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## FULL LENGTH ARTICLE

# Effects of weekly feeding frequency and previous ration restriction on the compensatory growth and body composition of Nile tilapia fingerlings



Tamer El Sayed Ali <sup>a</sup>, Silvia Martínez-Llorens <sup>b</sup>, A.V. Moñino <sup>b</sup>,  
 Miguel Jover Cerdá <sup>b</sup>, Ana Tomás-Vidal <sup>b,\*</sup>

<sup>a</sup> *Oceanography Department, Faculty of Science, Alexandria University, Alexandria, Egypt*

<sup>b</sup> *Research Group of Aquaculture and Biodiversity, Institute of Animal Science and Technology, Universitat Politècnica de València, Camino de Vera, 14, 46071 Valencia, Spain*

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### KEYWORDS

*Oreochromis niloticus*;  
 Compensatory growth;  
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**Abstract** The effect of different weekly feeding frequencies on Nile tilapia fingerlings of 2.02 g, was determined during 12 weeks. This was done by feeding the fish 7 days/week, 6 days/week or 5 days/week. After this restriction feeding period, all fish were fed as the control group (7 days/week) during 26 days to study the capability of the fish to compensate the growth during this re-feeding period. At the end of the feeding restriction period, there were significant differences in weights among the different treatments, although the significance was detected only at 7 days/week level, which presented the highest final body weight compared with the other 2 treatments. The daily feed intake and the feed conversion and protein efficiency ratios did not present significant differences. Crude protein efficiency (CPE) and gross energy efficiency (GEE) were affected by the feeding frequency, presenting high values in fish fed 7 days/week. Growth results obtained during this re-feeding period indicate that weight gain (WG) and specific growth rate (SGR) presented a linear increase from 7 to 5 days/week, i.e. with increasing feed deprivation period the fish could compensate the growth effectively, trying to reach to the weight as those of the control group.

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### Introduction

Feed is generally the highest variable costs at aquaculture facilities. Understanding nutrient requirements and implementing

appropriate feeding strategies can reduce waste and increase profits. Feed efficiency is vital in livestock farming in general and of course, in the case of aquaculture. From a management standpoint frequent feeding (number feeding per day) of fish may not be economical due to increased labour costs (Riche et al., 2004). So, one of the problems in fish production is to obtain a good balance between fish growth and food consumption. Therefore, equally important it is to know the growth and nutritional needs of fish, as knowing the best feeding strategies

\* Corresponding author at: Polytechnic University of Valencia, Camino de Vera, 14, 46071 Valencia, Spain. Fax: +34 96 3877439.

E-mail address: [atomasv@dca.upv.es](mailto:atomasv@dca.upv.es) (A. Tomás-Vidal).

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for a species (Jobling, 1993; Goddard, 1996; Jørgensen et al., 1996; Gokcek et al., 2008).

There is a positive relation between growth and feeding frequency (Riche et al., 2004; Riche, 2008). However, Crampton (1991) demonstrated that it may not be necessary to feed daily in order to obtain maximum growth rates. Also De Silva and Anderson (1995) observed that beyond a certain level, excessive feeding has no influence on growth and result in poor growth. Excess intake causes a worse FCR, above what the fish really needs.

Hyperphagy contributed to the restoration of an energy deficit caused by the starvation period. In fact, compensatory growth is a clear response to hyperphagia (Ali and Wootton, 2003). Hyperphagia should allow an animal that has suffered a food restriction regain the weight it would have if fish had eaten without restriction. Compensatory growth is higher when greater has been the period of restriction that has been subjected the animal (Jobling and Koskela, 1997; Nikki et al., 2004; Tian and Qin, 2003, 2004).

