

# Compensatory Responses of Nile Tilapia *Oreochromis niloticus* under Different Feed-Deprivation Regimes

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## Abstract

We investigated compensatory growth of Nile Tilapia *Oreochromis niloticus* in structural size and live weight in response to different deprivation periods and refeeding. Four treatments were assigned randomly to fish in 12 glass tanks, with each treatment performed in triplicate. The control group was fed to satiation three times a day throughout the experiment. The other three treatment groups were starved for 1 week (S1), 2 weeks (S2), or 4 weeks (S4) and then fed until the end of the experiment. After the experiment, no significant differences were observed among S1, S2, and the control group in average weight or length, whereas the weight and length of S4 were significantly reduced. Relative condition factors of the three starved groups decreased significantly until the end of the restricted period but recovered rapidly after refeeding. The specific growth rate in weight ( $SGR_w$ ) of the three restricted groups recovered quickly upon refeeding and were significantly higher than the control group, but these differences disappeared gradually until the end of the experiment. No significant difference in specific growth rate in length ( $SGR_l$ ) was noted between the control group and the three restricted groups after refeeding. All three groups showed hyperphagia for a short period upon refeeding, and no statistical differences were observed in feeding efficiency among the four groups.

**Key words:** Feed deprivation, Compensatory growth, Nile tilapia, *Oreochromis niloticus*

## Introduction

The successful feeding of intensively cultured fish requires detailed knowledge of nutritional requirements and optimal feeding practices, which can improve their growth rates and feeding efficiencies. In the Nile tilapia *Oreochromis niloticus*, one of the most popular and highly produced species globally, feeding improvement is important to farmers because of the high costs of feed, particularly in recirculating tank culture. Generally, culturists maximize food intake to maximize growth, but previous studies have suggested that this may not be the most efficient method of fish production (Azevedo et al., 1998; Rasmussen and Ostefeld, 2000; Van Ham et al., 2003). Maximizing feed intake can produce uneaten feed and reduce feeding efficiency (FE), resulting in more expensive production.

Compensatory growth may be used as a management tool to improve growth rates (Hayward et al., 1997) and FE and to reduce feeding costs. In various fish species, deprivation or limited-feeding strategies have been used to induce compensatory growth. Some factors underlying the rapid growth during compensatory growth phases include hyperphagia and increased FE in fish after feed limitation (Russell and Wootton, 1992; Boersma and Wit, 1997). Previous studies have generally focused on compensatory growth in weight, but not in length. However, Bavčević et al. (2010) reported that compensatory growth in gilthead sea bream *Sparus aurata* compensated weight, but not length. They proposed that any reduction in growth length is suggestive of a permanent loss in weight-increase potential, which we defined as the maximum

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attainable increase in weight during a given period.

In the present study, we explored the roles of previous feeding history on the capacity of tilapia to show compensatory growth responses in both weight and length, and we determined whether feeding history influenced characteristics of the compensatory response in relation to the effects of deprivation protocols on body condition. We also evaluated the effects of feed intake and efficiency on the compensatory response.

## Materials and Methods

### Experimental setting

Fish were acclimated to the recirculating system for 2 weeks prior to the start of the experiment. Water temperature was maintained at  $25 \pm 0.5^\circ\text{C}$  using a heater linked to a thermostat. The photoperiod was 12L:12D and continuous aeration was provided. Dissolved oxygen was above 5 mg/L. Water flow to each experiment tank was 5 L/min through a recirculating system equipped with a sand filter, and evaporating water was replenished continually.

Initially, fish were deprived of food for 24 h, weighed individually, and divided equally into 12 glass tanks ( $30 \times 30 \times 30$  cm), resulting in similar population structures. Four feeding regimes were applied in triplicate. Three restricted feeding groups were subjected to the following regimes: starved for 1 week and refed for 12 weeks (S1), starved for 2 weeks and refed for 11 weeks (S2), and starved for 4 weeks and refed for 9 weeks (S4). The control group (C) was fed to satiation three times a day on a commercial pellet feed (0.5 mm, 38% crude protein, 6% crude fat) during the experiment. The restricted groups were fed the same regime as the control group during the refeeding period. Weight and length were measured individually on the 7th, 14th, 28th, 42nd, 63rd, and 91st day after day 1 of feed deprivation. Uneaten feed was recorded, and feed amount was calculated at each measuring time. Dead fish were recorded on a daily basis.

