Chapter 6

The evaluation of mixed feeding schedules with respect to compensatory growth, feed conversion, nutrient utilisation and body composition in African catfish, *Clarias gariepinus* (Burchell, 1822)

6.1 INTRODUCTION

An important approach to reducing feed costs in aquaculture is to develop appropriate feeding management strategies and other general improvements to husbandry (Singh and Srivastava, 1984; 1985). 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, appear to be limited by food availability. Periods of food restriction or deprivation, which lead to growth retardation or loss of weight, do not appear to compromise the ability of fish to grow when they are returned to full rations. On the contrary, there is evidence to suggest that fish may show a period of rapid weight increase, known as compensatory or catch-up growth, following periods of feed restriction.

Among fish species, catch-up or compensatory growth has been reported for salmonids, cyprinids, pleuronectids, gadoids and centrarchids (Weatherley and Gill, 1981, 1987; Dobson and Holmes, 1984; Miglavs and Jobling, 1989a; Russell and Wootton, 1992; Jobling *et al.*, 1993; Jobling *et al.*, 1994; Bull and Metcalfe, 1997; Nicieza and Metcalfe, 1997; Rueda *et al.*, 1998; Saether and Jobling, 1999), but responses have been inconsistent. In other words, recovery of lost body weight has been reported to be partial in some cases whereas complete catch-up has been reported in others, and in a few cases overcompensation has also been observed.

A number of investigators have speculated that compensatory growth could be exploited in the commercial production of fish, to control rates of weight gain, or to manipulate final composition of body tissues, or to improve growth efficiency (Dobson and Holmes, 1984; Kindschi, 1988; Quinton and Blake, 1990; Jones and Farrell, 1992; Jobling *et al.*, 1993; Jobling *et al.*, 1994; Saether and Jobling, 1999). In almost all previous studies, food deprivation has been achieved by use of restricted feeding rather than the feeding of a maintenance ration. Studies on compensatory growth in African catfish, *Clarias gariepinus* are unreported. In order for this to become a useful tool, 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; Jobling *et al.,* 1994).

In the present experiment mixed feeding schedules consisted of alternating periods of feeding either maintenance rations as a restricted regime, and to appetite. Studies using maintenance requirements to impose restricted feeding combined with alternating periods of restricted and appetite ration with respect to compensatory growth in fish are limited. However, 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).

The objective of the present study was to examine the influence of food restriction and subsequent return to appetite feeding on compensatory growth responses, food conversion, nutrient utilisation and body composition in African catfish, *Clarias gariepinus,* with a view to reducing feed costs in culture.

6.2 MATERIALS AND METHODS

6.2.1 Experimental System

The experimental system described in Section 2.1 and Figure 2.1 was used in this experiment.

6.2.2 Experimental Fish

African catfish, *Clarias gariepinus* as described in Section 2.2 was used as the test fish species in this study. Twelve-week old (13.05 ± 0.05g) fingerlings were obtained from broodstock maintained at the Institute of Aquaculture, University of Stirling following the procedure detailed in Section 2.2. Fish were randomly assigned into groups of 30 fish and each group was placed in an individual 30-L tank as described in Section 2.1 and as shown in Figure 2.1.

6.2.3 Experimental Diet

An experimental diet was formulated to contain crude protein and gross energy of 35% and 17.5kJ/g respectively. The diet containing crude protein 35%, a P/E ratio of 20.0 mg protein per kJ of GE and L/CHO ratio g/g of 0.39 was fixed on the basis of results obtained from previous studies (Chapters 3, 4 and 5). The composition of the experimental diet and its proximate analysis are shown in Table 6.1. Amino acid composition is shown in Table 6.2. Diet formulation and preparation was described in Sections 2.3.1 and 2.3.2.

Table 6.1 Formulation and composition of the experimental diet and proximate analysis (% dry weight basis)

Ingredients:	Diet
Fish meal (Herring type)[1]	32.00
Soybean meal (Dehulled solvent extract)[2]	20.00
Wheat flour (Whole wheat)[3]	7.50
Fish oil	4.34
Corn oil	4.34
Vitamin premix[4]	1.00
Mineral premix[5]	1.00
Chromic oxide (Cr_2O_3)	0.50
Carboxymethyl cellulose (Binder)[6]	2.00
Corn starch	13.30
∝- Cellulose	14.02
Proximate composition:	
% as fed:	
Moisture	10.43
% Dry wt. basis:	
Crude Protein	35.07
Crude fat	11.82
Ash	8.85
Fibre	13.88
NFE[7]	30.38
Cr_2O_3	0.50
GE (kJ/g)[8]	17.94
P / GE ratio[9]	19.55
Lipid / CHO ratio (g/g)[10]	0.39

Proximate analysis (%dry weight basis):

1. Moisture: 8.53; Crude protein: 73.06; Crude fat: 8.31; Fibre: 0.96; Ash: 16.24.
2. Moisture: 12.44; Crude protein: 54.17; Crude fat: 1.40; Fibre: 3.96; Ash: 6.69.
3. Moisture: 14.35; Crude protein: 10.54; Crude fat: 1.17; Fibre: 2.33; Ash: 1.34.
4. As listed in Table 2.2, Section 2.3.1
5. As listed in Table 2.3, Section 2.3.1
6. Carboxymethyl cellulose – Sodium salt, high viscosity
7. NFE = Nitrogen free extractives, calculated as 100 – (% Protein + % Lipid + % Ash + % Fibre)
8. GE = Gross energy content
9. P / GE ratio = Protein to energy ratio in mg protein / kJ of GE
10. Lipid/CHO ratio (g/g) = % wt. in lipid / % wt. in CHO

Table 6.2 Essential amino acid compositions (EAA, g/100g protein) of experimental diet and EAA requirements of African catfish, *Clarias gariepinus*

Essential amino acids:	EAA (g/100g protein)	EAA requirements [a]
Arginine	4.74	4.30
Histidine	2.67	1.50
Isoleucine	3.25	2.60
Leucine	7.10	3.50
Lysine	5.53	5.00
Methionine[b]	1.13	2.30
Phenylalanine[c]	3.49	5.00
Threonine	3.44	2.00
Valine	3.79	3.00

a Requirement of a related species channel catfish (NRC, 1993)

b In the absence of dietary cystine (NRC, 1993)

c Dietary protein contained 1.72 percent tyrosine. With 0.6 percent tyrosine in the diet, phenylalanine requirement was 2.0 percent of the dietary protein (NRC, 1993)

6.2.4 Experimental Practices

Fish were acclimated to the experimental system using a commercial trout diet (Trout Fry 02, crumble 1.00 to 1.50 mm, BioMar Ltd., Scotland) for two weeks before the start of the experiment. Before commencement of the feeding trial, 30 fish from the acclimated lots were randomly sacrificed with an overdose of benzocaine. Six fish were taken for organ indices and triplicate pooled samples of 10 fish were taken for determination of initial whole body composition, eviscerated carcass, viscera and liver.

