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Compensatory growth in hybrid tilapia (*Oreochromis mossambicus* × *O. niloticus*) reared in seawater, following restricted feeding*

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Abstract Hybrid tilapia weighing 7.71 g were reared in seawater at 24.0-29.0℃ for 8 weeks. The controls were fed to satiation twice a day throughout the experiment, whereas treatment groups were fed at 0.5%, 1.5% or 3.0% body weight per day for 4 weeks, and then to satiation for the remainder of the experiment. During the first 4-week period, there was a curvilinear relationship between growth rate and ration size. Fish fed 0.5% and 1.5% rations displayed compensatory growth response of 2 weeks duration during realimentation. The weight-adjusted growth rate of fish fed at 3% ration was not significantly different from that of the controls by the end of the experiment, when none of the treatment groups had caught up in body weight with the controls. Hyperphagia was observed for the first 2 weeks of realimenatation in fish previously fed at 3% ration, but persisted for the whole realimentation period in groups previously fed at 0.5% and 1.5% rations. None of the feed restricted groups showed improved digestibility, feed efficiency, or protein and energy retention efficiency.

Key words: hybrid tilapia, compensatory growth, feed restriction, ration level

1 INTRODUCTION

Compensatory growth or catch-up growth is a phase of unusual rapid growth induced by a period of environmental restriction; it had been demonstrated in a wide range of fish species following food deprivation (Bilton and Robins, 1973; Dobson and Holmes, 1984; Miglavs and Jobling, 1989; Quinton and Blake, 990; Wieser et al., 1992; Reimers et al., 1993; Kim and Lovell, 1995; Paul et al., 1995), restricted feeding (Weatherley and Gill, 1981; Jobling and Koskela, 1996; Pirhonen and Forsman, 1998), or low water temperature (Mortensen and Damsgard, 1993). Growth compensation in relation to reduced dietary quality had also been investigated (Schwarz et al., 1985). The mechanism of compensatory growth in fish is still not clear. In many cases, intensity of compensatory growth was dependent on the severity of nutritional restriction (Weatherley and Gill, 1981; Wieser et al., 1992; Jobling et al., 1994), and increased feed efficiency during compensatory growth was observed in several studies (Bilton and Robins, 1973; Dobson and Holmes, 1984; Quinton and Blake, 1990; Russell and Wootton, 1992). By appropriate use of the principle of compensatory growth, the growth rate of F_1 hybrid sunfish (*Lepomis cyanellus* × *L. macrochirus*) could be doubled (Hayward et al., 1997). Such findings aroused interest in aquaculturists in exploring the possibility of using compensatory growth as a management tool in aquaculture.

Tilapia is important food fish cultured in freshwater, brackish water and seawater worldwide, especially in developing countries because of their rapid growth, omnivorous nature and strong disease resistance. In hybrid tilapia (*Oreochromis mossambicus* × *O. niloticus*) reared in seawater, some capacity for compensatory growth was observed following 1-4 weeks of food deprivation (Wang et al., 2000). The hybrid tilapia that deprived for 2 weeks or longer, however, was not able to catch up in body size with the continuously fed controls within 4 weeks of refeeding, and there was no improvement in feed efficiency during compensatory growth. The results implied that induction of

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compensatory growth by food deprivation could not be used as a tool for increasing growth or improving feed efficiency in seawater culture of tilapia. The high water temperature at which the tilapia were cultured means that, given the same experimental protocol, the effect of starvation may be more severe than in coldwater fishes held at lower temperatures, and this may result in reduced capacity for full compensation for lost weight. It could be hypothesised that hybrid tilapia may be able to fully compensate for a milder form of under-nutrition. The purpose of the present study was to investigate feed intake, growth and feed utilization in hybrid tilapia reared in seawater following restricted feeding at different levels.

2 MATERIAL AND METHODS

2.1 Preparation of experimental fish

The experiment was carried out at the Nanao Marine Biology Station, using hybrid tilapia produced at the Puning Hatchery Farm, Shantou. Fish were held in outdoor seawater tank for seven weeks, during which they were fed with commercial tilapia feed manufactured by the Shantou Meiyan Feed Corp. (crude protein content: 30%, crude lipid: 3.0 %) to satiation twice a day.