Following Ricker (1979), we estimated the von Bertalanffy growth rate ( $r_B$ ) starting with the alternative Ford Walford plot regression equation (Cadima, 2003),  $L_{t+\Delta t} - L_t = (L_\infty - L_t) \times (1 - e^{-r_B \Delta t})$ , where  $L_t$  and  $L_{t+\Delta t}$  are lengths at the beginning and end of each experimental period of duration  $\Delta t$ , respectively, and  $L_\infty = 59.8$  cm (Kraljević and Dulčić, 1997). Rearranging the above equation, we have  $r_B = [\ln(L_\infty - L_t) - \ln(L_\infty - L_{t+\Delta t})] / \Delta t$ . The relative condition factor (RCF) (Le Cren 1951) was used to evaluate fish condition. First, the weight and length relationship of the control group throughout the experimental period was calculated as  $W = 0.0099 \times L^{3.2691}$ ,  $r^2 = 0.996$ . The predicted weights of the other four groups could then be calculated using the above equation combined with the observed length. The RCF was the ratio of observed weight to predicted weight at a given length. When the relative-condition factor

equaled 1, the fish had the same body condition as the control group. FE, feed intake, and specific growth rates were calculated as follows:

$$\begin{aligned} \text{FE} &= (W_t - W_0)/I, \\ \text{FI} &= 100 \times \text{feed} \times [(W_t + W_0)/2]^{-1} \text{ day}^{-1}, \\ \text{SGR} &= 100 \times (\ln W_t - \ln W_0) \times (T_t - T_0)^{-1}, \end{aligned}$$

where  $W_0$  and  $W_t$  are fish initial and final weights (g),  $t$  is the feeding period (days), and  $I$  is total feed consumption (g) in  $t$  days.

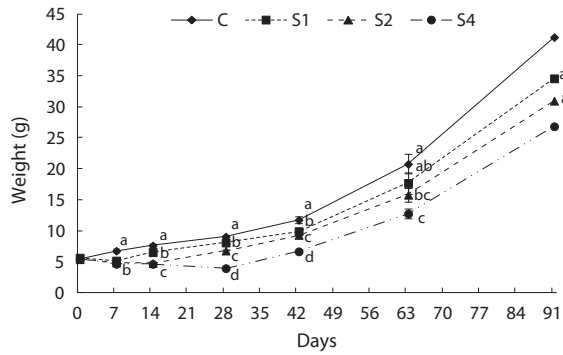
### Statistical analysis

Weight, length, and RCF differences during each measuring interval were analyzed by one-way analysis of variance (ANOVA). Differences in the specific growth rate, specific growth rate in weight/specific growth rate in length ( $\text{SGR}_w/\text{SGR}_l$ ), feed intake, and FE were evaluated by analysis of covariance (ANCOVA) using initial size (initial mass was used for the growth in mass, feed intake, and FE; initial length was used for the growth in length) as a covariate when necessary. Tukey's test was used for multiple comparisons. Differences were regarded as significant when  $P < 0.05$ . A multiple regression analysis (including interactions) was performed using feed intake and efficiency, initial weight, and length at the start of the refeeding period as explanatory variables and specific growth rate in weight and length as the outcome. If the explanatory items were not significant, then a new multiple regression analysis excluding the term was performed. Generally, the main effects of terms feed intake and feed efficiency were always included even if they were not significant. Analysis was performed using SPSS version 16.0 (SPSS Inc., Chicago, IL, USA).

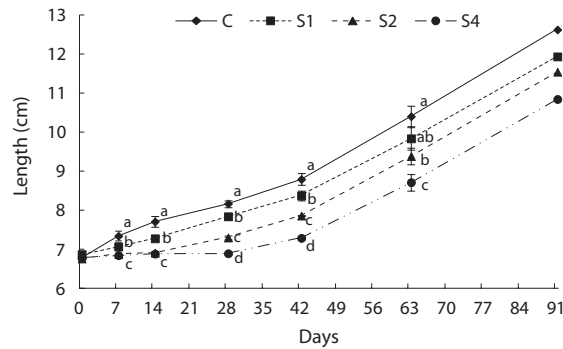
## Results

Feed restriction had a significant effect on weight trajectory (Fig. 1). Divergence between the control and restricted groups was significant after 1 week. After 8 weeks, S1 reached the growth level of the control group. After the experiment, no statistical difference was detected among S1, S2, and the control group, although the average weight of the control group was higher than that of S1 and S2. The average weight of S4 was significantly lower than that of the control group. The length growth trajectory showed similar trends to that of weight (Fig. 2). No group reached the length of the control group, although no statistical difference existed among S1, S2, and the control group. Fish condition decreased until the end of the restriction period (Fig. 3). After feeding was resumed, body condition recovered rapidly, and the more starved the fish were, the more rapidly body condition recovered.

