Compensatory growth in the Chinese longsnout catfish, *Leiocassis longirostris* following feed deprivation: Temporal patterns in growth, nutrient deposition, feed intake and body composition

Xiaoming Zhu\textsuperscript{a}, Shouqi Xie\textsuperscript{a,}\textsuperscript{*}, Wu Lei\textsuperscript{a}, Yibo Cui\textsuperscript{a}, Yunxia Yang\textsuperscript{a}, R.J. Wootton\textsuperscript{b}

\textsuperscript{a}State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, Hubei Province, 430072, P.R. China

\textsuperscript{b}Institute of Biological Science, University of Wales, Aberystwyth, SY23 3DA, Wales, UK

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**Abstract**

To investigate the compensatory growth responses of the carnivorous Chinese longsnout catfish a 7-week study was performed at 28 °C. Juvenile longsnout catfish weighing a mean of 13.14 g were starved for 0 (control), 1 (S1) or 2 (S2) weeks and then re-fed to satiation for 4 weeks. Weekly changes in specific growth rate, feed intake and body composition were monitored during re-feeding. No significant difference was found in final body weight among the three groups, indicating complete compensation in the starved fish. The deprived groups caught up in body weight with that of the control within 2 weeks of re-feeding. Body concentrations of protein, lipid and energy were restored to control levels within 1 week of re-feeding. In the first week of re-feeding, specific growth rates of body weight, lipid, protein and energy contents were significantly higher in the deprived fish than in the control. In the second week of re-feeding, the specific growth rate of protein content of the S2 group was still higher than in the control. In the third week of re-feeding, the growth rates for lipid and energy content of the deprived fish dropped below that of the control, but were elevated again during the last week of the experiment. Feed intake was higher than the control level in the first week of re-feeding in the S2 group, but no significant difference was found between the S1 group and control. Growth efficiency in the S2 group was significantly higher than in the controls for the first week of re-feeding. The results were compatible with the hypothesis that compensatory growth restores the ratio of fat to lean body mass ratio in the deprived fish.

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**Keywords:** Compensatory growth; Temporal pattern; Feed intake; Growth rate; Body composition; Chinese longsnout catfish

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**1. Introduction**

Compensatory growth is a period of unusually fast growth shown by individuals encountering abundant food following a period of deprivation (Wilson and Osbourn, 1960; Jobling et al., 1994; Ali et al., 2003).
Compensatory growth in fish is usually accompanied by hyperphagia (an increase in appetite) and sometimes improved growth efficiency (see review in Ali et al., 2003). Compensatory growth is of interest in aquaculture, because an understanding of its dynamics may allow the design of feeding schedules that improve growth rates (Hayward et al., 1997). The mechanism of compensatory growth is poorly understood. Russell and Wootton (1992) used the cybernetic model of Hubbell (1971) and Calow (1976) to explain the mechanism of compensatory growth. A related lipostat model, proposed by Jobling and Johansen (1999), suggests that the ratio of fat to lean body mass (LBM) is an indicator of nutritional status. A decrease in the fat:LBM ratio would result in compensatory growth responses, and restoration of the ratio to the control level would result in the termination of compensatory growth. A rigorous test of the lipostat model requires frequent monitoring of the changes in body composition during compensatory growth.

Although a majority of studies of compensatory growth in fish have used cold-water species, especially salmonids (Ali et al., 2003), some studies have also identified the phenomenon in warm-water species. For example, after a single period of 1 or 2 weeks of feed deprivation, the gibel carp can show full compensation when returned to a satiation ration (Qian et al., 2000; Xie et al., 2001). Compensatory growth has also been demonstrated in the channel catfish, a species important in aquaculture in the USA (Kim and Lovell, 1995; Gaylord and Gatlin, 2000, 2001; Chatakondi and Yant, 2001).

The Chinese longsnout catfish is a warm-water, carnivorous species and the optimum water temperature for growth is 25–30 °C (Xiong and He, 1994). It is a focus of current aquaculture interest because of its high market value in China. The purpose of the present study was to investigate the temporal patterns in growth, feed intake and body composition in the Chinese longsnout catfish upon re-feeding following 1 or 2 weeks of feed deprivation.

