Effect of restricted feeding on compensatory growth responses in Clarias gariepinus (Burchell, 1822)

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ABSTRACT

A four week feeding trial was carried out in a recycling water system to investigate the effect of restricted feeding regimes on compensatory growth and body composition in African catfish, Clarias gariepinus. A fishmeal-based diet containing 35% protein and 18 kJ g⁻¹ gross energy (GE) was fed to triplicate groups of 30 fish. Fish were fed in five feeding schedules of 28 days: restricted 14 days + appetite 14 days; restricted 7 days + appetite 7 days; restricted 3 days + appetite 4 days; restricted 2 days + appetite 2 days. The restricted regime was achieved by feeding at the rate of 1% (maintenance ration) of their body weight per day, adjusted after weekly weighing. African catfish did not exhibit compensatory growth response under alternating periods of a feed restriction and appetite feeding. However, not significant (P>0.05) values of feed and protein utilization were found under alternating periods of feed restriction and appetite feeding. Significantly higher (P<0.05) feed intake was observed in treatment with appetite throughout than those in other treatments. All the feeding schedules showed no significant differences (P>0.05) on body composition, organ indices, eviscerated carcass composition, viscera lipid and liver lipid. This study reveals that C. gariepinus failed to display compensatory growth response by alternating periods of restricted and appetite feeding.

Introduction

Feed management strategies of cultured fish is important in achieving efficient growth. The significance of feed utilisation in relation to compensatory growth in several fish species has recently been highlighted (Jobling and Johansen, 1999). Growth rates of fish may be highly variable and in many cases appears to be limited by food availability. When food supplies are increased following a period of starvation or restricted feeding, fish and other animals may display a growth spurt, known as compensatory growth or catch-up growth. The physiological basis of compensatory growth is not fully understood but starved-refed animals may have increased food intake (hyperphagia) and/or improve food conversion efficiency compared with animals reared continu-
Compensatory growth could be exploited in the commercial production of fish or to improve growth efficiency (Dobson and Homes 1984; Jobling et al., 1994; Saether and Jobling, 1999). For this detailed information is required about the effect of different feeding regimes or the imposition of different types of food-restricted schedules upon weight gain and tissue deposition in different fish species (Jobling et al., 1993, 1994). In almost all previous studies, food deprivation has been achieved by use of restricted feeding. Studies on compensatory growth in African catfish, Clarias gariepinus are unreported.

In the present studies, feeding regimes consisted of alternating periods of feeding either maintenance rations as a restricted regime, and feeding to appetite. The objective of the present study was to examine the influence of food restriction and subsequent appetite feeding on compensatory growth responses, food conversion, protein utilisation and body composition in African catfish, C. gariepinus.

Materials and methods

Experimental diets

An experimental diet was formulated with crude protein and gross energy (GE) of 35% and 18 kJ g⁻¹ respectively. The diet containing a protein to energy ratio (P/E ratio) of 20 mg protein kJ⁻¹ GE and lipid to carbohydrate ratio g/g (L:CHO ratio) of 0.40 was fixed on the basis of results obtained from previous studies (Ali, 2001). Ingredients and proximate composition of test diet are shown in Table 1.

The diet was prepared by mixing the dry ingredients in a Hobart mixer (Belle, Mini 150; England) blended with oils and then water to give a pelletable mixture. A steam conditioned California Pellet Mill (model CL2, San Francisco, California) was used to pellet the diet with 3 mm die. Pellets were dried by convection at 40°C overnight in a drying cabinet, packed in polythene bags, sealed and stored at -20°C until used.

Experimental system

The experiment was conducted in a temperature controlled recycling system with 15 cylindrical plastic tanks (40 cm diameter, 25 cm deep). Water was supplied to each tank at the rate of 1 L min⁻¹ from a 250-L header tank. About thirty percent of the water in the system was replaced biweekly with freshwater to adjust water quality and to avoid accumulation of waste products. Water quality parameters such as pH (6.45 - 7.30), dissolved oxygen (6.50 - 7.60 mg/L), ammonia (0.08 - 0.03 mg/L), nitrate (0.9 - 6.07 mg/L) and nitrite (0.03 - 0.24 mg/L) remained within optimum ranges for C. gariepinus (Viveen et al., 1985; Hoffman et al., 1991). A 12 h light: 12 h dark regime (08.30 - 20:30 h, light period) was maintained and water temperature was held at 28 ± 1°C. Six hundred 12-week old (13.05 ± 0.05 g) C. gariepinus were obtained from broodstock maintained at the Institute of Aquaculture, University of Stirling. Fish were randomly assigned into groups of 30 and stocked in the 30 L tank.

