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Compensatory growth in hybrid tilapia, *Oreochromis mossambicus* × *O. niloticus*, reared in seawater

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Abstract

Hybrid tilapia weighing 4.34 ± 0.03 g (mean ± SE) were reared in seawater at 23.8 to 27.0°C for 8 weeks. The control group was fed to satiation twice a day throughout the experiment. The other three groups were deprived of feed for 1, 2, and 4 weeks, respectively, and then fed to satiation during the refeeding period. At the end of the experiment, fish deprived for 1 week had similar body weights to the controls, whereas fish deprived for 2 and 4 weeks had significantly lower body weights than the controls. During the refeeding period, size-adjusted feed intakes and specific growth rates were significantly higher in deprived fish than in the controls, indicating some compensatory responses in these fish. Feed intake and growth rate upon refeeding were higher the longer the duration of deprivation. No significant differences were found in digestibility, feed efficiency or protein and energy retention efficiency between the deprived and control fish during refeeding, suggesting that hyperphagia was the mechanism responsible for increased growth rates during compensatory growth. During refeeding, relative gains in protein, lipid and ash, as proportions of total body weight gain, did not differ significantly among treatment groups.

Keywords: Compensatory growth; Feed deprivation; Food consumption; Feed utilisation; Hybrid tilapia

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1. Introduction

Compensatory growth is defined as a phase of unusually rapid growth, following a period of undernutrition (Dobson and Holmes, 1984; Hayward et al., 1997). Through this growth spurt, animals subjected to previous nutritional restriction may partially or completely catch up in body size with those that have not undergone food restriction (Dobson and Holmes, 1984; Russell and Wootton, 1992; Kim and Lovell, 1995). Compensatory growth in fish is not only of theoretical interest, but may also have applications in aquaculture (Quinton and Blake, 1990; Jobling et al., 1994; Hayward et al., 1997), as appropriate exploitation of this phenomenon may result in increased growth rate and feed efficiency.

Results of studies on compensatory growth in fish have yielded inconsistent results; compensation has been observed in most studies, but only a limited capacity for compensatory growth has been reported in others (Schwarz et al., 1985; Pirhonen and Forsman, 1998). Most studies of compensatory growth in fish have been carried out on coldwater species, and reports on warmwater species are few (Schwarz et al., 1985; Kim and Lovell, 1995; Hayward et al., 1997). Tilapia are warmwater, euryhaline, omnivorous fishes that are important in aquaculture, but compensatory growth does not seem to have been examined in representatives of this group of fishes. The purpose of the present study was to examine whether compensatory growth occurs in hybrid tilapia reared in seawater.

2. Materials and methods

The experiment was carried out between 28 April and 24 June 1998 at Nanao Marine Biology Station, Nanao Island, Guangdong, China, using hybrid tilapia (*Oreochromis mossambicus* × *O. niloticus*) obtained from Puning Fish Hatchery, Shantou. Fish were initially held in an 18 m^2 outdoor concrete pond containing freshwater, and were then acclimated to seawater at a rate of salinity change of 5‰ per day. Fish were then maintained in seawater for 1 week, during which they were fed twice a day on a commercial pellet feed containing 30% crude protein and 3.0% crude lipid (manufacturer's specification; Meiyan Feed, Shantou).

Prior to the experiment, 600 fish were held in 30 rectangular fibreglass tanks (80 × 50 cm; water depth 60 cm; water volume 240 l), with 20 fish per tank. Filtered seawater was distributed to the tanks at 1 l/min/tank. The fish were fed the experimental floating feed (Table 1) for 2 weeks. Crude protein in the feed was determined by the micro Kjeldahl method, lipid by ether extraction using a Soxtec system, ash by combustion at 550°C for 12 h, and energy by micro bomb calorimeter (AOAC, 1984). The concentration of Cr_2O_3, added to estimate digestibility, was determined as described by Furukawa and Tsukahara (1966).

At the start of the experiment, 400 fish weighing 4.34 ± 0.03 g (mean ± SE) were deprived of feed for 24 h and distributed among 20 tanks (20 fish per tank). Five tanks were randomly assigned to each of the four treatments. Five groups of five fish each were sampled for the analysis of initial body composition.