2. Materials and methods

Longsnout catfish, Leiocassis longirostris, were obtained from the Chinese Longsnout Catfish Hatchery Farm, Hubei, P.R. China about 2 months after hatching. They were reared in a recirculation system for one month prior to the start of the experiment. Two weeks before the start of the experiment, 160 fish were transferred to 80 Plexiglas tanks (surface area 650 cm²; water volume 26 l). These containers were perforated and four containers were placed in a 300 l fibreglass tank, which was part of a re-circulation system. Water temperature was controlled using a heater linked to a thermostat. Water temperature was increased to 28 °C at 2–3 °C per day and the fish were maintained at this temperature for a further week before the experiment started. Photoperiod was 12L:12D. Aeration was provided intermittently for 30 min every hour. Dissolved oxygen was >6 mg l⁻¹, and NH₄-N was below 0.5 mg l⁻¹. The fish were fed to satiation twice a day on experimental, formulated pellets (Table 1) during 1-month acclimatisation to the experimental diets.

The experiment lasted for 7 weeks. Initially, the fish were starved for 1 day to empty the gut. All the fish were then pooled, and 78 fish (average weight

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>(% wet weight)</th>
</tr>
</thead>
<tbody>
<tr>
<td>White fish meal (USA)</td>
<td>66.3</td>
</tr>
<tr>
<td>Fish oil</td>
<td>2.5</td>
</tr>
<tr>
<td>α-starch</td>
<td>2.0</td>
</tr>
<tr>
<td>Corn starch</td>
<td>15.6</td>
</tr>
<tr>
<td>Vitamin premix</td>
<td>0.8</td>
</tr>
<tr>
<td>Mineral premix</td>
<td>5.0</td>
</tr>
<tr>
<td>Cellulose</td>
<td>7.0</td>
</tr>
<tr>
<td>Cr₂O₃</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Proximate composition (% or kJ g⁻¹ dry matter)

<table>
<thead>
<tr>
<th>Component</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein</td>
<td>43.44</td>
</tr>
<tr>
<td>Crude lipid</td>
<td>7.31</td>
</tr>
<tr>
<td>Ash</td>
<td>18.59</td>
</tr>
<tr>
<td>Energy</td>
<td>17.55</td>
</tr>
</tbody>
</table>

* Vitamin mixture contained the following vitamins per kg of feed: vitamin A, 5500 I.U.; vitamin D₃, 1000 I.U.; vitamin E, 50 I.U.; vitamin K, 10 I.U.; choline, 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 B₁₂, 20 μg; ascorbic acid, 100 mg; vitamin C, 100 mg; inositol, 100 mg.

* Mineral mixture contained the following minerals per kg of feed: NaCl, 500.0 mg; MgSO₄·7H₂O, 7500.0 mg; NaH₂PO₄·2H₂O, 12500.0 mg; KH₂PO₄, 16000.0 mg; Ca(H₂PO₄)₂·H₂O, 10000.0mg; C₆H₅CaO₆·5H₂O, 1750.0 mg; FeSO₄, 1250.0 mg; ZnSO₄·7H₂O, 176.5 mg; MnSO₄·4H₂O, 81.0 mg; CuSO₄·5H₂O, 15.5 mg; CoCl₂·6H₂O,0.5 mg; KI, 1.5 mg; starch, 225.0 mg.
13.14 ± 3.49 g) were chosen randomly. Each fish was measured, blotted of excess water, weighed to 0.01 g and individually placed in a Plexiglas tank. The fish were fed to satiation twice a day on the experimental diet for 1 week and then randomly divided into three treatment groups. Each treatment had 26 replicates (one fish in each tank). The control group (C) was fed to satiation twice a day throughout the 7 weeks. The S1 group was starved during week 3, and then fed to satiation thereafter. The S2 group was starved for 2 weeks during weeks 2 and 3, and fed to satiation thereafter. During feeding, a small weighed quantity of diet was dropped into each tank every few minutes until the fish no longer accepted feed. Each feeding lasted for 1 h. It was confirmed that all pellets were consumed by the fish. The fish were weighed once a week following 22 h of starvation. Fish were not fed on the day of weighing.