The experiment was conducted for two phases each of 4 weeks (total 8 weeks) using fish in six treatments and three replicates per treatment. After the end of the first phase (phase I), ten fish from each tank were sampled for body composition, eviscerated carcass, viscera and liver composition per fish in duplicate and organ indices in triplicate. The remaining 20 fish in each tank were weighed and used again in the 2nd phase (phase II) of the experiment over the last 4 weeks. At the end of the 2nd phase (phase II) fish samples were analysed as at the end of the 1st phase (phase I). Acclimation and periodical weighing procedure were as described in Section 2.4.1.

6.2.4.1 Fish Feeding

Fish were offered the diet in six different treatments at two feeding regimes; viz., restricted (maintenance) and appetite feeding. In restricted feeding, fish were fed 1% of their body weight per day, adjusted after fortnightly weighing. This is an approximated maintenance ration for *Clarias* catfish, *Clarias batrachus* (Hassan and Jafri, 1994). The feeding trial continued for 56 days according to the following mixed feeding schedules:

(I) Appetite 56 days + 0 (A56 + 0, control)

(II) Restricted 28 days + 28 days Appetite (R28 + A28)

(III) Restricted 14 days + Appetite 14 days (R14 + A14)

(IV) Restricted 7 days + Appetite 7 days (R7 + A7)

(V) Restricted 3 days + Appetite 4 days (R3 + A4)

(VI) Restricted 2 days + Appetite 2 days (R2 + A2)

Under restricted feeding, fish were offered the meal 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 times) and was 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 loss of diet, food was offered taking great care by giving small amounts of food at a time to be sure that fish ate all the diet offered.

6.2.5 Water Quality Management

Water quality management was as described in Section 2.5. All values were within the optimum range for this species (Table 2.4, Section 2.1).

6.2.6 Experimental Analyses

6.2.6.1 Proximate Analyses

Proximate composition (moisture, crude protein, and ash) of whole body of fish, eviscerated carcass, viscera, liver and experimental diet were determined by the methods described in Sections 2.6.1.1, 2.6.1.2, and 2.6.1.5. Crude lipid in whole fish body, eviscerated carcass and the experimental diet was determined as described Section 2.6.1.3 while crude fibre in experimental diets was determined as described Section 2.6.1.4. Liver lipid and visceral lipid were measured as described in Section 2.7. Two fish in each group (each tank) were analysed individually in duplicate for determining whole body composition, eviscerated carcass, viscera and liver composition while organ indices were performed in triplicate.

6.2.6.2 Growth and Feed Performance, Nutrient Utilisation and Organ Indices

Growth and feed performance, nutrient utilisation and organ indices were calculated according to the methods described in Sections 2.6.1.2, 2.6.1.3, 2.6.1.4, 2.6.2.2, 2.6.2.3 and 2.6.2.5.

6.2.6.3 Statistical Analysis

Statistical analyses were carried out as described in Section 2.13.

6.3 RESULTS

The design of this experiment is such that the results of growth performance and food utilisation are generally considered in three parts. The first deals with phase I (weeks 0 - 4), the second with phase II (weeks 4 - 8) and the third with comparison of phase I and phase II as well as data for the overall (weeks 0 - 8) experimental period.

6.3.1 Growth, Survival and Feed Performance

No mortality nor external clinical symptoms occurred in any treatment during the whole period of this study. The fortnightly growth response over the phase I (weeks 0 - 4) is shown in Figure 6.1. Growth and feed response parameters are presented in Table 6.3 and graphically in Figures 6.2 and 6.3. The best ($P < 0.05$) growth response in terms of final body weight, percent weight gain and specific growth rate (SGR) was observed for feeding schedule I (control), for fish fed to appetite throughout. In contrast, the growth response to feeding schedule II (4 weeks restriction) was significantly the lowest ($P < 0.05$). No significant differences ($P > 0.05$) in growth rate were observed in treatments III to VI. (Table 6.3 and Figure 6.2). Daily highest and lowest feed consumption per 100g fish was found to be significantly different ($P < 0.05$) in the feeding schedule I (control) and feeding schedule II respectively. No significant difference ($P > 0.05$) was observed between feeding schedules III to VI (Table 6.3 and Figure 6.2). From Table 6.3 it is seen that food conversion efficiency (FCE) did not vary significantly ($P > 0.05$) among the feeding schedules I, III, IV, V and VI while feeding schedule II varied significantly ($P < 0.05$) from these.

The fortnightly growth response during phase II (weeks 4 - 8) is also shown in Figure 6.1. Growth and feed response parameters are presented in Table 6.4 and graphically in Figure 6.2 and 6.3. Feeding schedule II showed significantly the highest ($P < 0.05$) growth response in terms of final body weight, percent weight gain and specific growth rate (SGR) in comparison with other feeding schedules. No significant differences ($P > 0.05$) in growth rate were observed in treatments I, III, IV, V and VI. (Table 6.4 and Figure 6.2). Daily feed consumption per 100g fish was found to be significantly higher ($P < 0.05$) in treatment I (control) and treatment II in comparison with other treatments. No significant differences ($P > 0.05$) were observed between treatments III to VI. Food conversion efficiency (FCE) did not differ significantly ($P > 0.05$) between feeding schedule groups (Table 6.4 and Figure 6.2).