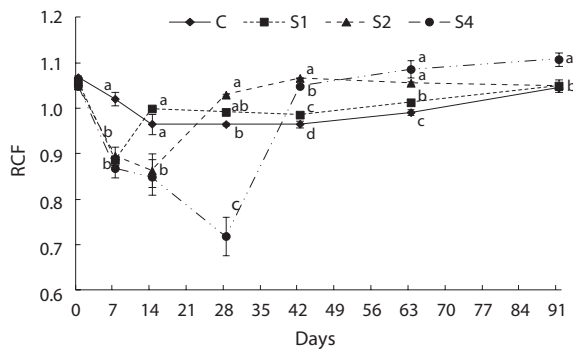
Fish showed negative weight growth in the feed-restricted



**Fig. 1.** Weight-growth trajectories. Differences in weight among measuring times were compared using one-way ANOVA. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.

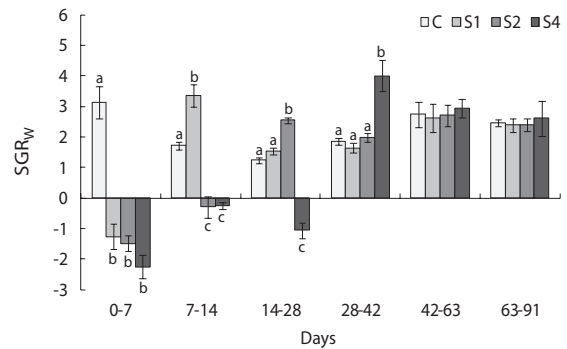


**Fig. 2.** Length-growth trajectories. Differences in length among measuring times were compared using one-way ANOVA. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.

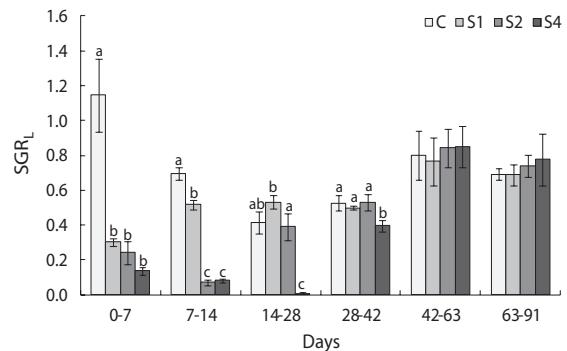


**Fig. 3.** Relative condition factor (RCF) of fish at each measuring time. Differences in the RCF among measuring times were assessed using one-way ANOVA. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.

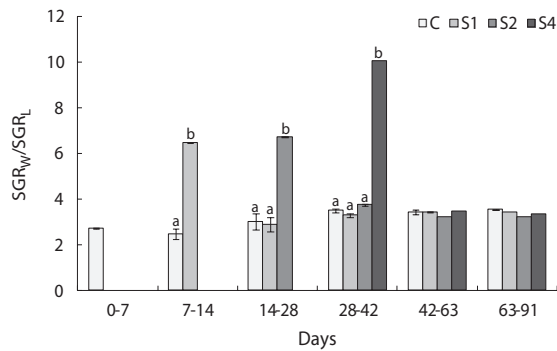
groups, and mass growth decreased significantly during the first week (Fig. 4). Upon refeeding, the growth rate increased immediately and was significantly higher than that of the control group, which was indicative of a compensatory response in weight. However, after a short period, the growth rate decreased to the control group level. During the last 6 weeks, no difference was detected between the control and restricted groups. Length growth decreased gradually in the starved groups and was negligible after 4 weeks of starvation in S4 (Fig. 5). After refeeding, the length growth rate increased but did not exceed that of the control group. Moreover,  $SGR_L$  of the most starved group, S4, was significantly lower than that of the control group during the first interval after refeeding and then increased significantly in the following period and was slightly higher although not statistically different from