Two weeks prior to the start of the experiment, 600 fish were moved to 20 indoor rectangular fibre-glass tanks (80×50 cm, water depth: 60 cm) at 30 fish per tank. Filtered and aerated seawater flowed through each tank at 1 L/min. The fish were fed to satiation twice a day with the experimental diet consisting of 24.65% fish meal, 28.51% soybean meal, 35.61% wheat, 1.80% soybean oil, 6.00% vitamin premix, 2.57% mineral premix and 0.86% Cr_2O_3. Cr_2O_3 was added as marker for digestibility measurement. The diet was made into floating pellets by a laboratory extruder. Analysed composition of the diet was: 94.20% dry matter, 31.55% protein, 3.18% lipid, 16.19% ash, and 15.64 kJ/g energy (of dry matter). Details of the feed formulation and analytical methods were described in Wang et al. (2000).

2.2 Experimental design and procedure

Four feeding groups were established with 5 fish tanks per group. The fish in feeding groups were fed 3.0%, 1.5% or 0.5 % body weight per day during the first 4 weeks (the feed restriction period), and were then fed to satiation twice a day during the second 4 weeks (the realimentation period). The control fish were fed to satiation twice a day throughout the 8-week experiment.

At the start of the experiment, 400 fish weighing 7.71±0.06 g (mean±S.E.) were randomly distributed among the 20 tanks, at 20 fish per tank. The fish were batch weighed every two weeks, and the rations were adjusted accordingly.

Fish were hand fed at 8:00 and 16:00 hours, during which water flow was stopped. For the fish fed to satiation, a small amount of feed was dropped into the tank every few minutes until the fish no longer accepted feed. Feeding time sometimes extended to 3 h. Intact faeces were collected daily, dried at 70℃ to constant weight and stored at 5℃. Faeces collected from each tank were pooled for analysis and measurements.

For analysis of initial body composition, five groups of five fish each were killed and frozen at –20℃ at the start of the experiment. At the end of the feed restriction period, 5 fish were sampled from each tank so that 15 fish remained in each tank. At the end of the experiment, five fish were sampled from each tank. Analysis of crude protein, crude lipid, ash and energy were made on the fish samples, and the diet and faeces were analysed for protein, energy and Cr_2O_3 as described by Wang et al. (2000).

During the experiment, water temperature was measured daily and fluctuated between 24.0℃ and 29.0℃ (mean 26.4℃). Salinity was 25 and 30 (mean of 27). Photoperiod was 16L: 8D. Dissolved oxygen, which was measured weekly, was usually above 5 mg/L, but occasionally dropped to 3.5mg/L when feeding time was greatly prolonged.

2.3 Data calculation and statistical analysis

Specific growth rate, feed efficiency, protein and energy retention efficiencies and digestibility of dry matter, protein and energy were calculated as described by Wang et al. (2000).

Possible differences among feeding groups were tested by ANOVA, and Tukey's HSD test was used for comparison of variables between feeding groups. Proportions were arcsine transformed prior to analysis. Differences were regarded significant when $P<0.05$. Relationships between ration level and specific growth rate during the feed restriction period were examined using regression analysis.

Feed intake and growth rate during the realimentation period were tested by two methods. One was to test the variance in relative feed intake (as a percentage of body weight) and specific growth rate directly. Since body weight between the restricted and control groups were significantly different at the start of realimentation, and feed intake and specific growth rate were both related to body weight, this method could not separate the effects of feeding treatments from those of body weight. The second method corrected for the effect of body weight using the empirical relationships between feed intake or specific growth rate and body weight (Wang et al., 2000). Such relationships were established using data for the control fish throughout the experiment, and described as: $\ln I$=-2.145+0.645$\ln W$ (r^2=0.901, n=20), and $\ln G$=2.109-0.382$\ln W$ (r^2=0.503, n=20), where I is feed intake (g/d), G is specific growth rate (%/d), and W is initial body weight (g) of each two-week period. Residual feed intake or specific growth rate was calculated as observed value minus the value predicted from the regression equation. The residuals, which eliminated the effect of body size, were tested by ANOVA, and P<0.05 was considered as significant difference.

3 RESULTS

During the feed restriction period, mortality was 7.0±2.5% for the control fish, 5.0±3.9% for the 0.5% treatment fish, 2.0±1.2% for the 1.5% treatment fish, and 2.0±1.2% for the 3.0% treatment fish. During the realimentation period, mortality was 6.7±3.7% for the control fish, 5.3±3.9% for the 0.5% treatment fish, 2.7±2.6% for the 1.5% treatment, and 4.0±1.6% for the 3.0% treatment. Mortality was largely caused by aggressive behaviour rather than previous feeding treatments.