Table 1
Formulation and proximate composition of the experimental feed

Formulation (% wet weight)	
White fish meal from Russia	24.65
Wheat flour	35.61
Soybean meal	28.51
Soybean oil	1.80
Vitamin premix[a]	6.00
Mineral premix[b]	2.57
Cr_2O_3	0.86
Proximate composition (% or kJ/g dry matter; mean ± SE; N = 5)	
Crude protein	31.2 ± 0.1
Crude lipid	3.2 ± 0.2
Ash	16.2 ± 0.1
Energy	15.6 ± 0.2

[a]Vitamin premix contained the following vitamins per kilogram feed: vitamin A (as vitamin A acetate and vitamin A palmitate, 1:1), 5500 I.U.; vitamin D_3, 1000 I.U.; vitamin E (as DL-α-tocopheryl acetate), 50 I.U.; vitamin K_3 (as menadione sodium bisulfite), 10 I.U.; choline (as choline chloride), 550 mg; niacin, 100 mg; riboflavin, 20 mg; pyridoxine, 20 mg; thiamin, 20 mg; D-calcium pantothenate, 50 mg; biotin, 0.1 mg; foliacin, 5 mg; vitamin B_{12}, 20 mg; ascorbic acid, 100 mg; inositol, 100 mg.

[b]Mineral premix contained the following minerals as milligram per kilogram feed: NaCl, 257; $MgSO_4 \cdot 7H_2O$, 3855; $Na_2H_2PO_4 \cdot 2H_2O$, 6425; KH_2PO_4, 8224; $Ca(H_2PO_4)_2 \cdot H_2O$, 5140; $C_6H_{10}CaO_6 \cdot 5H_2O$, 899.5; $FeC_6H_5O_7 \cdot 5H_2O$, 642.5; $ZnSO_4 \cdot 7H_2O$, 90.7; $MnSO_4 \cdot 4H_2O$, 41.6; $CuSO_4 \cdot 5H_2O$, 7.97; $CoCl_2 \cdot 6H_2O$, 0.26; KIO_3, 0.77.

The experiment lasted for 8 weeks and was divided into two periods, a feed restriction period (weeks 1 to 4) and a refeeding period (weeks 5 to 8). Fish in the control treatment were fed to satiation twice a day throughout the 8-week period. Fish in the other three treatment groups were deprived of feed for 1, 2, and 4 weeks, respectively, during the feed restriction period, and then fed to satiation twice a day during the refeeding period. Deprivation was timed so that the end of deprivation period occurred in all treatments at week 4.

On each feeding day, the fish were hand-fed at 0800 and 1600 h until they no longer accepted feed, with each feeding lasting for about 3 h. Once a day, intact faeces were collected from each tank by pipetting, dried at 70°C to constant weight and held at 5°C until analyzed. Fish in each tank were batch-weighed at the end of the feed restriction period and at the end of the experiment, following feed deprivation for 24 h. For the analysis of chemical composition, three to five fish were randomly taken from each tank at the end of the restriction period so that 15 fish remained in each tank at the start of the refeeding period. At the end of the experiment, five fish from each tank were taken. Fish from each tank were pooled, autoclaved, homogenised and dried to constant weight at 105°C (Cui et al., 1997). Protein, lipid, ash and energy concentrations were determined for the fish samples from each tank using methods described for feed, and protein, energy and Cr_2O_3 concentrations were determined for faecal samples from each tank.

During the experiment, water temperature ranged from 23.8°C to 27.0°C (mean 25.6°C), salinity from 25‰ to 32‰ (mean 27.7‰), and photoperiod was 16L:8D.

Specific growth rate, feed efficiency, digestibilities of dry matter, protein and energy, and protein and energy retention efficiencies were calculated as in Fu et al. (1998). Relative gain in protein, lipid or ash during the refeeding period was calculated as: $100 \times (W_8 \times C_{i8} - W_5 \times C_{i5})/(W_8 - W_5)$, where W_8 is mean final and W_5 initial body weight for each tank during the refeeding period, and C_{i8} is final and C_{i5} initial body concentration of protein, lipid or ash (mean values for each treatment).