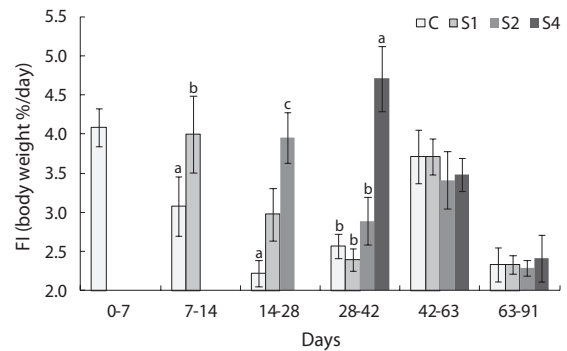
**Fig. 4.** Specific growth rates of weight during each measuring interval. Differences in specific growth rate in weight ( $SGR_W$ ) during among intervals were assessed using one-way ANCOVA with weight at the start of each interval as the covariate. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.



**Fig. 5.** Specific growth rate of length during each measuring interval. Differences in specific growth rate in length ( $SGR_L$ ) among intervals were assessed using one-way ANCOVA with length at the start of each interval as the covariate. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.



**Fig. 6.** Specific growth rate in weight/specific growth rate in length (SGR<sub>w</sub>/SGR<sub>l</sub>) during each measuring interval. Differences were assessed using one-way ANOVA. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.



**Fig. 7.** Feed intake (FI) during each interval. Differences in FI among intervals were assessed using one-way ANCOVA with weight at the start of each interval as the covariate. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.

the other groups. The von Bertalanffy growth rate showed no significant differences between the control group and restricted groups (Table 1), and the more starved fish had a higher growth rate during the refeeding period, although it was always lower than that of the control group. SGR<sub>w</sub>/SGR<sub>l</sub> was especially high when feed was supplied, and the more starved fish had higher ratio values (Fig. 6) which suggested that fish restored their lost weight, followed by their structure size, after refeeding.

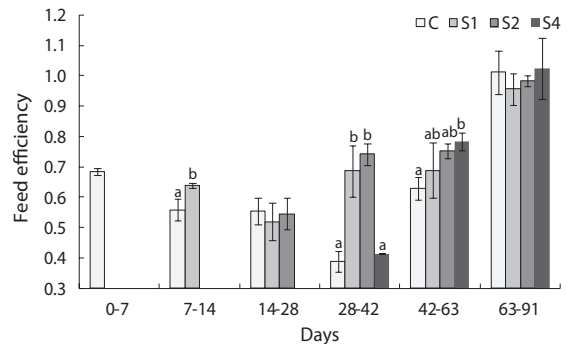
Hyperphagia was responsible for the compensatory growth.

**Table 1.** von Bertalanffy growth rate ( $r_b$ ) of fish in the control and restricted (restricted and refeeding period) groups (whole experiment period)

	Restricted period	Refeeding period
Control	12.84 ± 0.98 <sup>a</sup>	12.84 ± 0.98 <sup>a</sup>
S1	5.29 ± 1.93 <sup>b</sup>	11.53 ± 1.36 <sup>a</sup>
S2	2.02 ± 0.53 <sup>c</sup>	11.91 ± 1.21 <sup>a</sup>
S4	0.77 ± 0.04 <sup>c</sup>	12.32 ± 2.14 <sup>a</sup>

Growth rates differed significantly between the first period but not during the second period (one-way ANOVA, differences considered significant when  $P < 0.05$ ). Mean  $r_b$  ( $\times 10^4$ ) ± SD.

S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.



**Fig. 8.** Feed efficiency (FE) during each interval. Differences in FE among intervals were assessed using one-way ANCOVA with weight at the start of each interval as the covariate. Differences were considered significant when  $P < 0.05$ . C, control; S1, starved for 1 week and refed for 12 weeks; S2, starved for 2 weeks and refed for 11 weeks; S4, starved for 4 weeks and refed for 9 weeks.

In this experiment, feed intake increased immediately upon refeeding and was significantly higher in restricted groups than in the control group (Fig. 7). However, feed intake quickly returned to normal levels. Feed efficiency also improved in this experiment (Fig. 8). Feed efficiency in S1 increased quickly during the first week after refeeding but did not increase until

**Table 2.** Relationships among feed intake, feed efficiency, and specific growth rate

	SGR <sub>w</sub>				SGR <sub>l</sub>			
	B	SE	t	Sig.	B	SE	t	Sig.
Constant	-2.04	0.41	-4.94	<0.001	-0.17	0.18	-0.95	>0.05
FI	0.75	0.07	10.19	<0.001	0.10	0.03	3.01	<0.01
FE	3.23	0.38	8.59	<0.001	0.72	0.14	4.99	<0.001
W	-0.03	0.02	-2.03	<0.05	-	-	-	-

Length effect and interaction of FI and FE were removed from the model, as they were not significant.