Fig.1 shows the relationship between ration level and specific growth rate during the feed restriction period. Curvilinear relationship was observed between ration level (R) and specific growth rate (G), which could be expressed as: G=1.006+ 1.517 $\ln R$ (r^2=0.957, n=20, P<0.001). Fig.2 shows the hybrid tilapia body weight throughout the 8 weeks experiment. At the end of the feed restriction period, body weight in the feed restricted fish was significantly lower than that in the controls (P<0.001). After 4-weeks realimentation, the body weight of the feed restricted fish was still significantly lower (P<0.031).

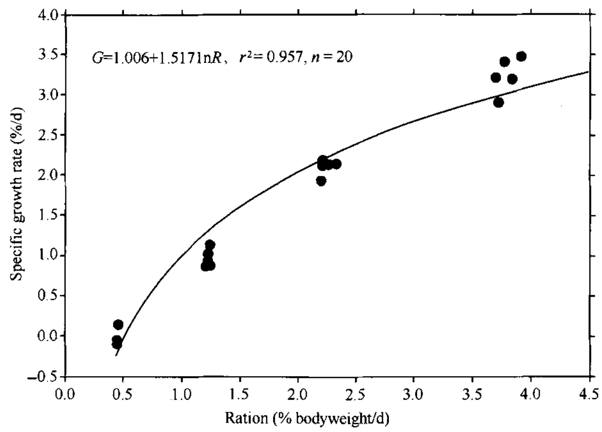

Fig.1 Relationship between specific growth rate and ration level in hybrid tilapia during the feed restriction period

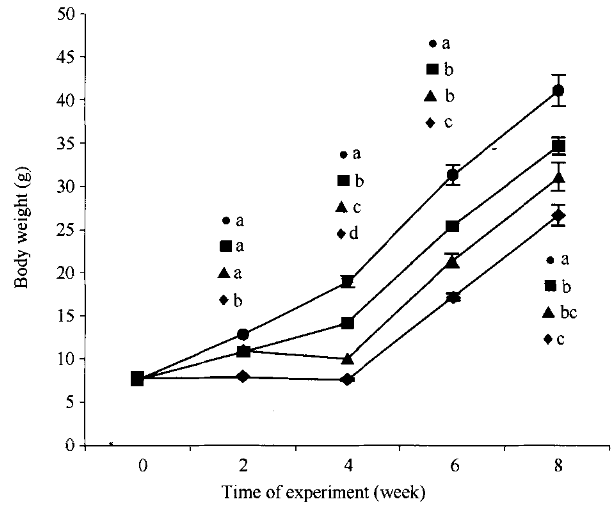

Fig.2 Body weight of hybrid tilapia during the experiment. Fish were fed different rations in the first 4 weeks and to satiation in the second 4 weeks

●,control; ■, 3.0%; ▲, 1.5% body weight per day; ◆, 0.5% body weightper day. Error bars represent 1 S.E. Letters a,b,c,d indicate results of HSD test. Values with different letters for the same week were significantly different from each other at the 0.05 level

At the end of the feed restriction period, the relative proportions of moisture in the feed restricted fish were significantly higher, while lipid and energy were lower than those in the controls (Table 1). Protein content in the fish fed the 1.5% and 0.5% rations was significantly lower, while ash content was higher than that in the controls. There were no significant differences in proportions of protein and ash among feeding groupds at the end of the realimentation period, but moisture in the 1.5% treatment groups was still significantly higher, while lipid content and energy were lower than those in the controls.

Unadjusted feed intake and specific growth rate increased significantly with increasing severity of feed restriction (Figs.3A, 4A). Residual feed intake in the 0.5% and 1.5% treatments remained significantly higher than in the controls in weeks 5-6 and 7-8, while elevation in residual feed intake in the 3% treatment group occurred only in weeks 5-6 (Fig.3B). The residual specific growth rate in the 0.5% and 1.5% treatment groups was significantly higher than in the controls only during the first 2 weeks of realimentation, while residual specific growth rate in the 3% treatment group was not significantly different from that of the controls in any of the realimentation periods (Fig. 4B).