Experimental procedure

Each feeding schedule had three replicates and the experiment was conducted for four weeks. Fish were weighed individually at the start and end of the feeding trial. Weekly sampling were used to adjust the daily feed ration. At the beginning of the experiment, twenty fish were randomly sacrificed and kept for analysis of body composition, organ indices, eviscerated carcass, visceral lipid and liver lipid. At end of the feeding trial, ten fish from each tank were sampled for
Fish were fed according to five feeding schedules incorporating restricted (maintenance) and appetite feeding. During restricted feeding, fish were fed at the rate of 1% of their body weight per day, adjusted after weekly weighing. This is an approximated maintenance ratio in 20 g of catfish, Clarias batrachus at 30 ± 2°C (Hassan and Jafri 1994). The feeding trial was conducted for 56 days according to the following feeding schedules: (i) Appetite 28 days (Control); (ii) Restricted 14 days + Appetite 14 days (R14 + A14); (iii) Restricted 7 days + Appetite 7 days (R7 + A7); (iv) Restricted 3 days + Appetite 4 days (R3 + A4); (v) Restricted 2 days + Appetite 2 days (R2 + A2).

Under restricted feeding, fish were fed by subdividing it into three equal parts at 10:00, 14:00 and 18:00 h every day. Appetite feeding was also offered three times daily (at the same intervals) and achieved by presenting a small quantity of feed every few minutes and allowing fish to eat until they stopped showing interest in added feed (about 20 minutes). Feed intake for appetite feeding was recorded daily for each treatment. To avoid excess feeding, food was offered with great care by giving small amounts of food at a time to ensure that fish ate all the diet offered.

Proximate composition of diet ingredients, experimental diets and fish carcasses were analysed following AOAC (1990). Gross energy was determined using an Automatic Adiabatic Bomb Calorimeter (Gallenkamp & Co. Ltd., England). Liver lipid and visceral lipid were determined gravimetrically (Floch et al. 1969) and proximate composition of diet ingredients were determined following AOAC (1990).

<table>
<thead>
<tr>
<th>Ingredients: (g/100g diet)</th>
<th>(g/100g diet)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish meal</td>
<td>32.00</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>20.00</td>
</tr>
<tr>
<td>Wheat flour</td>
<td>7.50</td>
</tr>
<tr>
<td>Fish oil</td>
<td>4.34</td>
</tr>
<tr>
<td>Corn oil</td>
<td>4.34</td>
</tr>
<tr>
<td>Vitamin premix</td>
<td>1.00</td>
</tr>
<tr>
<td>Mineral premix</td>
<td>1.00</td>
</tr>
<tr>
<td>Carboxymethyl cellulose</td>
<td>2.00</td>
</tr>
<tr>
<td>Corn starch</td>
<td>13.30</td>
</tr>
<tr>
<td>Cellulose</td>
<td>14.02</td>
</tr>
</tbody>
</table>

**Proximate composition:**

- Crude Protein: 35.07
- Crude fat: 11.82
- Ash: 8.85
- Fibre: 13.88
- NFE: 30.38
- GE (kJ g⁻¹): 17.94
- P : GE ration: 19.55
- Lipid : CHO ratio (g/g): 0.40

1. NFE = Nitrogen free extractives, calculated as 100 - (% Protein + % Lipid + % Ash + % Fibre)
2. GE = Gross energy content
3. P : GE ration = Protein to energy ratio in mg protein / kJ of GE
4. Lipid : CHO ratio (g/g) = % wt. in lipid / % wt. in CHO.
et al., 1957). Two fish in each tank were analysed individually in duplicate for determining whole body composition, eviscerated carcass, viscera lipid and liver lipid, while organ indices were performed in triplicate.

Specific growth rate (SGR), % weight gain, food conversion efficiency (FCE), protein efficiency ratio (PER) and apparent net protein utilisation (ANPU) were calculated as follows: SGR (%/Day) = \[\frac{\ln \text{Final body weight} - \ln \text{Initial body weight}}{\text{days} \times 100}\]

\[
\text{% Weight gain} = \frac{(\text{Final body weight} - \text{Initial body weight})}{\text{Initial body weight}} \times 100
\]

\[
\text{FCE} = \frac{\text{Live weight gain (g)}}{\text{Crude protein fed (g dry weight)}}
\]

\[
\text{PER} = \frac{\text{Live weight gain (g)}}{\text{Crude protein fed (g dry weight)}}
\]

\[
\text{ANPU} (%) = \frac{\text{Final carcass protein} - \text{Initial carcass protein}}{\text{Total dry protein consumed} \times 100}
\]