SGR<sub>w</sub>, specific growth rate in weight; SGR<sub>l</sub>, specific growth rate in length; FI, feed intake; FE, feed efficiency; W, weight at the start of the refeeding period.

the second period in S2 and S4.

After entered the refeeding period, the relationships among feed intake, feed efficiency, and SGR were determined based on multiple regression analysis (Table 2). The  $SGR_w$  of the three restricted groups was positively correlated with feed intake (FI) and FE and negatively correlated with initial weight at the start of the refeeding period ( $SGR_w = 0.75FI + 3.23FE - 0.03W - 2.04$ ,  $r^2 = 0.72$ ).  $SGR_L$  was significantly correlated with FE and FI, and initial length at the start of the refeeding period did not affect the length growth rate ( $SGR_L = 0.1FI + 0.72FE - 0.17$ ,  $r^2 = 0.33$ ).

## Discussion

Compensatory growth is significantly associated with feed-deprivation period. Barramundi *Lates calcarifer*, which were completely deprived of food for 1 week, displayed marked compensatory growth after refeeding and reached the body weight of fish that had been fed normally. However, fish starved for more than 1 week displayed only partial compensatory growth (Tian and Qin, 2003). Jobling et al. (1994) reported that complete compensatory growth in Atlantic cod *Gadus morhua* required deprivation for 3 weeks. Complete compensatory growth in the gibel carp *Carassius auratus gibelio* and stickleback *Gasterosteus aculeatus* only occurred after feed deprivation for more than 2 weeks (Xie et al., 2001; Zhu et al., 2001). Xie et al. (2001) found that the weights of gibel carp *C. auratus gibelio* were 92% and 74% of the control fish weight after 1 and 2 weeks of feed deprivation, respectively, but complete compensatory growth was achieved in all fish within 2 weeks after refeeding. Our results showed that the weights of S1, S2, and S4 fish were 76%, 62%, and 43% of the control fish weight, respectively, at the end of deprivation. However, complete compensatory growth occurred in fish that had been deprived for 1 and 2 weeks. This finding was similar to that for another tropical fish reported by Wang et al. (2000), who found that the weights of fish that had been deprived for 1, 2, and 4 weeks were 71%, 48%, and 26% of the control fish weight, respectively. The statement that “However, complete compensatory growth in tilapia only occurred in fish that had been deprived for 1 week” is referred to in Wang et al. (2000). “The weight of deprived fish dropped below 60% of the control fish weight, and complete compensatory growth was unlikely to occur” is an inference from Wang et al. (2000) and the present study.

At the end of restricted period, the respective lengths of groups S1, S2, and S4 were 96%, 90%, and 77% that of the control group, and the RCFs were 0.89, 0.86, and 0.72 that of the control group, respectively. The compensatory response showed different trends for weight than for length in our study. No difference in the von Bertalanffy growth rate ( $r_B$ ) was observed between the control and restricted groups. This result was consistent with the results reported by Bavčević

et al. (2010), who observed compensatory growth in weight, but not length, in gilthead sea bream (*S. aurata*). Álvarez and Nicieza (2005) found that brown trout *Salmo trutta* L., showed no compensation in structure size and only partial compensation for mass, but rapid recovery of body condition. They also found that the compensatory response ended when feed-restricted fish were returned to control conditions. In our study,  $SGR_w$  increased significantly after feeding was resumed, and then decreased when the body condition recovered to a normal level (Figs. 3 and 4). However,  $SGR_L$  showed no acceleration in growth compared with the control group after feeding was resumed (Fig. 5).  $SGR_w/SGR_L$  showed a significantly higher value for a short period and then decreased to control levels (Fig. 6), indicating that fish initially recovered their mass reserve (but not structure size) when feed levels increased. Bavčević et al. (2010) demonstrated that mass recovery was used to replenish energy reserves (but not size) at a given age. They also reported that feed intake was higher for all groups during the refeeding period and that the von Bertalanffy growth rates ( $r_B$ ) were equal regardless of condition. This suggested that length growth depends on feeding rate and not on condition factors (Kooijman, 2000). These results supported the “mass-for-length” rule proposed by McCauley et al. (1990) and Gurney et al. (1990) or the “ideal” reserve-to-structure ratio proposed by Broekhuizen et al. (1994) to explain compensatory growth responses in salmonid fishes. These studies hypothesized that starving animals give priority to the recovery of body mass over reproduction or structural growth whenever their mass-to-length ratio falls below an appropriate or “healthy” level. Our data suggested that the mass-for-length rule can be fulfilled not only in the context of starvation but also when the growth of structural tissues has depleted reserves.