Most studies of compensatory growth have focused on the duration of complete feed deprivation (Wieser et al., 1992; Jobling and Koskela, 1996; Zhu et al., 2001; Tian and Qin, 2003, 2004; Azodi et al., 2016) and mostly were carried out on cold water species and reports on warm water species are few (Schwarz et al., 1985; Kim and Lovell, 1995; Hayward et al., 1997). Hybrid tilapia *Oreochromis mossambicus* × *Oreochromis niloticus*, exhibited compensatory responses after feed deprivation (Wang et al., 2000, 2004, 2005, 2009; Gao et al., 2015; Ye et al., 2016), but fish that were kept on restricted feeding regimes failed to completely recover in the great majority of cases.

Despite the great potential of tilapia production, information regarding the effects of feeding strategies and management practices on fish performance is limited.

Along with carps and salmonids tilapia is considered the most produced worldwide species (El-Sayed, 1999). Although until recently are raised in ponds without artificial feeding, consequence of its recent intensification is necessary to increase the nutritional knowledge of this species.

For these reasons, the present study aimed to investigate the effect of different feeding regimes (frequency of feeding per week) by feed deprivation for days (week end was selected for later commercial application) on the growth parameters, nutrients retention and body composition of the fish during different life stages and the influence of previously mentioned restriction feeding (feeding frequency) and subsequent return to all-week feeding on compensatory growth responses of Nile tilapia.

## Materials and methods

### Experimental fish and culture system

Nile tilapia (*O. niloticus*) fingerlings that weighed 2.02 g ( $n = 360$ ) came from a local commercial fish farm, Valencià de Acuicultura S.L., Valencia, Spain. Fish were randomly stocked in 3 fibreglass tanks with 750 l capacity (40 fishes per tank), for facilities limitation 3 cages of 120 l capacity were put in each tank to obtain 3 replicates for each treatment. They were fed ad libitum with a commercial diet (45% CP and 20% CL) for a week before the experiment began.

The duration of the trial was 110 d. The facilities consist in a recirculating marine water system (65 m<sup>3</sup> capacity). The average water parameters measured during the experiment was: temperature was  $28.3 \pm 1.7$  °C (mean  $\pm$  SD) and dissolved oxygen was  $6.04 \pm 0.7$  mg L<sup>-1</sup> (both parameters were measured with an OxyGuard, Handy Polaris V 1.26).

All tanks have aeration and photoperiod was natural.

### Experimental diets and feeding regime

Two experimental diets previously tested and recommended in preliminary feeding trial were tested (40% CP, 15% EE and 21.37 kJ g<sup>-1</sup> for young fish till 40 g body weight and then the diet used was 35% CP, 15% EE and 21.20 kJ g<sup>-1</sup> for the fish till the end of the experiment, Table 1).

Some ingredients, like wheat and extracted soybean were milled in a hammer mill (Technochufa, Valencia, Spain). Diets were prepared by extrusion cooking with a semi-industrial twin-screw extruder (Clextral BC-45, St. Etienne, France, 100 rpm screw speed, 110 °C temperature, 30 atm–40 atm pressure and 2 mm–3 mm diameter pellets).

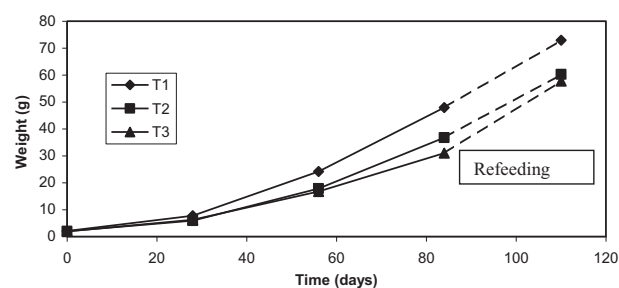
The first period lasted for 84 days and tested a restricted feeding regime. During this period, fish were fed 3 times/day (9:00 a.m., 1:00 p.m. and 5:00 p.m.) to apparent satiation at different feeding frequencies as follow: T1, feeding 7 days/week, T2, feeding 6 days/week and T3, feeding 5 days/week, i.e. fasting one day or 2 days at weekends is the meaning of T2 and T3, respectively. Every four weeks, fish were weighed and counted (previously anaesthetisation with 30 mg/L of clove oil (Guinama, Valencia, Spain) containing 87% Eugenol).