Table 1 Changes in body composition of differently treated hybrid tilapia during the experiment*

Sampling dates	Treatment	Moisture (%)	Protein (%)	Lipid (%)	Ash (%)	Energy (KJ/g)
Initial		76.48±0.16	14.68±0.18	2.82±0.16	4.74±0.04	4.39±0.06
At the end of the feed restriction period	Control	74.99±0.38^{a}	14.22±0.27^{ab}	5.16±0.27^{a}	4.04±0.10^{a}	5.23±0.17^{a}
	3.0% ration	76.58±0.29^{b}	14.77±0.54^{a}	3.70±0.37^{b}	4.52±0.19^{a}	4.60±0.08^{b}
	1.5% ration	78.28±0.17^{c}	13.02±0.33^{b}	2.01±0.14^{c}	5.42±0.24^{b}	3.71+0.05^{c}
	0.5% ration	80.32±0.28^{d}	11.19+0.25^{c}	0.94±0.15^{d}	5.38+0.24^{b}	3.11±0.09^{d}
At the end of the realimentation period	Control	72.68±0.73^{a}	15.16+0.59	6.28±0.31^{a}	4.09+0.10	5.84±0.12^{a}
	3.0% ration	73.93+0.33^{ab}	15.04±0.19	5.34±0.31^{ab}	4.14+0.11	5.65+0.24^{ab}
	1.5% ration	75.00±0.71^{b}	14.77±0.30	4.54+0.69^{b}	4.45±0.12	5.05±0.19^{b}
	0.5% ration	74.51±0.28^{ab}	14.58±0.33	5.12±0.25^{ab}	4.13±0.11	5.49±0.10^{ab}

*Values are expressed as mean+S.E (n=5). Letters (a, b, c, d) after each value indicate results of HSD test. Values at the same time with different letters are significantly different from each other at the 0.05 level.

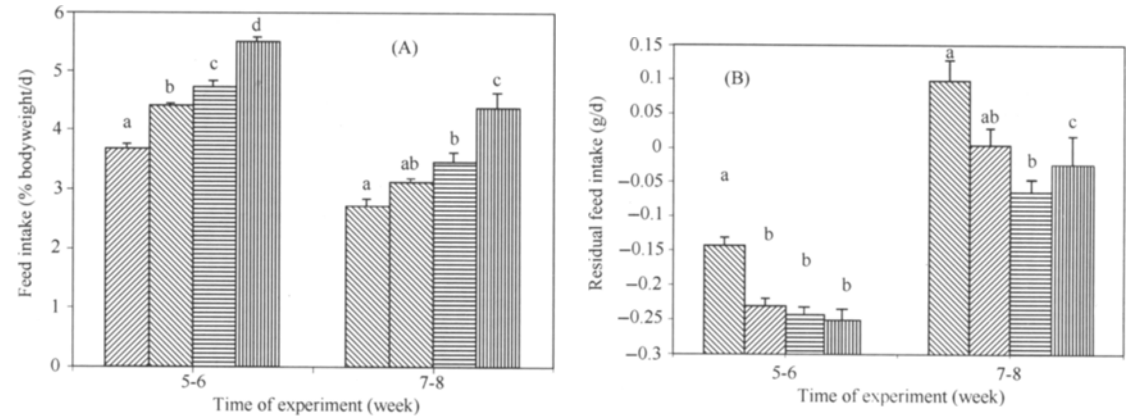

Fig.3 Unadjusted relative feed intake of hybrid tilapia (A) and residual feed intake (B) during the experiment
▨, control; ▧, 3.0% body weight per day; ▤, 1.5% body weight per day; ▥, 0.5% body weight per day. Residual value of feed intake is the difference between observed value and predicted value from the regression equation relating feed intake to body weight of the control fish. Error bars present 1S.E. Letters indicate results of HSD test. Values with different letters for the same period are significantly from each other at the 0.05 level