Organ indices (EVSI = Eviscerosomatic index; VSI = Viscerosomatic index; HSI = Hepatosomatic index) were calculated as follows:

\[
\text{Organ indices (OI %) = } \frac{\text{Organ weight (g)}}{\text{Body weight (g)}} \times 100
\]

Data were subjected to analysis of variance (ANOVA) using Minitab software for Windows. Comparisons among treatment means were carried out by one way analysis of variance followed by

<table>
<thead>
<tr>
<th>Treatments (Feeding schedule)</th>
<th>T-I (Control)</th>
<th>T-II</th>
<th>T-III</th>
<th>T-IV</th>
<th>T-V</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Parameters:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial body wt. (g)</td>
<td>12.99 ± 0.06</td>
<td>13.05± 0.13</td>
<td>12.91± 0.08</td>
<td>13.01± 0.05</td>
<td>12.92± 0.10</td>
</tr>
<tr>
<td>Final body wt. (g)</td>
<td>40.60 ± 0.83</td>
<td>28.89 ± 0.75</td>
<td>29.23 ± 0.67</td>
<td>30.31 ± 0.90</td>
<td>29.64 ± 2.88</td>
</tr>
<tr>
<td>Weight gain (g)</td>
<td>27.61 ± 0.89</td>
<td>15.85 ± 0.74</td>
<td>16.32 ± 0.68</td>
<td>17.30 ± 0.85</td>
<td>16.72 ± 0.42</td>
</tr>
<tr>
<td>Weight gain (%)</td>
<td>212.57 ± 7.77</td>
<td>121.47 ± 5.74</td>
<td>126.36 ± 5.60</td>
<td>132.99 ± 6.09</td>
<td>129.38 ± 3.40</td>
</tr>
<tr>
<td>Specific growth rate (SGR, %/day)</td>
<td>4.07 ± 0.09</td>
<td>2.84 ± 0.04</td>
<td>2.29 ± 0.04</td>
<td>3.02 ± 0.04</td>
<td>2.97 ± 0.04</td>
</tr>
<tr>
<td>Food conversion (FCE)</td>
<td>± 0.06</td>
<td>± 0.04</td>
<td>± 0.04</td>
<td>± 0.04</td>
<td>± 0.04</td>
</tr>
<tr>
<td>efficiency (FCE)</td>
<td>1.05 ± 0.12</td>
<td>1.07</td>
<td>1.13 ± 0.09</td>
<td>1.20</td>
<td>1.17</td>
</tr>
<tr>
<td>Feed intake (g/100g fish/day)</td>
<td>2.32 ± 0.30</td>
<td>1.89</td>
<td>1.95</td>
<td>1.91</td>
<td>1.83</td>
</tr>
<tr>
<td>Protein efficiency ratio (PER)</td>
<td>± 0.19</td>
<td>± 0.11</td>
<td>± 0.12</td>
<td>± 0.12</td>
<td>± 0.11</td>
</tr>
<tr>
<td>Apparent net protein utilisation (ANPU, %)</td>
<td>48.43 ± 5.36</td>
<td>47.17</td>
<td>47.86</td>
<td>48.96</td>
<td>50.75</td>
</tr>
</tbody>
</table>

**Note:** Values are means ± SD of three replicates. Figures in the same row having different superscripts are significantly different (P < 0.05).

The treatments (feeding regimes) were viz., T-I (control), T-II, T-III, T-IV and T-V refers A28, R14 + A14, R7 + A7, R3 + A4 and R2 + A2 respectively where, R and A refers respectively to the restricted and appetite feeding and the numerical values refers to the number of days.
Tukey’s test (0.05). Standard deviation (± SD) was calculated to identify the range of means. Percentage data were transformed by arc-sine transformation (Zar, 1984) prior to ANOVA and reversed afterwards.

**Results**

No mortality or external clinical symptoms occurred in any treatment of this study. The highest (P<0.05) growth was observed in fish fed to appetite throughout, and no significant differences (P>0.05) in growth were observed between fish on the other feeding schedules. Daily feed consumption per 100 g fish was found to be significantly higher (P<0.05) in fish on feeding schedules I (control). Fish on feeding schedules II to V did not show statistical differences (P>0.05) (Table 2). It is seen that food conversion efficiency (FCE) in any feeding schedule did not differ significantly (P>0.05). Protein efficiency ratio (PER) and apparent net protein utilization (ANPU) did not vary significantly (P>0.05) among the different feeding schedules (Table 2).