One-way analysis of variance (ANOVA) was used to test for treatment effects, and Tukey's procedure was used for multiple comparisons. Proportions were arcsine transformed prior to analysis. A major problem was realised when analyzing feed intake and growth rate data obtained during the refeeding period. There were marked differences in the body weight at the start of refeeding among treatments, and both weight-specific rates of feed intake and growth were expected to decrease with increasing body weight (Jobling, 1983). Feed intake and growth rate were corrected for size effects using the relationship between intake or growth rate and body weight in the normally growing fish. Such relationships were established using regression analysis on data from the control group and another five tanks of fish that were held in the same rearing system at about the same time under the same regimes as for the controls. Initial body size of these fish at the start of each 4-week period varied from 4.18 to 43.79 g. The regression equation relating feed intake (I: g/day) to body weight (W: g) was: $\ln I = 1.270 - 0.666 \ln W$, $n = 20$, $r^2 = 0.974$, and the equation relating specific growth rate (G: %/day) to body weight was: $\ln G = 1.834 - 0.297 \ln W$, $n = 20$, $r^2 = 0.823$. These equations were used to calculate the predicted feed intake and specific growth rate of fish from each tank during the refeeding period based on the initial weight at the beginning of the refeeding period. The residual feed intake or growth rate was calculated as the difference between the observed and predicted values. Analysis of variance was carried out on the residual feed intake and growth rate. Differences were regarded significant when $P < 0.05$.

3. Results

Mortality ranged from zero to two fish per tank during the feed restriction period, and zero to one fish per tank during the refeeding period. Mortality was largely caused by injuries due to aggressive behaviour.

At the end of the feed restriction period, there were significant differences in body weight among fish deprived of feed at different durations. At the end of the experiment, mean body weight of the fish that were deprived of feed for 1 week was still numerically lower than that of the controls, but the difference was not significant ($P = 0.140$). Body weights of the fish that were deprived for 2 and 4 weeks were significantly lower than those of the controls (Table 2), and there was a tendency for the final weight to decrease with the length of deprivation period.

Analysis of variance on both the observed specific growth rate and relative feed intake during the refeeding period (weeks 4–8), and on residual growth rate and feed intake corrected for body weight effects, showed that growth rate and feed intake were

Table 2
Body weights at different times of the experiment in relation to duration of deprivation (mean ± SE, $N = 5$)*

Duration of deprivation (week)	Initial weight (g)	Weight after deprivation (g)	Final weight (g)
0	4.37 ± 0.08	14.20 ± 0.35[a]	30.81 ± 0.94[a]
1	4.35 ± 0.02	10.05 ± 0.11[b]	27.84 ± 0.95[a]
2	4.35 ± 0.06	6.78 ± 0.17[c]	21.52 ± 0.98[b]
4	4.29 ± 0.09	3.66 ± 0.11[d]	15.51 ± 0.77[c]

* Letters after each value indicate results of Tukey's HSD tests. Values with the same letter are not significantly different at the 0.05 level.

significantly higher in deprived fish than in the controls, and there was a tendency for these values to increase with increases in the duration of deprivation period (Table 3).

During the refeeding period, there were no significant differences between deprived and control fish in digestibilities of dry matter, protein and energy. Digestibility of dry matter was within the range 68.7–70.3% (mean ± SE: 70.4 ± 0.5), that of protein 86.8–88.6% (mean ± SE: 88.0 ± 0.3), and that of energy 83.7–85.1% (mean ± SE: 84.1 ± 0.5). No significant differences were observed in feed efficiency, or protein and energy retention efficiencies among groups. Feed efficiency ranged 85.3–91.0% (mean ± S.E.: 88.7 ± 1.2), protein retention efficiency ranged 38.5–41.3% (mean ± SE: 40.1 ± 3.3), and energy retention efficiency ranged 30.1–33.0% (mean ± SE: 31.6 ± 3.0). The relative gains in protein, lipid, and ash, expressed as percentages of body weight gain, did not differ significantly among the groups. Relative protein gain was within the range 14.5–15.0% (mean ± SE: 15.0 ± 0.2), lipid 5.5–5.7% (mean ± SE: 5.6 ± 0.2), and ash 4.1–4.6% (mean ± SE: 4.3 ± 0.2).