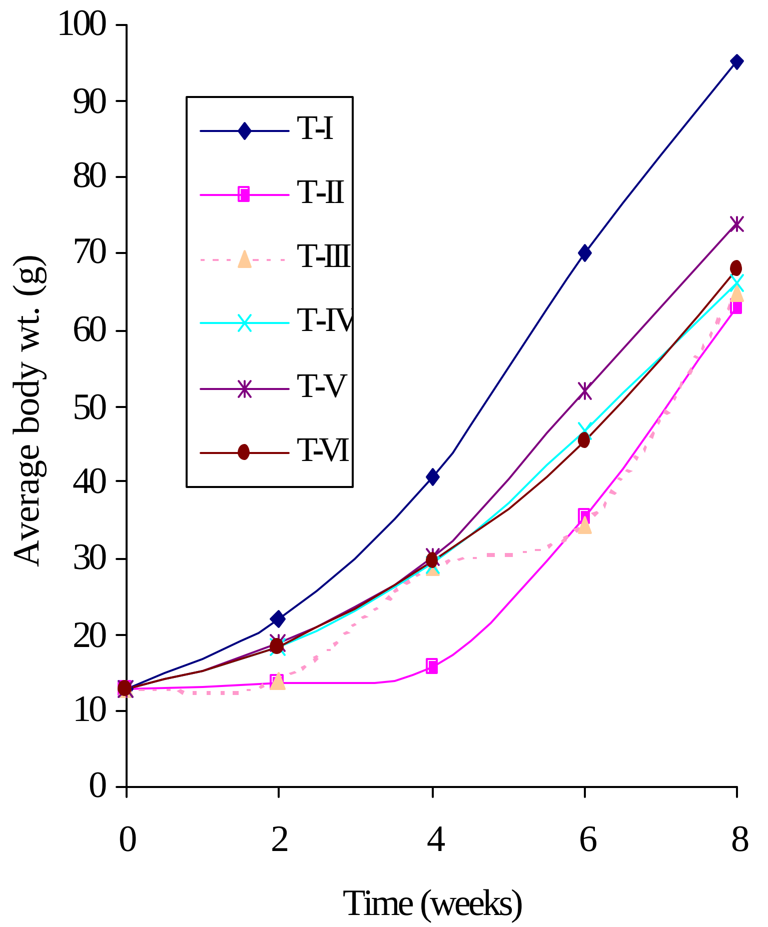

Figure 6.1 The mean fortnightly growth response of African catfish, *Clarias gariepinus* maintained mixed feeding schedules over 8 weeks

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

Table 6.3 Phase I (weeks 0 - 4). Growth performance, feed intake and feed utilisation in *Clarias gariepinus* maintained on mixed feeding schedules

	Treatment (Feeding schedule)						
Treatment:	T-I (Control)	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters:							
Initial body wt. (g)	12.99[a] ± 0.06	12.91[a] ± 0.08	13.05[a] ± 0.13	12.91[a] ±0.08	13.01[a] ± 0.05	12.92[a] ± 0.10	0.02
Final body wt. (g)	40.60[c] ± 0.83	15.57[a] ± 0.24	28.89[b] ± 0.75	29.23[b] ± 0.67	30.31[b] ± 0.90	29.64[b] ± 0.44	1.77
Weight gain (g)	27.61[c] ± 0.89	2.66[a] ± 0.20	15.85[b] ± 0.74	16.32[b] ± 0.68	17.30[b] ± 0.85	16.72[b] ± 0.42	1.76
Weight gain (%)	212.57[c] ± 7.77	20.61[a] ± 1.47	121.47[b] ± 5.81	126.36[b] ± 5.53	132.99[b] ± 6.09	129.38[b] ± 3.40	13.6
Specific growth rate (SGR, % day)	4.07[c] ± 0.09	0.67[a] ± 0.05	2.84[b] ± 0.10	2.92[b] ± 0.09	3.02[b] ± 0.10	2.97[b] ± 0.05	0.25
Feed intake (g/100g fish/day)	2.32[c] ± 0.12	0.76[a] ± 0.02	1.89[b] ± 0.03	1.95[b] ± 0.04	1.91[b] ± 0.04	1.83[b] ± 0.04	0.06
Food conversion efficiency (FCE)	1.05[b] ± 0.06	0.80[a] ± 0.06	1.04[b] ± 0.04	1.02[b] ± 0.04	1.07[b] ± 0.04	1.10[b] ± 0.04	0.03
Protein efficiency ratio (PER)	3.02[b] ± 0.19	2.31[a] ± 0.19	2.93[b] ± 0.11	2.95[b] ± 0.12	3.06[b] ± 0.12	3.16[b] ± 0.11	0.07
Apparent net protein utilization (ANPU, %)	48.43[b] ± 5.36	37.39[a] ± 2.30	47.17[b] ± 3.23	47.86[b] ± 2.04	48.96[b] ± 2.24	50.75[b] ± 0.67	1.21
Apparent net lipid utilization (ANLU, %)	89.86[b] ± 3.70	-5.13[a] ± 29.57	73.32[b] ± 4.36	54.96[b] ± 17.41	79.96[b] ± 22.93	63.95[b] ±4.82	8.24
Apparent net energy utilization (ANEU,%)	45.31[b] ± 1.56	15.77[a] ± 6.89	40.43[b] ± 2.40	36.06[b] ± 5.40	42.97[b] ± 6.27	39.66[b] ± 1.15	2.54

Note: Values are means ± SD of three replicates. Means in the same row having different superscripts are significantly different ($P < 0.05$) and values in the same row with same superscript is not significantly different($P > 0.05$).