Whole body composition of fish in treatments II to V did not vary significantly (P>0.05) in comparison to the control (T-I) (Table 3). Among the feeding schedule groups eviscerosomatic index (EVSI) and viscerosomatic index (VSI) values did not differ significantly (P>0.05). Eviscerated (EV) carcass composition (moisture, lipid, protein and ash content), visceral lipid and liver lipid did not differ significantly (P>0.05) between the groups. (Table 4).

**Discussion**

The results demonstrated that the imposition of restricted feeding, involv-

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Treatment (Feeding schedule)</th>
<th>T-I (Control)</th>
<th>T-II</th>
<th>T-III</th>
<th>T-IV</th>
<th>T-V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture</td>
<td>Initial</td>
<td>74.03</td>
<td>±0.59</td>
<td>±0.95</td>
<td>±1.27</td>
<td>±0.98</td>
</tr>
<tr>
<td>Crude Protein</td>
<td>15.63</td>
<td>15.91±</td>
<td>15.70</td>
<td>15.96</td>
<td>15.81</td>
<td>16.36</td>
</tr>
<tr>
<td>Crude Lipid</td>
<td>7.84</td>
<td>7.33±</td>
<td>7.11</td>
<td>6.96</td>
<td>7.15</td>
<td>6.61</td>
</tr>
<tr>
<td>Ash</td>
<td>2.50</td>
<td>2.98±</td>
<td>3.04</td>
<td>3.08</td>
<td>2.96</td>
<td>3.25</td>
</tr>
<tr>
<td>EVSI</td>
<td>92.59</td>
<td>91.63±</td>
<td>91.13</td>
<td>90.87</td>
<td>90.43</td>
<td>91.06</td>
</tr>
<tr>
<td>VSI</td>
<td>6.11</td>
<td>6.94±</td>
<td>7.09</td>
<td>7.98</td>
<td>7.54</td>
<td>7.79</td>
</tr>
<tr>
<td>HSI</td>
<td>0.79</td>
<td>1.14±</td>
<td>1.13</td>
<td>1.24</td>
<td>1.20</td>
<td>1.15</td>
</tr>
</tbody>
</table>

**Note:** Values are means ± SD of six replicates. Figures in the same row having different superscripts are significantly different (P<0.05). (EVSI = Eviscerosomatic index; VSI = Viscerosomatic index; HSI = Hepatosomatic index).

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV and T-V refers A28, R14 + A14, R7 + A7, R3 + A4 and R2 + A2 respectively where, R and A refers respectively to the restricted and appetite feeding and the numerical values refers to the number of days.
ing alternating periods of maintenance ration and appetite feeding failed to display compensatory growth responses in Clarias gariepinus. The highest growth rates were observed in fish fed to appetite throughout, while others failed to display full growth compensation. The results are similar to those reported for Arctic charr, Salvelinus alpinus and Atlantic cod, in which alternating short periods (1-3 weeks) of food deprivation with unlimited provision of food resulted in reduced growth than control (Jobling et al., 1993, 1994). Thus, they suggested periods of good deprivation of short duration were insufficient to induce compensatory growth.

Compensatory growth in fish may be influenced by factors such as species, sex, age or state of maturity and severity of the food restriction (Quinton and Blake, 1990; Jobling et al., 1994; Jobling and Koskela, 1996). Physiological mechanisms underlying the compensatory growth response in fish remain obscure, and may, at least in part, differ from those operative in broiler chickens (Jobling et al., 1993).

All most similar feed conversion efficiency (FCE) values were found in different treatment groups (Table 2). On the other hand, Miglavs and Jobling (1989a, b) have also reported that Arctic charr showing compensatory growth displayed higher food conversion efficiency than their counterparts fed to satiation throughout. Dobson and Homes (1984) and Bilton and Robin (1973) have suggested that salmonid fishes also show improved food conversion efficiency (FCE) during recovery from a period of starvation. Similar protein utilisation efficiency (PER and ANPU) in feeding schedules II to V (Table 2) was found in comparison to the control. This may be due to the low metabolic expenditure, which possibly occurred during the period of recovery. Comparable results on protein and energy utilisation efficiency of fish species with similar alternating