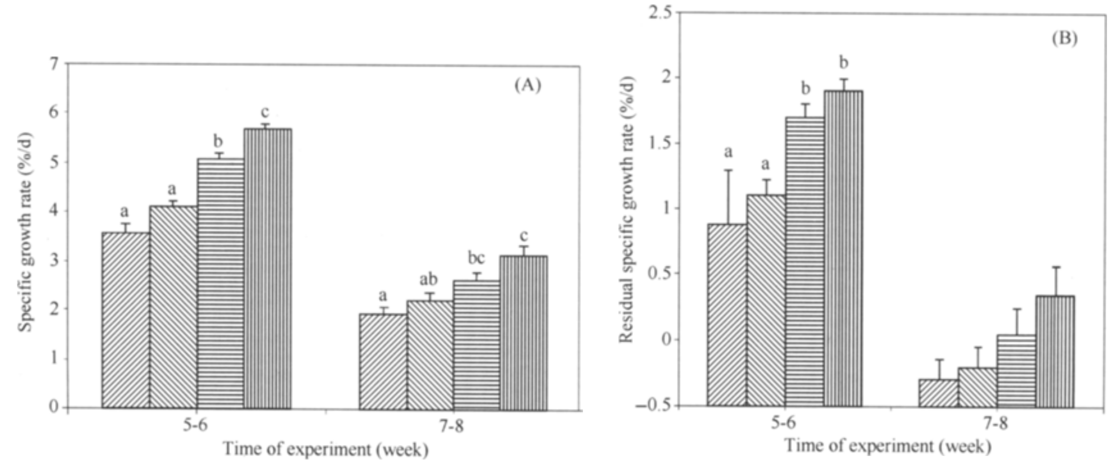

Fig.4 Unadjusted specific growth rate of hybrid tilapia (A) and residual specific growth rate (B) during the experiment
▨, control; ▧, 3.0% body weight per day; ▤, 1.5% body weight per day; ▥, 0.5% body weight per day. Residual specific grow rate is the difference between observed value and predicted value from the regression equation relating specific growth rate to body weight of the control fish. Error bars present 1S.E. Letters indicate results of HSD test. Values with different letters for the same period are significantly from each other at the 0.05 level

During the feed restriction period, feed efficiency as well as protein and energy retention efficiency were not significantly different between high ration treatment group, but decreased at low rations. During realimentation, there were no significant differences in feed efficiency, protein retention efficiency or energy retention efficiency among the treatment groups (Table 2). Digestibility of dry matter and protein were not significantly different among treatment groups during realimentation, but digestibility of energy in the 0.5% treatment group was significantly lower than that in the controls (Table 3).

Table 2 Feed efficiency, and protein and energy retention efficiency in differently treated hybrid tilapia during the feed restriction and realimentation period*

Experimental phases	Treatment	Feed efficiency (%)	Protein retention (%)	Energy retention (%)
Feed restriction period	Control	80.39±1.81[a]	35.40±0.75[ab]	29.77±1.23[a]
	3.0% ration	92.47±1.77[a]	43.64±2.99[a]	28.74±1.07[a]
	1.5% ration	80.05±3.61[a]	19.93±3.89[b]	8.06±0.97[b]
	0.5% ration	-5.12±5.96[b]	-90.49±7.24[c]	-66.74±7.02[c]
Realimentation period	Control	82.62±5.13	42.06±4.04	33.77±2.97
	3.0% ration	79.80±3.05	38.74±2.77	32.80±2.97
	1.5% ration	87.92±5.03	44.64±3.24	32.80±2.58
	0.5% ration	82.72±4.55	42.06±2.74	34.31±2.01

* The feed restriction period covered weeks 1 to 4 and the realimentation period cover weeks 5 to 8. Values are expressed as mean±S.E.(n=5). Letters (a, b, c) indicate results of HSD test. Values at the same time with different letters are significantly different from each other at the 0.05 level.

Table 3 Digestibility of dry matter, protein and energy of differently treated hybrid tilapia during the realimentation period*

Treatment	Digestibility of dry matter (%)	Digestibility of protein (%)	Digestibility of energy (%)
Control	71.54±1.14	87.79±0.49	85.77±0.62[ab]
3.0% ration	72.54±1.11	89.23±0.72	87.21±1.12[a]
1.5% ration	72.58±0.96	87.50±0.71	84.62±0.58[ab]
0.5% ration	70.81±0.73	86.86±0.32	83.10±1.06[b]

* The realimentation period covered weeks 5 to 8. Values are expressed as mean±S.E. (n=5). Letters (a, b, c) indicate results of HSD test, values with different letter are not significantly different from each other at the 0.05 level.