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

Table 6.4 Phase II (weeks 4 - 8). Growth performance, feed intake and feed utilisation in *Clarias gariepinus* maintained on mixed feeding schedules

	Treatment (Feeding schedule)						
Treatment:	T-I (Control)	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters:							
Initial body wt. (g)	40.72^{c} ± 1.71	15.37^{a} ± 0.23	30.05^{b} ± 1.10	29.28^{b} ± 0.90	30.66^{b} ± 0.54	29.86^{b} ± 1.50	1.80
Final body wt. (g)	95.18^{b} ± 13.37	62.94^{a} ± 4.45	64.76^{a} ± 0.77	66.05^{a} ± 1.34	73.81^{a} ± 5.34	67.91^{a} ± 2.88	2.95
Weight gain (g)	54.45^{b} ± 11.67	47.57^{ab} ± 4.60	34.71^{a} ± 0.33	36.77^{a} ± 1.56	43.15^{ab} ± 5.06	38.04^{a} ± 1.50	2.00
Weight gain (%)	133.08^{a} ± 23.30	309.75^{b} ± 32.99	115.65^{a} ± 5.33	125.72^{a} ± 5.53	140.68^{a} ± 15.36	127.46^{a} ± 3.31	16.90
Specific growth rate (SGR, % day)	3.01^{a} ± 0.37	5.03^{b} ± 0.28	2.74^{a} ± 0.09	2.91^{a} ± 0.13	3.13^{a} ± 0.23	2.93^{a} ± 0.06	0.20
Feed intake (g/100g fish/day)	1.98^{b} ± 0.09	2.39^{c} ± 0.11	1.62^{a} ± 0.02	1.84^{ab} ± 0.06	1.81^{ab} ± 0.08	1.67^{a} ± 0.11	0.07
Food conversion efficiency (FCE)	1.03^{a} ± 0.12	1.13^{a} ± 0.08	1.18^{a} ± 0.01	1.08^{a} ± 0.07	1.15^{a} ± 0.10	1.20^{a} ± 0.09	0.02
Protein efficiency ratio (PER)	2.95^{a} ± 0.36	3.25^{a} ± 0.23	3.20^{a} ± 0.04	3.11^{a} ± 0.19	3.31^{a} ± 0.29	3.45^{a} ± 0.25	3.42
Apparent net protein utilization (ANPU,%)	50.75^{a} ± 10.53	52.34^{a} ± 5.11	55.27^{a} ± 4.28	51.25^{a} ± 7.88	57.12^{a} ± 9.53	54.85^{a} ± 1.80	1.56
Apparent net lipid utilization (ANLU,%)	93.97^{a} ± 20.90	103.51^{a} ± 14.14	103.15^{a} ± 10.35	103.68^{a} ± 15.95	88.32^{a} ± 21.81	126.38^{a} ± 13.16	4.36
Apparent net energy utilization (ANEU,%)	49.33^{a} ± 9.71	50.59^{a} ± 5.76	51.84^{a} ± 2.93	49.11^{a} ± 5.51	48.86^{a} ± 2.42	57.62^{a} ± 3.99	1.33

Note: Values are mean ± SD of three replicates. Means in the same row having different superscripts are significantly different ($P < 0.05$) and values in the same row with same superscript are not significantly different($P > 0.05$)

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

Table 6.5 Overall (weeks 0 - 8). Growth performance, feed intake and feed utilisation in *Clarias gariepinus* maintained on mixed feeding schedules

	Treatment (Feeding schedule)						
Treatment:	T-I (Control)	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters:							
Initial body wt. (g)	12.99[a] ± 0.06	12.91[a] ± 0.08	13.05[a] ± 0.13	12.91[a] ± 0.08	13.01[a] ± 0.05	12.92[a] ± 0.10	0.02
Final body wt. (g)	95.18[b] ± 13.37	62.94[a] ± 4.45	64.76[a] ± 0.77	66.05[a] ± 1.34	73.81[a] ± 5.34	67.91[a] ± 2.88	2.95
CV (%) of final wt.	54.84[b] ± 9.88	44.98[ab] ± 3.29	36.59[a] ± 7.07	34.63[a] ± 3.43	35.55[a] ± 2.38	42.08[ab] ± 1.78	2.02
Weight gain (%)	633.03[b] ± 106.26	387.84[a] ± 37.62	396.36[a] ± 5.75	411.54[a] ± 13.23	467.28[a] ± 39.82	425.43[a] ± 20.87	22.70
Specific growth rate (SGR) (% day)	3.54[b] ± 0.26	2.83[a] ± 0.13	2.86[a] ± 0.02	2.92[a] ± 0.05	3.10[a] ± 0.12	2.96[a] ± 0.07	0.06
Feed intake (g/100 g fish/day)	1.49[b] ± 0.14	1.27[a] ± 0.06	1.23[a] ± 0.01	1.35[ab] ± 0.03	1.30[ab] ± 0.06	1.24[a] ± 0.08	0.05
Food conversion efficiency (FCE)	1.04[a] ± 0.11	1.10[a] ± 0.08	1.16[a] ± 0.02	1.06[a] ± 0.03	1.13[a] ± 0.08	1.17[a] ± 0.09	0.02
Protein efficiency ratio (PER)	2.98[a] ± 0.33	3.17[a] ± 0.22	3.33[a] ± 0.04	3.06[a] ± 0.08	3.40[a] ± 0.22	3.37[a] ± 0.24	0.05
Apparent net protein utilization (ANPU, %)	51.71[a] ± 9.54	51.10[a] ± 4.68	53.69[a] ± 2.04	48.66[a] ± 4.58	54.94[a] ± 7.50	53.72[a] ± 1.90	1.24
Apparent net lipid utilization (ANLU, %)	85.45[a] ± 14.50	93.45[a] ± 12.07	87.43[a] ± 8.14	83.62[a] ± 11.12	79.28[a] ± 14.78	100.71[a] ± 8.26	2.88
Apparent net energy utilization (ANEU, %)	45.65[a] ± 7.47	47.37[a] ± 5.11	47.07[a] ± 2.54	43.78[a] ± 2.68	45.54[a] ± 0.79	50.49[a] ± 2.69	0.96

Note: Values are mean ± SD of three replicates. Means in the same row having different superscript are significantly different ($P < 0.05$) and values in the same row with same superscript are not significantly different($P > 0.05$).