### Table 4

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Initial (Control)</th>
<th>T-I</th>
<th>T-II</th>
<th>T-III</th>
<th>T-IV</th>
<th>T-V</th>
</tr>
</thead>
<tbody>
<tr>
<td>EV moisture</td>
<td>75.55</td>
<td>73.19 ± 0.53</td>
<td>73.91 ± 0.75</td>
<td>74.74 ± 0.29</td>
<td>74.04 ± 0.69</td>
<td>74.37 ± 1.36</td>
</tr>
<tr>
<td>EV crude protein</td>
<td>16.23</td>
<td>16.50 ± 0.33</td>
<td>16.36 ± 0.47</td>
<td>159.9 ± 0.25</td>
<td>16.22 ± 0.30</td>
<td>16.13 ± 0.62</td>
</tr>
<tr>
<td>EV crude lipid</td>
<td>5.70</td>
<td>7.25 ± 0.51</td>
<td>6.64 ± 0.67</td>
<td>6.17 ± 0.67</td>
<td>6.57 ± 0.48</td>
<td>6.29 ± 0.74</td>
</tr>
<tr>
<td>EV ash</td>
<td>2.64</td>
<td>3.07 ± 0.17</td>
<td>3.09 ± 0.17</td>
<td>3.10 ± 0.20</td>
<td>3.16 ± 0.11</td>
<td>3.20 ± 0.11</td>
</tr>
<tr>
<td>Liver lipid</td>
<td>14.09</td>
<td>11.58 ± 1.15</td>
<td>9.99 ± 2.09</td>
<td>8.97 ± 2.49</td>
<td>8.91 ± 1.39</td>
<td>8.60 ± 1.96</td>
</tr>
</tbody>
</table>

**Note:** Values are means ± SD of six replicates. Figures in the same row are not significantly different (P > 0.05).

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV and T-V refers to A28, R14 + A14, R7 + A7, R3 + A4 and R2 + A2 respectively where, R and A refers respectively to the restricted and appetite feeding and the numerical values refers to the number of days.
feeding with respect to compensatory growth are currently very limited.

Fish fed on alternating feeding schedules (II to V) showed almost similar whole body lipid and moisture content compared to control. There was thus no indication, especially in treatment II, that growth compensation involved just fat or water deposition. Quinton and Blake (1990) showed that carcass lipid decreased and moisture increased in rainbow trout after 3 weeks of starvation. In short-time starvation visceral fats and muscle fats are utilised as the energy source (Parker and Vanstone, 1996; Weatherley and Gill, 1981) and replacement of the muscle lipids with water occurs (Idler and Bithers, 1959). After six weeks, no significant difference of lipid and moisture content was observed. They concluded that growth occurring during the rapid growth phase of compensatory growth is due to protein synthesis, not just increase in fat deposition or water uptake.

Whole body protein and ash did not vary much among the treatment groups. Phillips et al. (1960) reported that whole body protein levels in brook trout, Salvelinus fontinalis tended to increase or remain the same after 12 weeks of fasting. Satoh et al. (1984) also stated that whole body protein levels of fasted Nile tilapia, Oreochromis niloticus, were similar after 60 days of fasting compared to fish before fasting. Quinton and Blake (1990) also reported that alternating period of three weeks fasting and 3 weeks feeding in rainbow trout showed compensatory growth and resulted in no significant differences in body protein content in comparison to continuously fed control fish.

The eviscerosomatic index (EVSI) of fish fed on alternating feeding schedules II to V were similar to control. Similar EVSI values were reported in juvenile Artic char, Salvelinus alpinus in sixteen week fasting followed by refeeding and continuously fed controls (Miglavs and Jobling, 1989b). Viscerosomatic index (VSI) and hepatosomatic index (HSI) values in the experimental fish were similar to controls. This is in accordance with the observations in several fish species (Miglavs and Jobling, 1989; Rueda et. al., 1989). In the present study, fish fed on alternating schedules exhibited almost similar eviscerated (EV) carcass composition when compared to the control. Similar observations have been reported in eviscerated carcass composition for Arctic char fed on alternating fasting and re-feeding for 16 weeks (Miglavs and Jobling 1989b). Visceral fat in fish fed on alternating feeding schedules showed similar values of that of control. Weatherley and (Gill 1987) and Love (1980) reported that visceral lipids were the principal energy source during short periods of food deprivation, protein being used only when the lipid deposits are depleted. Similarly visceral lipid of fish fed on alternating schedules showed almost similar lipid in comparison with the control. Likewise Artic char also showed no changes in liver lipid during alternating feeding to fasting and re-feeding for 16 weeks (Miglavs and Joblish, 1989b).

This study with African catfish, C. gariepinus, thus failed to display compensatory growth response. It also revealed that fish at alternating periods of restricted and appetite-feeding schedules has no positive trend of growth compensation.

Acknowledgements

The first wishes to thank the World Bank under Agricultural Management Project for funding.

References


Compensatory growth in African catfish