After this restricted feeding period, fish were fed all the week days to satiation twice a day (9:00 a.m. and 5:00 p.m.). This was the second period, with duration of 26-days and with the objective studying the compensatory growth in tilapia.

### Body composition analyses

Five fish per tank at the beginning and the end of the first period were randomly sampled and dissected to determine biometric parameters and body composition.

Ingredients, diets and the whole fish were analysed according to the following steps (AOAC, 1990): dry matter (105 °C to constant weight); ash (incinerated at 550 °C to constant weight); CP (N x 6.25) by the Kjeldahl method after acid digestion (Kjeltec 2300 Auto Analyser, Tecator, Höganäs, Sweden); CL extraction with methyl ether (Soxtec 1043 extraction unit;



**Figure 1** Evolution of average body weight of tilapia during the two periods of the experiment.

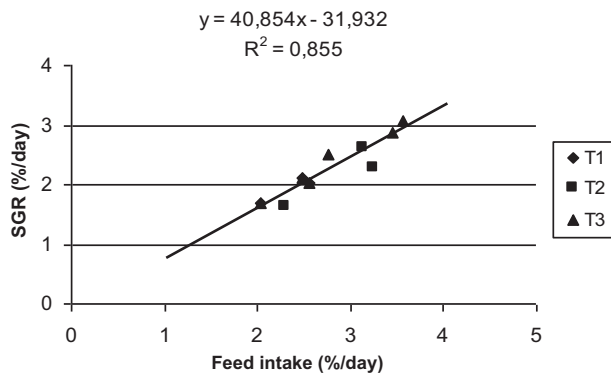
**Table 1** Formulation and proximate composition of extruded diets.

Ingredients (g/kg)	Diet (CP/CL)	
	35/15	40/15
Fish meal, herring	270	263
Extracted soybean meal	135	264
Wheat meal	472	348
Soybean oil	51	52
Fish oil	64	65
Vitamin-mineral mix <sup>u</sup>	8	8
Analysed composition (%)		
Crude protein (CP)	35.07	40.01
Crude Lipid (CL)	15.01	15.06
Crude fibre (CF)	2.81	3.07
Ash	6.98	7.58
<i>Calculated values</i>		
N-free extract (NFE) <sup>x</sup>	40.13	34.28
Gross Energy GE (MJ/kg) <sup>y</sup>	21.2	21.37
CP/GE (g/MJ)	16.5	18.7

<sup>u</sup> Vitamin and mineral mix (values are g kg<sup>-1</sup> except to those in parenthesis): Premix: 20; Choline. 10; DL- $\alpha$ -tocopherol. 5; ascorbic acid. 5; Premix composition: retinol acetate. (1,000,000 IU/7 kg); calciferol. (500 IU kg<sup>-1</sup>); DL-  $\alpha$ -tocopherol. 10; menadione sodium bisulphite. 0.8; thiamin hydrochloride. 2.3; riboflavin. 2.3; pyridoxine hydrochloride. 1.5; cyanocobalamin. 25; nicotinamide. 15; pantothenic acid. 6; folic acid. 0.65; biotin. 0.07; ascorbic acid. 75; inositol. 15; betaine. 100; polypeptides. 12; Zn. 5; Se. 0.02; I. 0.5; Fe. 0.2; Cu. 0.15; Mg. 5.75; Co. 0.02; Met. 0.2; Cys. 0.8; Lys. 1.3; Arg. 0.6; Phe. 0.4; Try. 0.7; except. to 1000 g (Source: Dibaq-Diproteg).

<sup>x</sup> Calculated NFE:1000- CP-CL-Ash-CF (g kg<sup>-1</sup>).