For the measurement of body composition and energy content, three fish were killed at the start of week 2, prior to the start of starvation in the S2 group. Three fish from each group were randomly taken and killed at the beginning of week 4 (start of re-feeding) and each week thereafter. There were three replicate samples per treatment. Allocation of fish to the treatment groups was such that 12 fish remained in each group at the end of the experiment. There were 12 replicates per treatment at the end of the experiment. All surviving fish were killed at the end of the experiment (C0), following weighing. Sacrificed at the end of the experiment. There were 12 replicates per treatment. Allocation of fish to the treatment groups was such that 12 fish remained in each group at the end of the experiment. There were 12 replicates per treatment at the end of the experiment. All surviving fish were killed at the end of the experiment, following weighing. Sacrificed fish were autoclaved at 120 °C, dried to constant weight at 70 °C and homogenised. Nitrogen was determined using the Kjeldahl method (AOAC, 1984), lipid by Lambert and Dehnel’s (1974) modification of the chloroform-methanol extraction technique, ash by combustion at 550 °C and energy by bomb calorimetry (Gentry Instruments Inc., Aiken, USA). Protein was calculated from nitrogen by multiplying by 6.25.

For each week, for the fish that survived to the end of the experiment (N = 12 per treatment), daily specific growth rate in fresh weight was calculated as: 100(Wt − Wt−1)/I, where Wt is body weight at week t, and I is weekly feed intake.

Analysis of variance (ANOVA) was used to test the differences in body weight at the start of the experiment, start of re-feeding and end of the experiment among treatments. Repeated measures ANOVA or ANCOVA, with week as the within-subjects factor and feed regime as the between-subjects factor, was used to assess the effects of feeding regime on the trajectories in body weight, feed intake, growth efficiency, and weekly specific growth rate in body weight, body protein, lipid, ash and energy. Body weight at the start of each week was used as covariate in repeated measures ANCOVA for feed intake and weekly specific growth rate in body weight and nutrients. Pre-planned orthogonal comparisons tested for the overall effect of deprivation (Control vs. mean of S1 and S2) and for the effect of the mildest deprivation (Control vs. S1). Differences were regarded as significant when P < 0.05, but P values between 0.05 and 0.1 were also noted. Log transformations were used to stabilise the variances of weight measurements and to allow for the allometric relationship between feed intake and body weight.

3. Results

There was no significant difference in the initial body weight of the fish among treatments. Differences in body weight were significant at the start of re-feeding, but final body weight did not differ significantly among groups (Table 2).

Repeated measures ANCOVA showed that body weight was significantly affected by week, the interaction between feeding regime and week, but not by feeding regime (F and P values in Table 3). The significant interaction reflected the different trajectories of body weight for the three groups over the 7 weeks (Fig. 1). Planned comparisons showed no significant difference in body weight between the control and deprived groups at the beginning of week 6 and thereafter, suggesting complete catch up by the deprived groups within 2 weeks of re-feeding (Fig. 1). Planned comparisons showed body concentrations of dry matter, protein, energy, lipid and the ratio of fat to lean body mass (LBM: sum of protein and ash), were significantly lower in the deprived groups than
in the controls at the start of re-feeding (week 4), but were restored to the control level 1 week after re-feeding (week 5) (Fig. 2). The pattern for ash concentration was irregular. It was significantly different between the control and deprived groups at week 5, but the difference was not significant for other weeks.

Repeated measures ANCOVA of weekly changes in specific growth rates in body weight and nutrients used only data for the re-feeding period (weeks 4–7), because weekly data on nutrient specific growth rates were not available for weeks 1–3 (details of F-ratios and P values are in Table 3). Specific growth rates in body weight, protein, lipid and energy were all significantly affected by feeding regime, week and by the interaction between feeding regime and week.

Specific growth rate in body ash was significantly affected by week and by the interaction between feeding regime and week, but was not affected by feeding regime (Table 3).