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

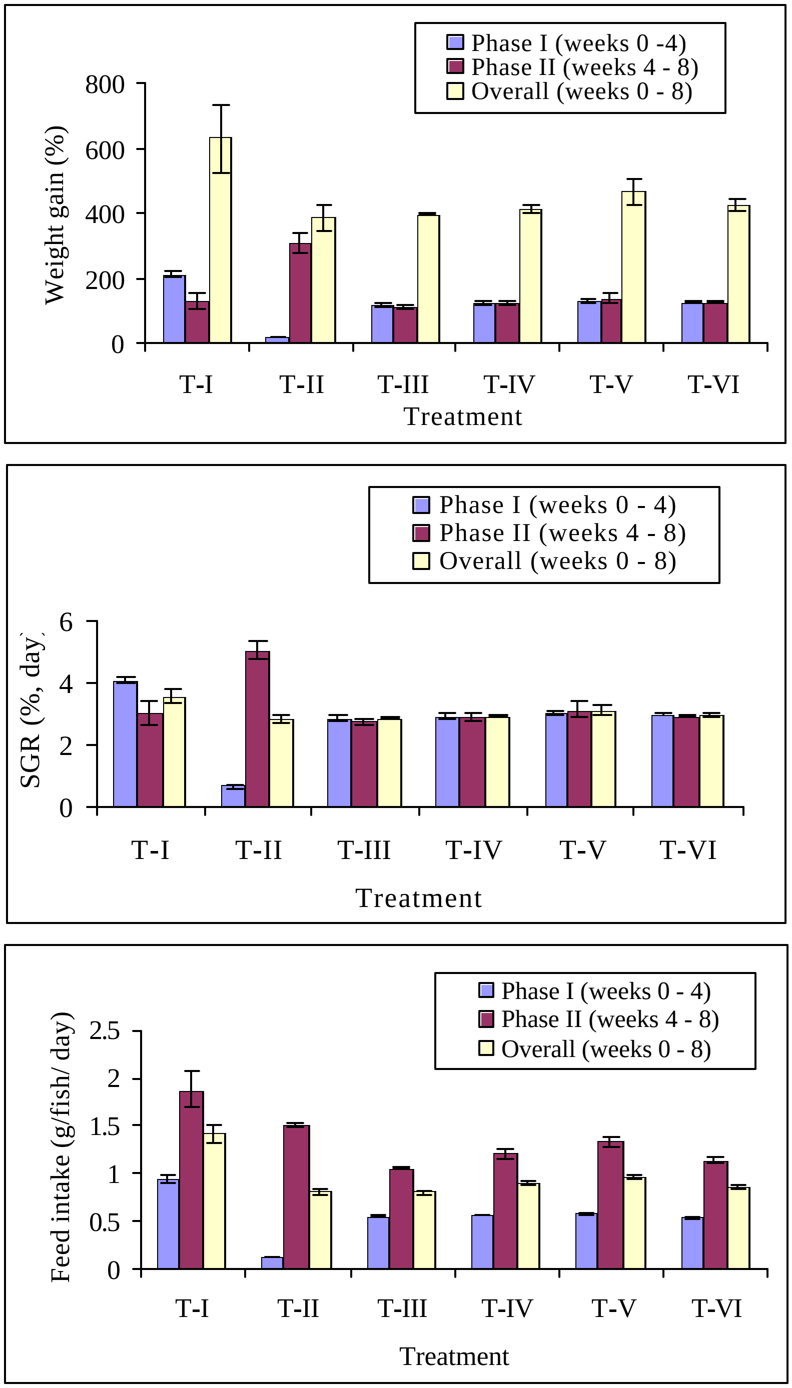

Figure 6.2 Growth performance (weight gain and specific growth rate) and feed intake of African catfish, *Clarias gariepinus* maintained on mixed feeding schedules in different experimental period (SGR = Specific growth rate).

Bars vertical are means of ± SD of three replicates. The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