Hyperphagia and growth efficiency play major roles in compensatory growth during the refeeding period. Hyperphagia occurs in several fish species during compensatory growth (Russell and Wootton, 1992; Wang et al., 2000), whereas improved feeding efficiency has not been widely observed (Russell and Wootton, 1992; Qian et al., 2000; Wang et al., 2000). In this study, hyperphagia was observed in all starved fish after refeeding (Fig. 6). Some models of compensatory growth in fish have suggested that the associated hyperphagia would abate as the body composition of the deprived fish returned to control levels. Broekhuizen et al. (1994) hypothesized that hyperphagia restored the ratio of reserve to structural material. The lipostatic model for fish (Jobling and Johansen, 1999; Johansen et al., 2002) proposed that lipid levels play a regulatory role in feed intake. Supporting experimental evidence has been obtained from salmonids displaying compensatory growth (Johansen et al., 2001) and those fed high- and low-fat diets (Johansen et al., 2002). Patterns in compensatory responses in  $SGR_w$  and feed intake were similar to those in our study.

Previous studies have demonstrated increased growth ef-



iciency during compensatory growth responses in *Lepomis* hybrids (Hayward et al., 1997), juvenile gibel carp (Qian et al., 2000), channel catfish (Gaylord and Gatlin, 2001), and juvenile three-spined sticklebacks (Zhu et al., 2001; Wu et al., 2003). However, the causal explanation for these observed improvements in growth efficiency remains unclear (Ali et al., 2003). A relatively low basal metabolism may be sustained for a period beyond the restricted phase, after which a relatively higher proportion of energy and protein may be used for growth requirements (Koong et al., 1983; Drouillard et al., 1991; Jobling et al., 1994). However, this effect is usually small and short-lived (Miglavys and Jobling, 1989). Hybrid tilapia reared in seawater showed partial growth compensation resulting from increased feed intake, but without improved FE (Wang et al., 2000). In our experiments, improved FE was observed in S1 immediately after feeding was resumed, whereas efficiency was not improved in S2 or S4. Feeding efficiency was especially low in S4 after feeding was resumed, and did not recover until the second interval. Time may be required to reestablish effective digestive processes in the stomach following a period of feed deprivation (Ali et al., 2001; Zhu et al., 2004).

In our study, multiple regression analysis indicated that feeding efficiency played an important role in the specific growth rates of weight and length. This was in agreement with the hypothesis that growth and increases in energy reserves depend on the assimilation (not ingestion) of feed (Gurney et al., 2003). Assimilation efficiency diminishes as ingestion increases, which reduces the yield per ingested feed. The optimal feeding strategy requires a balance of maximizing ingestion and growth rate while maintaining the most efficient possible feed assimilation.

The mechanism of compensatory growth in different fish species may be more complicated than can be explained by the lipostatic model, but compensatory growth in Nile tilapia depended on the length of feed deprivation. Periodic short-term starvation in tilapia farming may not reduce fish weight gain. To date, a body-condition indicator to determine when feed should be reapplied to feed-deprived fish to elicit a compensatory growth response has not been determined. Hayward et al. (1997) determined when fish should be feed-deprived based on the cessation of the hyperphagic period, but the most desirable length of feed deprivation was determined empirically. In channel catfish, hepatosomatic index is used as the most responsive index of feed deprivation and re-alimentation (Gaylord and Gatlin, 2001; Cho, 2012). Gurney et al. (2003) suggested that when the maintenance ratio inhibits structural growth without reducing total carbon mass (the ingestion rate exactly matches the current basal metabolic cost), then reintroduction of abundant feed would not induce a compensatory response. However, when the ratio exceeds the basal metabolic cost of the animal's current structure, a strong compensatory response would be expected.

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