<sup>y</sup> Calculated using: 23.9 kJ g<sup>-1</sup> proteins, 39.8 kJ g<sup>-1</sup> lipids and 17.6 kJ g<sup>-1</sup> carbohydrates.

**Figure 2** Feed-growth relationship for tilapia subjected to full-week satiation feeding during the re-feeding (compensatory) period.

Tecator); and CF by acid and basic digestion (Fibertec System M. 1020 Hot Extractor; Tecator). All analyses were performed in triplicate.

#### Statistical analyses

Prior to the analysis, all variables were checked for normality and variance homogeneity (Barlett's test). One way analysis of

variance (ANOVA), was applied to compare between the real final body weights and the other variables were subjected to multifactor analysis of variance. All the growth parameters were corrected for size effects using the initial weight as a covariate (Snedecor and Cochran, 1971). The Student Newman-Keuls test was used for comparisons between means at 0.05 significant level. Mean values for each tank were the units of observation for statistical evaluation. Multiple regression analysis was employed to derive a relationship between feed intake and body weight, the resulting regression equation allowed the estimation of the optimum ration size at any given weight. Also a linear regression analysis was applied for estimation the relationship between WG and FI during the compensatory feeding period. This statistical analysis was carried out using statistical software, STATGRAPHICS, Version 4.1.

## Results

### (First period) Feed restriction period

Approximately, no mortality was recorded during the experimental period, neither during the restricted feeding period nor during the satiation feeding period.

### Feed consumption and growth

Growth and feed response parameters are presented in Table 2. At the end of the feed restriction period, there were significant differences in body weights among the different treatments, final fish weights and WG increased in all groups by increasing the feeding frequency from 5 days to 7 days (i.e. T3 to T1), although the significance ( $P < 0.05$ ) was detected only at T1 level, which presented the highest final body weight compared with the other 2 treatments and a higher WG compared with T3.

Fish fed T3 presented a significantly ( $P < 0.05$ ) lower SGR compared with the other 2 treatments, meaning that feeding 5 days/week has a severe effect on the fish growth.

Daily feed intake, feed conversion and protein efficiency ratios did not present significant differences.

### Biological parameters and biochemical composition of fish

Nutrient utilisation, biometric parameters and body composition are presented in Table 3. No significant differences were obtained on biometric parameters, neither CF, VSI, HSI nor did mesenteric fat present any significant difference, meaning that these parameters were not influenced by the feeding frequency but there was a tendency to be decreased with increasing the duration of feed deprivation. Only the DP was affected by the number of feeding days that presented significantly ( $P < 0.05$ ) lower values when fish fed 6 days/week (T2) or 5 days/week than the control group (T1).

With respect to the body composition of the fish, no significant differences were found in the protein, ether extract (EE), ash or water content between the different treatments ( $P > 0.05$ ), although the CP and EE have presented a linear decrease from T1 to T3 and also a linear increase in ash content from T1 to T3, probably due to different fish size.

Although neither protein nor fat content varied between the different treatments, the CPE and GEE were affected by the

**Table 2** Effect of feeding frequencies on growth and nutritive parameters (mean  $\pm$  SE) of tilapia during the restricted feeding period.

	Feeding regime		
	T1	T2	T3
Initial weight (g)	2.08 $\pm$ 0.08	2.04 $\pm$ 0.08	1.94 $\pm$ 0.08
Final weight (g)	47.19 <sup>a</sup> $\pm$ 1.85	36.55 <sup>b</sup> $\pm$ 1.85	31.98 <sup>b</sup> $\pm$ 1.85
WG (%) <sup>s</sup>	2554 <sup>a</sup> $\pm$ 235	1850 <sup>ab</sup> $\pm$ 235	1625 <sup>b</sup> $\pm$ 235
SGR (%/day) <sup>t</sup>	3.88 <sup>a</sup> $\pm$ 0.09	3.52 <sup>ab</sup> $\pm$ 0.09	3.38 <sup>b</sup> $\pm$ 0.09
FI <sup>u</sup>	2.50 $\pm$ 0.12	2.53 $\pm$ 0.12	2.74 $\pm$ 0.12
FCR <sup>v</sup>	1.14 $\pm$ 0.05	1.18 $\pm$ 0.05	1.30 $\pm$ 0.05
PER <sup>x</sup>	2.20 $\pm$ 0.08	2.13 $\pm$ 0.08	1.98 $\pm$ 0.08