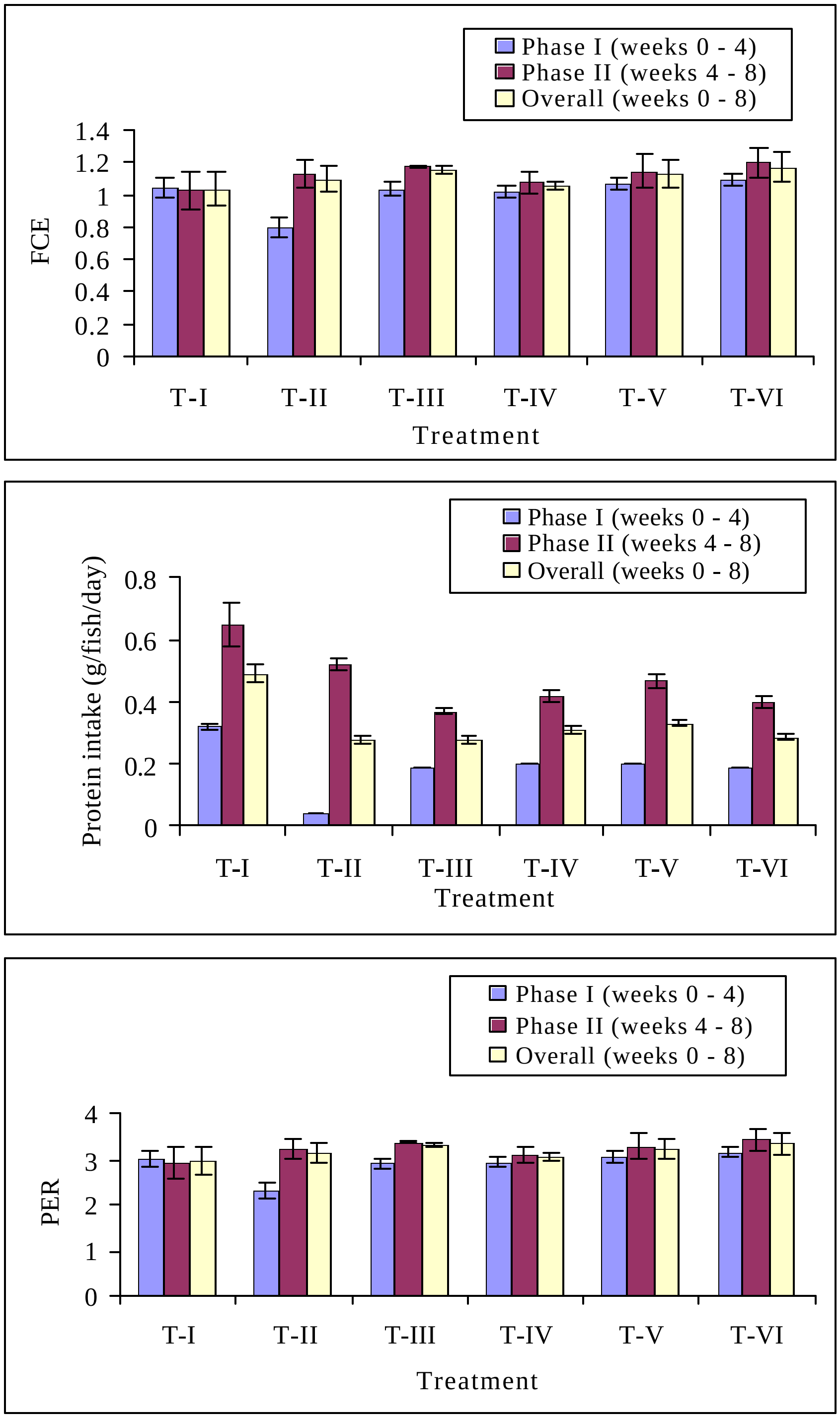

Figure 6.3 Food conversion efficiency (FCE), protein intake and protein efficiency ratio (PER) of *Clarias gariepinus* maintained mixed feeding schedules in different experimental periods

Bars vertical is means ± SD of three replicates. The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

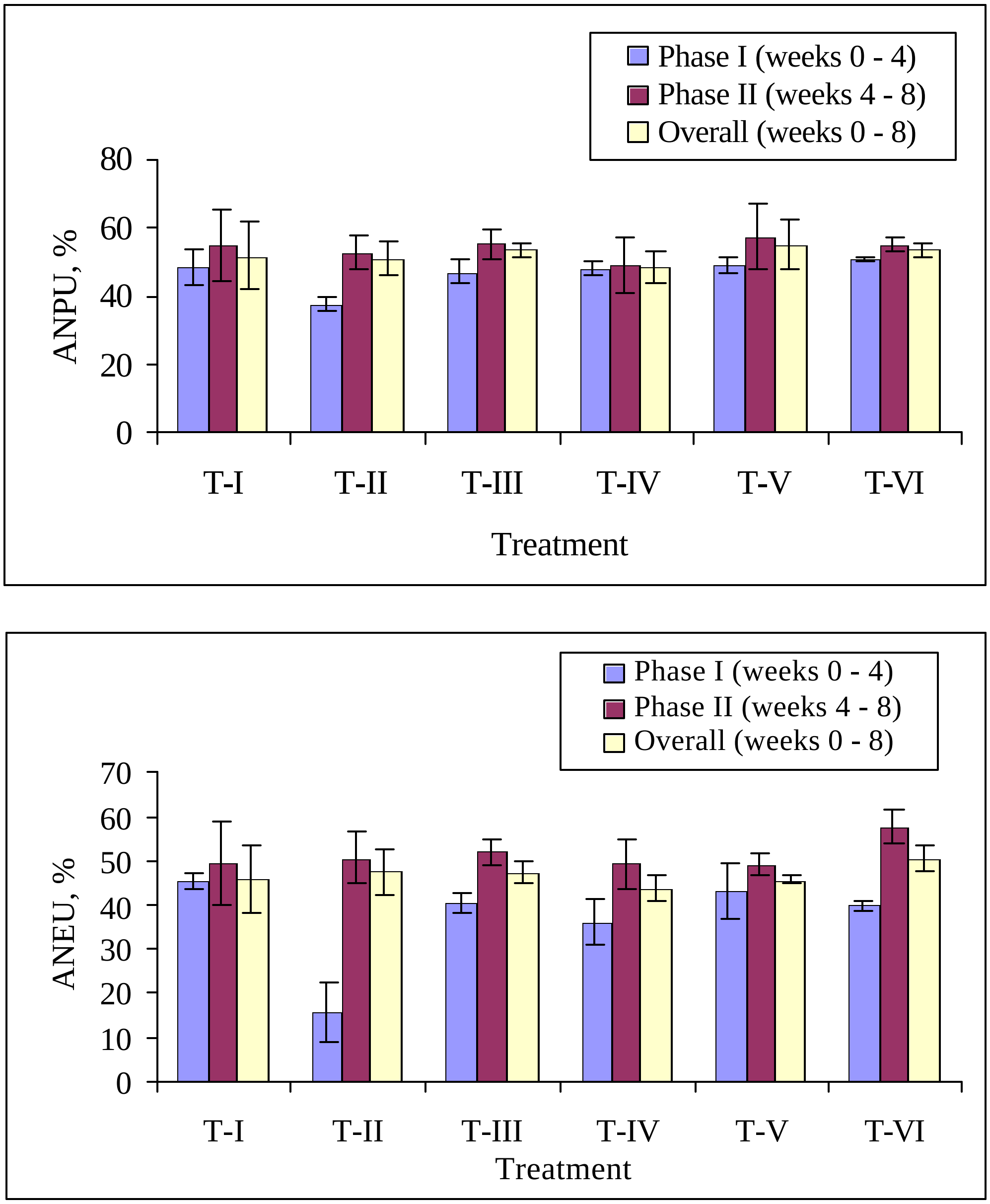

Figure 6.4 Apparent net protein utilisation (ANPU) and apparent net energy utilisation (ANEU) of *Clarias gariepinus* maintained mixed feeding schedules in different experimental periods.

Bars vertical is means ± SD of three replicates. The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

Growth rate and food conversion efficiency (FCE) in feeding schedule II were markedly higher during phase II in comparison with phase I. Phase I (0 - 4 weeks) growth rate slightly increased in fish fed restricted ration throughout (T-II). In contrast, in phase II (4 - 8 weeks) fish were fed to appetite throughout (T-II) showed a rapid increase in fortnightly growth response (Figure 6.1) and higher growth rates, feed consumption and FCE (Tables 6.3 and 6.4).