At the end of the feed restriction period, body concentrations of moisture and ash tended to be higher, while lipid, protein and energy concentrations tended to be lower the longer the duration of deprivation. At the end of the experiment, moisture concentration was still significantly higher, and energy concentration was lower in the previously

Table 3
Specific growth rate and feed intake during the refeeding period (weeks 5 to 8) in relation to duration of deprivation (mean ± SE, $N = 5$)*,**

Duration of deprivation (week)	Specific growth rate		Feed intake	
	Observed value	Residual value	Observed value	Residual value
0	2.76 ± 0.04[a]	−0.09 ± 0.03[a]	3.09 ± 0.03[a]	−1.35 ± 0.43[a]
1	3.58 ± 0.08[b]	0.42 ± 0.08[b]	3.69 ± 0.04[b]	3.08 ± 0.43[b]
2	4.08 ± 0.13[c]	0.53 ± 0.14[b,c]	4.11 ± 0.07[c]	3.53 ± 0.45[b,c]
4	5.13 ± 0.10[d]	0.87 ± 0.12[c]	4.89 ± 0.08[d]	4.66 ± 0.28[c]

* Both growth rates and feed intake were expressed as observed values (%/day for growth rate and % body weight/day for feed intake) and as residuals (%/day for growth rate and g/day for feed intake) from regression equations relating growth rate or feed intake to body weight for the control fish.

** Letters after each value indicate results of Tukey's HSD tests. Values with the same letter are not significantly different at the 0.05 level.

Table 4
Body composition and energy concentration of hybrid tilapia at different times of the experiment in relation to duration of deprivation (mean ± SE, $N = 5$)*,**

Duration of deprivation (week)		Moisture	Protein	Lipid	Ash	Energy
Initial		76.5 ± 0.2	14.4 ± 0.1	2.7 ± 0.1	4.49 ± 0.07	4.69 ± 0.12
At the end of deprivation	0	76.9 ± 0.3[a]	14.8 ± 0.4[a]	4.3 ± 0.4[a]	4.2 ± 0.2[a,b]	5.0 ± 0.1[a]
	1	77.7 ± 0.4[a]	13.7 ± 0.3[a,b]	3.7 ± 0.2[a]	4.0 ± 0.2[a]	4.5 ± 0.1[a]
	2	80.3 ± 0.4[b]	12.6 ± 0.5[b]	1.6 ± 0.3[b]	4.7 ± 0.0[b]	3.4 ± 0.1[b]
	4	84.0 ± 0.6[c]	9.5 ± 0.4[c]	0.6 ± 0.1[c]	n.a.***	2.1 ± 0.1[c]
Final	0	74.4 ± 0.5[a]	14.9 ± 0.3[a]	5.1 ± 0.3	4.4 ± 0.1	5.4 ± 0.1[a]
	1	76.05 ± 0.12[b]	14.14 ± 0.14[b,c]	4.85 ± 0.09	4.06 ± 0.07	4.97 ± 0.09[b]
	2	75.93 ± 0.30[b]	14.39 ± 0.11[a,b,c]	4.25 ± 0.30	4.27 ± 0.07	4.85 ± 0.09[b]
	4	76.11 ± 0.12[b]	13.84 ± 0.11[c]	4.37 ± 0.12	4.19 ± 0.10	4.86 ± 0.11[b]

* Letters after each value indicate results of Tukey's HSD tests. Values with the same letter are not significantly different at the 0.05 level.

** Values were expressed as % wet weight except that for energy concentration, which was expressed as J/g wet weight.

*** Data not available because of insufficient samples.

deprived fish than in the controls, but there was no significant difference in lipid or ash concentrations between the deprived and control fishes (Table 4). Except for fish deprived for 2 weeks, protein concentration of the deprived groups was significantly lower than that of the controls.