Mean  $\pm$  S.E (means of triplicate groups). Means followed by the same superscript do not differ at  $P < 0.05$  (Newman–Keuls). Covariate initial weight: SGR, final weight.

<sup>s</sup> Relative weight gain (%). WG = 100\*(Final weight – Initial weight)/Initial weight.

<sup>t</sup> Specific growth rate (%/day). SGR = 100 \* ln (Final weight/Initial weight)/days.

<sup>u</sup> Feed intake (%/day<sup>-1</sup>) FIR = 100  $\times$  Feed consumption (g)/(average biomass (g)  $\times$  days).

<sup>v</sup> Feed conversion ratio. FCR = Feed consumption (g)/Biomass gain (g).

<sup>x</sup> Protein efficiency ratio. PER = Biomass gain (g)/Protein intake (g).

**Table 3** Effect of feeding frequencies on biometric parameters, body composition and retention parameters (mean  $\pm$  SE) of tilapia during the restricted feeding period.

	Feeding regime		
	T1	T2	T3
CF (%) <sup>t</sup>	1.99 $\pm$ 0.05	1.93 $\pm$ 0.05	1.90 $\pm$ 0.05
IVS <sup>u</sup>	9.05 $\pm$ 0.29	8.58 $\pm$ 0.29	8.22 $\pm$ 0.29
IHS <sup>v</sup>	1.97 $\pm$ 0.18	1.91 $\pm$ 0.18	1.75 $\pm$ 0.18
MF <sup>w</sup>	0.98 $\pm$ 0.12	0.93 $\pm$ 0.12	0.62 $\pm$ 0.12
DP <sup>x</sup>	77.71 <sup>a</sup> $\pm$ 0.80	71.68 <sup>b</sup> $\pm$ 0.80	73.58 <sup>b</sup> $\pm$ 0.80
<i>Body composition</i>			
Dry matter (%)	28.01 $\pm$ 0.41	27.69 $\pm$ 0.41	27.98 $\pm$ 0.41
Ash (% dm)	9.76 $\pm$ 0.99	11.40 $\pm$ 0.99	13.84 $\pm$ 0.99
Crude protein CP (% dm)	53.69 $\pm$ 2.02	50.95 $\pm$ 2.02	50.70 $\pm$ 2.02
Crude lipid CL (% dm)	34.93 $\pm$ 0.99	32.21 $\pm$ 0.99	31.42 $\pm$ 0.99
<i>Nutrient retention</i>			
CPE (%) <sup>y</sup>	34.49 <sup>a</sup> $\pm$ 0.80	31.70 <sup>ab</sup> $\pm$ 0.80	30.62 <sup>b</sup> $\pm$ 0.80
GEE (%) <sup>z</sup>	34.78 <sup>a</sup> $\pm$ 0.54	32.14 <sup>b</sup> $\pm$ 0.54	32.54 <sup>b</sup> $\pm$ 0.54

Mean  $\pm$  S.E ( $n = 15$  for biometric parameters and means of triplicate groups for the rest). Means followed by the same superscript do not differ at  $P < 0.05$  (Newman–Keuls).

<sup>t</sup> Condition factor, CF = 100  $\times$  total weight (g)/total length<sup>3</sup> (cm).

<sup>u</sup> Viscerosomatic index (%), VSI = 100  $\times$  visceral weight (g)/empty fish weight (g).