4 DISCUSSION

The specific growth rate of the control was 3.25 during the feed restriction period and 2.74 during realimentation. The relatively high specific growth rate shown by the control fish suggested that external environmental conditions, i.e. temperature, salinity and dissolved oxygen were adequate for normal feeding and growth of the hybrid tilapia throughout the experiment. Curvilinear growth-ration relationship was found in the present study. This is in agreement with earlier conclusions obtained from freshwater Nile tilapia (Xie et al., 1997) and many other fish species (Flowerdew and Grove, 1980; Allen and Wootton, 1982; Russell et al., 1996). The hybrid tilapia's maintenance ration predicted from the growth-ration relationship established in the present study was 0.52%, indicating that the fish fed less than the 0.52% ration would lose weight with prolongation of the food condition.

In the present study, hybrid tilapia previously fed the 1.5% or 0.5% rations showed at least partial compensatory growth during realimentation, as growth rates were higher than the controls. However, even tilapia experiencing the mildest feed restriction (fed the 3% ration) failed to catch up in body size with those of the controls within four weeks realimentation. As no significant difference in the weight-adjusted growth rate between the feed restricted fish and control fish were shown during the last two weeks of realimentation, it is unlikely that the feed restricted fish could fully catch up with the controls with an extension of the growth trial. The results did not support our hypothesis that hybrid tilapia could fully compensate for retarded growth caused by a mild form of under-nutrition.

Whether feed restricted fish could catch up the controls in body size depends on the body size difference at the start of realimentation, and the intensity of compensatory growth response. At the start of realimentation, body weights of feed restricted hybrid tilapia were 0.41-0.75 times that of the control fish. These values were somewhat lower than those for two species showing complete compensation following starvation or restricted feeding, i.e. 0.77-0.82 for gibel carp (Qian et al., 2000) and 0.70-0.81 for Arctic charr (Jobling et al., 1993). The high growth rate in the controls in hybrid tilapia at high temperatures may partly account for the difference. The intensity of compensatory growth can be reflected by the duration of the response, and the magnitude of compensatory growth (relative elevation of growth rate in feed restricted fish over that of the controls). Duration of compensatory growth in hybrid tilapia was short (2 weeks), and this was similar to results from several studies on other fish species (Russell and Wootton, 1992; Wieser et al, 1992; Sæther and Jobling, 1999), although a much longer duration was reported for Arctic charr (Miglavs and Jobling, 1989). It was difficult to compare the magnitude of compensatory growth in different studies, as growth rate in the controls were different, and many studies failed to consider the effect of body size on growth rate during compensatory growth. Based on a review on fishes of different taxa, Jobling (1983) proposed that there may be a general weight exponent in the power relationship between specific growth rate and body weight in fish, which was close to –0.4. When specific growth rate is regressed against body weight at the start of realimentation in fish subjected to different degrees of food restriction, the weight exponent is expected to be lower than that in normally growing fish if compensatory growth exists. Assuming the weight exponent is similar in different fish species displaying normal growth, then the magnitude of the weight exponent in the specific growth rate vs body weight relationship can be considered as a rough measure of magnitude of compensatory growth. The weight exponent in the specific growth rate vs body weight relationship during realimentaion was –0.53 in the present study, and –0.43 in hybrid tilapia following different periods of feed deprivation (Wang et al., 2000). Recalculations showed the weight exponent was –1.42 in gibel carp (Qian et al., 2000) and –1.13 to –0.97 in Arctic charr (Jobling et al., 1993) during compensatory growth. These values were much lower than that in hybrid tilapia, suggesting that the magnitude of compensatory growth was relatively low in tilapia. Thus during realimentation, a low magnitude of compensatory growth, coupled with a relatively large difference in body size between the feed restricted fish and controls, resulted in a weak capacity for compensatory growth in hybrid tilapia.

Compensatory growth could be achieved through hyperphagia (Jobling and Koskela, 1996), or a combination of hyperphagia and improved feed efficiency (Miglavs and Jobling,1989; Russell and Wootton,1992; Jobling et al., 1994; Qian et al., 2000). The present study confirmed the result from a previous study on compensatory growth of the hybrid tilapia following feed deprivation, that hyperphagia was the major mechanism for compensatory growth in this species (Wang et al., 2000).

In conclusion, hybrid tilapia reared in seawater displayed partial compensatory growth only following restricted feeding for 4 weeks, and the compensatory growth was not accompanied by improved feed efficiency. Thus feeding regimes incorporating periods of restricted feeding to induce compensatory growth may have limited application in the culture of hybrid tilapia in seawater.

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