fish liver was in a apparently healthy.

TNF-α and IL-1β are pro-inflammatory cytokines produced primarily by activated macrophages, and they participate in early inflammatory host reactions (Lee et al. 2006; Raida and Buchmann, 2009) and contribute to defense mechanisms of the host in response to bacterial colonization or invasion (Sigh et al. 2004; Reda et al. 2016). In the present study, upregulated mRNA expression levels of TNF-α and IL-1β were found in fish fed 25% protein diet once daily at day10. It can be speculated that this dietary manipulation aggravated the inflammation response. In contrast, long-term (50 days) feed restriction at 70% of ad libitum intake in lean mice increased the expression levels of IL-1β and TNF-α in adipose tissues (Kurki et al. 2012), and food deprivation (39.5 h) increased the basal mRNA expressions of IL-1β and TNF-α in rat hypothalamus (Gayle et al. 1999). In addition, feed-restricted (63 days) rabbits tended to show higher IL-1β mRNA expression and lower TNF-α mRNA expression in the ileum (Knudsen et al. 2015). In this study, at day 30, the L20H20 fish showed lower hepatopancreas IL-1β mRNA expression than the other groups. These results suggest that either the cytokines are differentially expressed in the different tissues, an inflammation response is dependent on the duration and type of dietary manipulation.

Heat-shock proteins (HSPs) are commonly used as indicators of stress in animals (Cara et al. 2005;

Antonopoulou et al. 2013), and an increase in HSP content in the tissues may be used to overcome the starvation stress (Yengkokpam et al. 2008; Antonopoulou et al. 2013). Moreover, HSP induction inhibits genetic expression of pro-inflammatory cytokines (Yoo et al. 2000). In *O. niloticus*, upregulated expression of HSP70 could enhance the immunological ability against *Streptococcus iniae* infection (Chen et al. 2014b). In our study, increased HSP70 mRNA expression in the hepatopancreas was found only in the L10H30 and L20H20 groups at day 10, and no significant differences occurred during the rest of experiment among the groups. In contrast, a research on *L. rohita* fingerlings showed that the expression of HSP70 increased linearly in the hepatopancreas during 3 weeks of starvation, but in muscle, the change was observed only after 3 weeks of starvation (Yengkokpam et al. 2008).

In conclusion, feeding 25% protein diet once daily to juvenile GIFT for 10 days did not affect growth rate, whereas for 20 days reduced body weight relative to the control. However, refeeding 35% protein diet thrice daily achieved a complete CG at the end of realimentation period in both restricted groups. This could ascribe to increased FI rather than improved FE.

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