<sup>v</sup> Hepatosomatic index (%), HSI = 100  $\times$  liver weight (g)/empty fish weight (g).

<sup>w</sup> Mesenteric fat (%), MF = 100  $\times$  mesenteric fat weight (g)/empty fish weight (g).

<sup>x</sup> Dressout percentage (DP, %) = 100  $\times$  (total fish weight – head-viscera weight)(g)/total fish weight (g).

<sup>y</sup> Crude protein efficiency, CPE (%) = (fish protein gain, g)  $\times$  100/(protein intake, g).

<sup>z</sup> Gross energy efficiency, GEE (%) = (fish energy gain, kJ)  $\times$  100/(energy intake, kJ).

feeding frequency, presenting significant ( $P < 0.05$ ) high values in T1 treatments, but it must be considered that these values were reflection of the high values of CP and EE at T1 level even no significance was detected and the higher growth with this diet.

#### Second period: Re-feeding period

Growth results obtained during this re-feeding period (all week days feeding period) are presented in Fig. 1 and Table 4, showing that no significant differences ( $P > 0.05$ ) in the calculated

final body weight were detected between the different treatments, knowing that these values are corrected by the initial body weight as a covariate. With respect to the real values obtained (Table 4) no significant differences ( $P > 0.05$ ) were detected also but it may be due to the high variations between treatments which may have masked any treatment effects (high standard errors), but statistically for studying the compensatory growth, the theoretical values which are corrected by initial body weight must be considered as a result of the significance difference in the later parameter at the beginning of this period.

With respect to the growth parameters WG and SGR, their ANOVA was corrected for initial body weight effects and

**Table 4** Effect of re-feeding on growth and nutritive parameters (mean  $\pm$  SE) of tilapia.

	Feeding regime		
	T1	T2	T3
Initial weight (g) <i>n</i> = 3	45.70 <sup>a</sup> $\pm$ 2.02	35.27 <sup>b</sup> $\pm$ 2.02	29.41 <sup>b</sup> $\pm$ 2.02
Final weight (g) <i>n</i> = 3	75.90 $\pm$ 15.03	60.23 $\pm$ 15.03	57.74 $\pm$ 15.03
Corrected final weight (g) <sup>*</sup> <i>n</i> = 3	62.20 $\pm$ 2.35	62.06 $\pm$ 2.20	69.06 $\pm$ 2.31
WG (%) <sup>s,*</sup> <i>n</i> = 3	73.64 <sup>b</sup> 5.14	76.38 <sup>b</sup> $\pm$ 4.82	101.32 <sup>a</sup> $\pm$ 5.06
SGR (%/day) <sup>t,*</sup> <i>n</i> = 3	2.11 <sup>b</sup> $\pm$ 0.10	2.16 <sup>b</sup> $\pm$ 0.10	2.66 <sup>a</sup> $\pm$ 0.10
FI <sup>u</sup> <i>n</i> = 3	2.35 $\pm$ 0.21	2.89 $\pm$ 0.35	2.99 $\pm$ 0.21
FCR <sup>v</sup> <i>n</i> = 3	1.24 $\pm$ 0.09	1.37 $\pm$ 0.09	1.10 $\pm$ 0.09
PER <sup>x</sup> <i>n</i> = 3	2.31 $\pm$ 0.24	2.09 $\pm$ 0.24	2.70 $\pm$ 0.25

Mean  $\pm$  S.E (means of triplicate groups). Means followed by the same superscript do not differ at  $P < 0.05$  (Newman-Keuls).

<sup>\*</sup> Calculated using initial weight as covariate.

<sup>s</sup> Relative weight gain (%). WG = 100<sup>\*</sup>(Final weight – Initial weight)/Initial weight.

<sup>t</sup> Specific growth rate (%/day). SGR = 100 \* ln (Final weight/Initial weight)/days.