The fortnightly growth response of *Clarias gariepinus* overall (weeks 0 - 8) is shown in Figure 6.1. Growth and feed response parameters are summarised in Table 6.5 and graphically in Figures 6.2 and 6.3. Significantly higher ($P < 0.05$) growth response in terms of final body weight, percent weight gain and specific growth rate (SGR) was observed in feeding schedule I (control), for fish fed to appetite throughout. No significant differences ($P > 0.05$) in growth rate were observed between feeding schedule II to VI. Coefficients of variation (CV) for final weight in feeding schedule I (control) were significantly higher ($P < 0.05$). Improved growth rates were accompanied by lower CV for final weight feeding schedules III, IV and V and there were no significant differences ($P > 0.05$) between them (Table 6.5). Daily feed consumption per 100g fish was found to be significantly higher ($P < 0.05$) in feeding schedules I (control). Fish in feeding schedules II to VI did not show statistical differences ($P > 0.05$). Food conversion efficiency (FCE) in any feeding schedule did not differ significantly ($P > 0.05$) (Table 6.5).

For treatment III, it is possible to calculate both food intake and growth rate for the 2-week periods of maintenance and appetite feeding as this corresponds to the 2-week weighing interval. The average SGR (%, day) and food intake (g/100g fish/day) for the 2 appetite fed periods were 4.89 and 3.15 respectively.

6.3.2 Apparent Nutrient and Energy Utilisation

Protein efficiency ratio (PER) and apparent net protein utilisation (ANPU) for phase I (weeks 0 - 4) are presented in Table 6.3 and graphically in Figures 6.2 and 6.3. Fish on feeding schedule II showed significantly the lowest ($P < 0.05$) PER and ANPU while feeding schedules I, III, IV, V and VI did not vary significantly ($P > 0.05$). As shown in Table 6.3, a significantly lower ($P < 0.05$) ANLU value of –5.13% was found in fish fed schedule II. However, no significant differences ($P > 0.05$) were noticed in other groups. Similarly, apparent net energy utilisation (ANEU) was lowest ($P < 0.05$) for feeding schedule II with no significant differences ($P > 0.05$) between the other group (Table 6.3).

In phase II (weeks 4 - 8) PER and ANPU are shown in Table 6.4 and graphically in Figures 6.2 and 6.3. PER ranged from 2.95 to 3.45 and did not show significant differences ($P > 0.05$) among groups. ANPU ranged from 50.75 to 57.12% and did not vary significantly ($P > 0.05$) between treatments. However, comparatively higher PER and ANPU values were recorded in the feeding schedules II to VI than for the control (T-I). As shown in Table 6.4, apparent net lipid utilisation (ANLU) and apparent net energy utilisation (ANEU) also did not differ significantly ($P > 0.05$) between groups.

In phase II, feeding schedule II displayed considerable changes in PER, ANPU, ANLU and ANEU value in comparison to phase I (Figure 6.3; Table 6.3 and Table 6.4). PER and ANPU of *Clarias gariepinus* in the overall experimental period (weeks 0 - 8) are presented in Table

6.5 and graphically in Figure 6.3. PER and ANPU did not differ significantly (P > 0.05) among groups. However, slightly higher PER and ANPU values were observed in the for feeding schedule V (R3 + A4). As shown in Table 6.5, ANLU and ANEU did not show significant differences (P > 0.05).

6.3.3 Whole Body Carcass Composition

Whole body composition at the end of phase I (weeks 0 - 4), the termination of experiment (weeks 0 - 8) and in initial samples are presented in Table 6.6. After 4 weeks body moisture content in feeding schedule II was significantly higher (P < 0.05) than for feeding schedule I (control), but no significant differences (P > 0.05) were found between other groups. Body lipid content for group I (control) was significantly higher (P < 0.05) compared to feeding schedules II, IV and VI. Whole body protein and whole body ash content did not differ significantly (P > 0.05) among groups (Table 6.6).

After 8-week whole body composition of fish fed treatments II to VI did not vary significantly (P > 0.05) in comparison to the control (T-I). Body moisture and body lipid content did not show significant differences (P > 0.05) between groups. Similarly, whole body protein and whole body ash content did not differ significantly (P > 0.05) between feeding schedule groups (Table 6.6).

At the end of the experiment (weeks 0 - 8) whole body moisture and whole body lipid content in treatment I (control) and treatment, III to VI did not show notable changes while treatment II displayed a marked changes in comparison to phase I (weeks 0 - 4) (Table 6.6).

Table 6.6 Whole body carcass composition of *Clarias gariepinus* (% mean wet wt. basis) fed mixed feeding schedules at the middle and the end of the experiment

Feeding schedules															
Sampling time		Sampling time end of 4th week Middle of the experiment (0 – 4 week)							Sampling time end of 8th week End of the experiment (0- 8 week)						
Treatments	Initial	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters (%)															
Moisture	74.03	71.79[a] ± 0.59	74.80[b] ± 1.01	73.15[ab] ± 0.95	74.00[b] ± 1.27	72.89[ab] ± 0.98	73.79[ab] ± 1.93	0.24	70.95[a] ± 1.55	71.30[a] ± 1.57	71.93[a] ± 1.53	72.17[a] ± 1.15	71.97[a] ± 0.87	71.26[a] ± 1.74	0.23
Crude Protein	15.63	15.91[a] ± 0.58	15.70[a] ± 0.50	15.70[a] ± 0.36	15.96[a] ± 0.76	15.81[a] ± 0.42	16.36[a] ± 1.14	0.11	16.71[a] ± 1.11	15.99[a] ± 0.85	16.05[a] ± 0.65	15.18[a] ± 0.87	16.07[a] ± 0.80	15.90[a] ± 0.86	0.14
Crude Lipid	7.84	9.33[b] ± 0.85	6.36[a] ± 0.93	8.11[ab] ± 0.93	6.96[a] ± 0.92	8.35[ab] ± 1.25	6.61[a] ± 1.85	0.26	9.21[a] ± 1.47	9.49[a] ± 1.37	8.73[a] ± 1.98	8.95[a] ± 1.40	8.86[a] ± 1.01	9.71[a] ± 1.51	0.24
Ash	2.50	2.98[a] ± 0.25	3.13[a] ± 0.19	3.04[a] ± 0.17	3.08[a] ± 0.20	2.96[a] ± 0.24	3.25[a] ± 0.19	0.04	3.13[a] ± 0.40	3.213[a] ± 0.29	3.30[a] ± 0.48	3.08[a] ± 0.17	3.11[a] ± 0.25	3.14[a] ± 0.21	0.05