Planned comparisons showed that specific growth rates in body weight, protein, lipid and energy were significantly higher in the deprived groups than in the controls during the first week after re-feeding (Fig. 3). These compensatory effects lasted for only 1 week in the S1 group. For the S2 group, weekly

### Table 2

Changes in body weight (g) of longsnout catfish at different times of the experiment

<table>
<thead>
<tr>
<th>Group</th>
<th>Initial weight</th>
<th>Weight at week 3 (start of re-feeding)</th>
<th>Final weight</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>12.97±0.64</td>
<td>17.03±0.71</td>
<td>23.87±1.99</td>
<td>12</td>
</tr>
<tr>
<td>S1</td>
<td>13.19±0.77</td>
<td>15.27±0.77</td>
<td>23.68±1.84</td>
<td>12</td>
</tr>
<tr>
<td>S2</td>
<td>13.31±0.65</td>
<td>13.43±0.64</td>
<td>22.53±1.50</td>
<td>12</td>
</tr>
</tbody>
</table>

**ANOVA**

<table>
<thead>
<tr>
<th>F</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.046</td>
<td>6.745</td>
<td>0.182</td>
</tr>
</tbody>
</table>

**d**f 2.32 0.002 0.835

Table 3

Results of repeated measures ANCOVA of weekly changes in body weight for the whole experiment, and changes in specific growth rate in weight and nutrient, feed intake and growth efficiency during the re-feeding period in longsnout catfish subjected to different feeding regimes

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Treatment effect</th>
<th>Week effect</th>
<th>Treatment × Week interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>df</td>
<td>P</td>
</tr>
<tr>
<td>Body weight</td>
<td>0.494</td>
<td>2, 33</td>
<td>0.615</td>
</tr>
<tr>
<td>Specific growth rate in weight</td>
<td>14.474</td>
<td>2, 33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Specific growth rate in protein</td>
<td>15.984</td>
<td>2, 33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Specific growth rate in lipid</td>
<td>41.922</td>
<td>2, 33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Specific growth rate in ash</td>
<td>1.108</td>
<td>2, 33</td>
<td>0.342</td>
</tr>
<tr>
<td>Specific growth rate in energy</td>
<td>26.026</td>
<td>2, 33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Feed intake</td>
<td>0.760</td>
<td>2, 33</td>
<td>0.476</td>
</tr>
<tr>
<td>Growth efficiency</td>
<td>3.552</td>
<td>2, 33</td>
<td>0.040</td>
</tr>
</tbody>
</table>

(P values<0.05 in bold type).

C: control fish that were fed throughout the 9-week experiment; S1: fish that were starved for 1 week during week 2 and fed thereafter; S2: fish that were starved for 2 weeks during weeks 2 and 3 and fed thereafter (mean ± S.E.).

Fig. 1. Weekly changes in body weight (g) in three groups of longsnout catfish during the seven-week experiment. C: control group (N=12) fed to satiation throughout the experiment; S1: group (N=12) starved for 1 week (week 3) and fed to satiation subsequently; S2: group (N=12) starved for 2 weeks (weeks 2 and 3) and subsequently fed to satiation. Data were log transformed. Results of planned comparisons: NS, no significant difference between C and (S1+S2). *, significant difference between C and (S1+S2), **, significant difference between C and (S1+S2), but not between C and S1. ***, significant difference between C and (S1+S2) and between C and S1. Data were log transformed and collected at start of the week.
specific growth rate in body weight, lipid, ash and energy were higher than in the controls for 1 week, and specific growth rate in protein was higher than in the controls for 2 weeks. Specific growth rate in body protein, energy and lipid of the S2 group declined in the third week after re-feeding then increased again during the last week of experiment. In week 6, specific growth rates in energy and lipid were significantly lower in the deprived groups than in the controls.

Repeated measures ANCOVA showed, that after adjustment for the effect of body weight at the beginning of each week, feed intake was significantly affected by week, but not by feeding regime, or by the interaction between feeding regime and week. However, the orthogonal comparisons showed that feed intake was significantly higher in the deprived groups than in the controls, which was a consequence of the high intake by the S2 rather than the S1 group during the first week after re-feeding (Fig. 4).