<sup>u</sup> Feed intake (%/day<sup>-1</sup>) FIR = 100  $\times$  Feed consumption (g)/(average biomass (g)  $\times$  days).

<sup>v</sup> Feed conversion ratio. FCR = Feed consumption (g)/Biomass gain (g).

<sup>x</sup> Protein efficiency ratio. PER = Biomass gain (g)/Protein intake (g).

presented a linear increase from T1 to T3, i.e. with increasing feed deprivation period although the contrary was obtained during the restricted feeding period, this indicates that the fish presented compensatory growth.

A great correlation ( $r^2 = 0.855$ ;  $P < 0.01$ ) between SGR and FI was observed:  $y = 40.854x - 31.932$  (Fig. 2). Although FI have not presented significant differences between the different treatments, a linear increase was shown from T1 to T3 meaning that with increasing feed deprivation period the fish had a great potential to intake more feed during the re-feeding period and compensate their growth, presenting also a linear increase in SGR values from T1 to T3. No evidence of significant trend in FCR or in PER for fish subjected to different treatments was observed.

## Discussion

### Restricted feeding regime

The effect of the number of feeding days per week on growth of Nile tilapia, testing the influence of feed deprivation at weekends (Saturday and Sunday), on fish growth and feeding efficiency was studied. Results demonstrated that feeding all the week days have affected greatly on the final body weight, WG and SGR. These results do not agree with the observations recorded by the formerly mentioned authors, De Silva and Anderson (1995) in which experiment an excessive feeding has no influence on growth, but is in accordance with those of Riche et al. (2004) who observed a positive relation between growth and feeding frequency as mentioned before.

Also, Okumus and Bascinar (2001) examined the effects of the number of feeding days per week and fasting at weekends on growth of rainbow trout (*Oncorhynchus mykiss*) and

demonstrated that feeding 7 days/week is required for obtaining the best growth.

In this study neither CF, HSI nor VSI has been affected by the feeding frequency, this indicates that the liver and the viscera are in normal state and no abnormal storage has been done, this observation is in accordance with others reported in several fish species (Miglav and Jobling, 1989; Rueda et al., 1998). Also, C. Fatness presented a tendency to be decreased with increasing duration of feed deprivation. Many authors suggested that in short-term starvation visceral fats and muscle fats are utilised as energy sources (Weatherley and Gill, 1987) and this could be confirmed by the significantly lower values of EUE obtained at T2 and T3 levels.

Feeding regime affects feed utilisation and hence influences fish body composition (Lovell, 1992; Adebayo et al., 2000).

Although decreasing the number of feeding days from 7 to 5 days/week was accompanied by a linear decrease in protein and fat contents and linear increase in the ash, no significant differences were recorded. Moisture content has not followed a certain rule but there was a great tendency to be increased with increasing the duration of feed deprivation, meaning that there was a replacement of muscle lipids by water. Likewise, Wang et al. (2000) demonstrated that tilapia body moisture and ash tended to be higher, while lipid and protein contents tended to be lower as the duration of feed deprivation increases.

### Compensatory growth

Compensatory growth is a good alternative to improve growth rates of fish through the appropriate choice of where food deprivation periods are followed by periods of food satiation. This technique, well done, can compensate for the lost growth

during starvation and could be an opportunity to recover the lost growth when the supply resumes.

Compensatory growth usually precedes a period of food restriction (Dobson and Holmes, 1984; Hayward et al., 1997). Fish subjected to previous nutritional restriction may partially (Miglav and Jobling, 1989; Jobling, 1993) or completely (Johansen et al., 2001; Maclean and Metcalfe, 2001) regain the weight and can match those who have not been subjected to restriction (Dobson and Holmes, 1984; Kim and Lovell, 1995).