4. Discussion

Tilapia are reported to grow well in both brackish water and seawater (Chervinski and Yashouv, 1971; Shiau and Huang, 1989), and the high growth rates of the hybrid tilapia in the control group in the present study confirm that seawater is a suitable environment for the culture of tilapia.

After 4 weeks of refeeding, body weights of tilapia that were feed-deprived for 2–4 weeks were still significantly lower than those of the controls. Complete compensation was reported within 3 weeks of refeeding in 1–2 g minnows (*Phoxinus phoxinus*) after a 16-day deprivation (Russell and Wootton, 1992), and in 16–120 g rainbow trout after a 3-week deprivation (Dobson and Holmes, 1984; Quinton and Blake, 1990). The inability of hybrid tilapia deprived for 2–4 weeks to catch up in body weight probably resulted from the relatively weak capacity for compensatory growth, and/or greater weight losses during deprivation at high temperatures.

Food-restricted fish are considered to show partial compensation if their growth rates upon refeeding are higher than those of the controls, but final body weights at the end of the compensatory period are still lower than the fully fed controls (Weatherley and Gill, 1981; Miglavs and Jobling, 1989). As body weight of food-restricted fish is usually smaller than that of the controls at the start of the refeeding period, higher growth rates would be expected among restricted fish because of the body size dependency of growth rate (Jobling, 1983). Thus, care must be taken in interpreting the data on partial compensatory growth. In the present study, feed intake and growth rate data were adjusted for size effects, and the analysis revealed that there was a partial compensatory response in fish deprived for 2–4 weeks. There was also a tendency for both feed intake and growth rate during refeeding to increase with the length of deprivation. In three cyprinids, growth rate during refeeding increased in proportion to the length of starvation (Wieser et al., 1992). In the minnow, compensatory growth was detected in fish that were starved for 16 days, but not in fish that were starved for 4 days (Russell and Wootton, 1992). Thus, the magnitude of compensatory growth tends to be dependent on the severity of undernutrition.

It is not known whether tilapia that were deprived for 2 or 4 weeks in the present study would eventually catch up in body size with the controls with the extension of the refeeding period. Whether the fish can catch up in body size with the controls depends on the duration of compensatory growth response. Data on the duration of compensatory growth in fish is limited. It was less than 3 weeks in the minnow (Russell and Wootton, 1992) and in juveniles of two cyprinid species (Wieser et al., 1992), but was at least 8 weeks in juvenile Arctic charr (Miglavs and Jobling, 1989).

Hyperphagia may be the major contributor to the high growth rates during compensatory growth (Miglavs and Jobling, 1989; Russell and Wootton, 1992; Jobling and Koskela, 1996; Jobling et al., 1994), and improved feed efficiency has been reported for some fishes showing compensatory growth (Bilton and Robins, 1973; Dobson and Holmes, 1984; Russell and Wootton, 1992; Jobling et al., 1994; Qian et al., 2000). In the present study, hyperphagia was observed, but without any improvement in feed efficiency relative to the controls.

Jobling et al. (1994) suggested that the composition of accretion may differ between animals displaying compensatory growth and normal body growth, and that animals with preferential accretion of lean body mass would be expected to display better feed efficiency than those depositing greater amounts of body fat. The argument was supported by findings in gibel carp, *Carassius auratus gibelio*, which showed improved feed efficiency and preferential protein growth during compensatory growth (Qian et al., 2000). In the hybrid tilapia examined in the present study, the composition of the gain during refeeding did not differ among treatment groups, and the lack of difference in the composition of gain between tilapia showing compensatory and normal growth may be one reason that compensatory growth in tilapia was not accompanied by improved feed efficiency.

Hybrid tilapia were unable to achieve complete growth compensation within 4 weeks following feed deprivation for periods longer than 1 week. Further, the compensatory growth was not accompanied by any improvement in feed efficiency. This suggests that rearing regimes that incorporate periods of feed deprivation to induce compensatory growth may have limited application in the culture of juvenile hybrid tilapia in seawater.

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