Repeated measures ANOVA showed that growth efficiency was significantly affected by feeding regime, by week and by the interaction between feeding regime and week (Table 3). In the first week of re-feeding, there was a significant difference between the deprived groups and the control (Fig. 5).
Again, this was because of the high growth efficiency of the S2 group.

4. Discussion

This study demonstrated complete growth compensation following 1 or 2 weeks starvation by juvenile Chinese longsnout catfish, a warm-water carnivorous fish. Full or over-compensation was also observed in channel catfish (Kim and Lovell, 1995; Chatakondi and Yant, 2001), and hybrid sunfish (Lepomis cyanellus × L. macrochirus) (Hayward et al., 1997). However, in Silurus meridionalis, a warm-water carnivorous fish, starved for 10–60 days, only those starved for 50 days showed elevated growth rate in dry matter and energy (Deng and Zhang, 1999). A limited capacity for compensatory growth was observed in hybrid tilapia (Oreochromis mossambicus × O. niloticus) following starvation (Wang et al., 2000). Studies on juvenile gibel carp (Xie et al., 2001), juvenile three-spined stickleback (Gasterosteus aculeatus), and minnow (Phoxinus phoxinus) (Zhu et al., 2001) demonstrated full
compensatory growth following 1 or 2 weeks starvation.

Upon re-feeding the longsnout catfish, the temporal patterns in the compensatory responses in growth in weight, protein, lipid and ash were similar, with elevated growth lasting for 1 week (except protein growth in the S2 group, which remained elevated for 2 weeks). Thus, compensatory growth responses in longsnout catfish lasted for only a short period, and responses in growth rates terminated as body weight converged to the control level. A short duration of compensatory growth has been reported in several studies. In 1–2 g minnows (*Phoxinus phoxinus*) starved for 16 days, elevated growth rate and growth efficiency lasted for 2 weeks after deprivation (Russell and Wootton, 1992). In very small juveniles (50–100 mg) of three coldwater cyprinids, compensatory growth lasted for 6–12 days of re-feeding (Wieser et al., 1992). Studies on cold-water salmonids report much longer durations of compensatory growth. In 5–10 g Arctic char, following 8 weeks restricted feeding, hyperphagia persisted for 6 weeks after re-alimentation, though growth efficiency was elevated for only 2 weeks (Miglavs and Jobling, 1989). Feed restricted Atlantic salmon weighing about 3 g showed higher growth rate than the controls during the period 80–215 days after re-alimentation (Nicieza and Metcalfe, 1997). It is not clear whether these differences reflect variations among species or are a result of different body sizes and experimental protocols.

The present study also suggested that the duration of compensatory growth tended to increase with an increase in the severity of starvation, with elevated protein growth in the longsnout catfish persisting into the second week of re-feeding. Similar results have been reported for other species (see Ali et al., 2003 for review).

Compensatory growth could be achieved through hyperphagia (Miglavs and Jobling, 1989; Jobling and Koskela, 1996; Wang et al., 2000), or a combination of hyperphagia and improved growth efficiency (Russell and Wootton, 1992; Jobling et al., 1994; Qian et al., 2000). In the longsnout catfish study, both hyperphagia and increased growth efficiency played a role. Gross growth efficiency in the S2 group was higher than in the S1 and control groups in the first week of re-feeding. The hyperphagic response was also only significant in the first week of re-feeding, although the feed intake of the S2 group was consistently higher than for the S1 or control group throughout the re-feeding period.

In the present study, body lipid concentration and fat:LBM ratio in the starved fish (S2 group) were restored to controls levels within 1 week after re-feeding. Compensatory responses in growth rate and feed intake followed a mostly similar pattern. Thus, the results partly supported the lipostat model proposed by Jobling and Johansen (1999). However, the high rate of protein growth of the S2 group in the second week of re-feeding also suggests that some compensatory growth of structural material was taking place. In the third week of re-feeding, growth in energy and lipid were depressed compared to the control fish, but then were higher in the following week. These changes may be artifacts reflecting the small number of fish sampled. However, they may indicate that the com-
compensatory response was “hunting” for the optimal growth trajectories, a behaviour typical of some control systems (Calow, 1976).

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References