By applying this phenomenon in tilapia, the growth rate and feed efficiency may be increased (Wang et al., 2000, 2009; Gao et al., 2015). This also seemed to be the case in the present study, after a long period of restricted feeding (12 weeks) which caused significant differences in the body weights, these differences were diminished at the end of the re-feeding period. Tilapia final weight was not significantly different in all treatments but fish with no food deprivation presented a higher weight than food deprived animals, only when initial weight was used as covariate, the differences disappeared. This result indicates a partial compensatory growth, since the animals deprived of food did not reach the same weight of the continuously fed animals.

Tian and Qin (2004) concluded that complete compensatory growth occurs only in fish experiencing a moderate feed restriction. Complete compensation was reported after a 16-day deprivation in minnows (*Phoxinus phoxinus*) (Russell and Wootton, 1992), and in rainbow trout after a 3-week deprivation (Dobson and Holmes, 1984; Quinton and Blake, 1990). Also Ali and Jauncey (2004) revealed that African catfish (*Clarias gariepinus*) shows partial compensatory growth responses at alternating periods of feeding regimes.

Wang et al. (2009) and Gao et al. (2015) obtained compensatory growth of the feed-restricted groups during the refeeding period, although the growth of none of the restricted groups caught up with that of the control group over the experimental period. Wang et al. (2000) demonstrated that hybrid tilapia (*O. mossambicus* × *O. niloticus*) had compensatory growth when fishes were deprived of food a week. This 1 week represents about 25% of the duration of the restricted feeding trial. In the present study, fish fed T3 deprived from feed 24 days, i.e. fasted about 28% of the days of the first period, and presented a good ability to compensatory growth response in 26 days, although a longer period would be needed to equal the weight of fish fed without restriction.

Therefore, at commercial fish farms, farmers could restrict feed delivery to fish during the labour days (5 days/week, excluding the week ends) and then full week feeding for superior to 1/3 previous duration. It is evident that an economic benefit will be realised, because although the total intake can equal after the re-feeding period between treatments with and without restriction, the general expenses of the company would be reduced, especially staff costs dedicated to the daily feeding of the fish.

The same could be discussed for T2 feeding regime which approximately presented the same results although T3 has presented better significance with respect to WG and SGR than T2 compared with T1, this may due to the longer feed deprivation period.

Growth rate increased with increasing feed restriction and was the highest in group T3 in which fish were deprived for 2 days/week (T3), indicating that these fish have great poten-

tial to compensate the previous restricted feeding period and to catch up a higher body size. These results are similar to those obtained by Gao et al. (2015).

These high growth rates are greatly related with FI. The feed intake of the restricted groups was higher than that of the control group throughout the refeeding period, although no significant differences were found. These results are in accordance with the results for Arctic charr, *Salvelinus alpinus* (Miglav and Jobling, 1989; Damsgård et al., 2000), hybrid sunfish Hayward et al., 1997), gibel carp, *Carassius auratus gibelio* (Xie et al., 2001), and three-spined stickleback, *Gasterosteus aculeatus* (Ali and Wootton, 2001).

The sharp decrease in FCR (1.10) after being (1.30) at the first period is explained by the higher growth rate accompanied by better feed conversion ratio during the re-alimentation period, which are specially compensatory growth indicators (Ali and Wootton, 2003). Also PER has increased confirming the increase in WG, considering that fish in all treatments fed the same protein level.

Two possible explanations of the compensatory growth recorded by several authors are the hyperphagia or a combination of hyperphagia and improved feed efficiency (Ye et al., 2016). The present study confirmed the result from a previous study on compensatory growth of tilapia following feed deprivation, that hyperphagia was the major mechanism for compensatory growth in this species (Wang et al., 2000, 2004; Tian and Qin, 2004).

So, Nile tilapia subjected to 1 or 2 fasting days displayed complete compensatory growth and high growth rate during the recovery phase when applied for certain period equal or longer than the duration of feed deprivation period, but to equal the final weight of the fish that ate every day, the re-feeding period should have been higher.

## Conflicts of interest

The authors have no personal conflicts of interest to declare.

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