Note: Degree of freedom (d. f) is 5, 35. Values are means ± SD of six replicates. Means in the same row in the same block having different superscripts are significantly different ($P < 0.05$) and value in the same row in the same block with same superscript are not significantly different ($P > 0.05$)

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

6.3.4 Organ Indices

Eviscerosomatic index (EVSI), viscerosomatic index (VSI) and hepatosomatic index (HSI) data at the end of phase I (weeks 0 - 4), at the termination of whole experiment (weeks 0 - 8) and in initial sample are presented in Table 6.7. EVSI did not vary with feeding schedules (T-I to T-VI) ($P > 0.05$). Significantly the lowest ($P < 0.05$) VSI was observed for feeding schedule II but no significant differences ($P > 0.05$) were found between the control (T-I) and other feeding schedules (T-III to T-VI). Treatment II had insignificantly ($P > 0.05$) lower HSI compared to the control and the other groups (Table 6.7).

At the end of the experiment (weeks 0 - 8) EVSI and VSI values did not differ significantly ($P > 0.05$) whereas a significantly lower ($P < 0.05$) HSI was observed for feeding schedule I (Table 6.7).

6.3.5 Eviscerated Carcass Composition

Eviscerated (EV) carcass composition data for fish in initial samples, at the end of phase I and at the termination of experiment are summarised in Table 6.8. After phase I all treatment groups exhibited a higher percentage of lipid and a lower percentage of moisture content in comparison to the initial sample. Moisture content did not vary significantly ($P > 0.05$). Significantly the lowest ($P < 0.05$) lipid content was observed for feeding schedule II in comparison with other feeding schedules. No significant differences ($P > 0.05$) in protein and ash contents were recorded (Table 6.8).

Table 6.7 Organ indices: eviscerosomatic index (EVSI), viscerosomatic index (VSI) and hepatosomatic index (HSI) of *Clarias gariepinus* fed mixed feeding schedules at the middle and the end of the experiment

Feeding schedules															
		Sampling time end of 4th week Middle of the experiment (0 – 4 week)							Sampling times (end of 8th week)) End of the experiment (0- 8 week)						
Treatments	Initial	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters (%)															
EVSI	92.59	91.63^{a} ± 0.87	92.39^{a} ± 1.05	91.13^{a} ± 0.64	90.87^{a} ± 1.15	90.43^{a} ± 1.06	91.06^{a} ± 1.48	0.20	91.29^{a} ± 1.94	91.84^{a} ± 1.31	91.39^{a} ± 1.96	91.26^{a} ± 2.05	91.22^{a} ± 3.04	90.59^{a} ± 0.97	0.31
VSI	6.11	6.94^{b} ± 1.08	5.54^{a} ± 0.74	7.09^{ab} ± 0.67	7.98^{b} ± 1.19	7.54^{b} ± 1.20	7.79^{b} ± 0.99	0.21	7.52^{a} ± 1.53	6.59^{a} ± 0.93	7.80^{a} ± 1.85	7.69^{a} ± 2.15	8.21^{a} ± 1.13	8.13^{a} ± 1.13	0.25
HSI	0.79	1.14^{ab} ± 0.21	0.76^{a} ± 0.17	1.13^{ab} ± 0.24	1.24^{b} ± 0.18	1.20^{b} ± 0.27	1.15^{ab} ± 0.31	0.0.5	1.21^{a} ± 0.31	1.26^{ab} ± 0.19	1.31^{ab} ± 0.20	1.43^{ab} ± 0.18	1.45^{ab} ± 0.08	1.62^{b} ± 0.29	0.04

Note: Degree of freedom (d. f) is 5, 35. Values are means ± SD of six replicates. Means in the same row in the same block having different superscripts are significantly different ($P < 0.05$) and value in the same row in the same block with same superscript are not significantly different ($P > 0.05$)

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

Table 6.8 Eviscerated carcass (Landscap Table)

Blank

At the end of the experiment (weeks 0 - 8) the EV carcass composition in respect of moisture, protein, lipid and ash content did not vary significantly (P > 0.05) between feeding schedules. Moisture and lipid contents in treatment I (control) and treatment III to VI did not show notable changes while treatments II showed considerable changes in comparison to phase I (weeks 0 - 4) (Table 6.8).

6.3.6 Viscera Composition

Viscera composition in initial sample, at the end of phase I (weeks 0- 4) and at the termination of the experiment (weeks 0- 8) are shown in Table 6.9. After 4 weeks moisture and lipid content did not show significant differences (P > 0.05) among feeding schedules. However, comparatively lower lipid content was found for feeding schedule II that was accompanied by highest moisture content. Protein content also did not show significant differences (P > 0.05) among groups (Table 6.9).

After 8-weeks it was found that water, lipid and protein content did not vary significantly (P > 0.05) among feeding schedules. At the termination of the experiment (weeks 0 - 8) moisture and lipid contents in treatment I (control) and treatments III to VI were similar while treatment II displayed an increase in comparison to phase I (weeks 0 - 4) (Table 6.9).

Table 6.9 Viscera composition of *Clarias gariepinus* (% mean wet wt. basis) fed mixed feeding schedules at the middle and the end of the experiment

Feeding schedules															
		Sampling time end of 4th week Middle of the experiment (0 – 4 week)							Sampling time end of 8th week End of the experiment (0- 8 week)						
Treatments	Initial	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters (%)															
Moisture	58.52	51.95 ± 4.54	63.08 ± 9.09	58.62 ± 4.11	61.42 ± 8.24	61.00 ± 7.35	57.77 ± 4.44	1.25	53.68 ± 8.01	54.21 ± 5.45	55.76 ± 9.94	59.49 ± 5.93	60.74 ± 6.91	58.37 ± 1.48	1.26
Crude Protein	20.75	18.84 ± 7.88	15.69 ± 8.71	15.29 ± 5.90	13.39 ± 6.60	12.71 ± 5.94	12.64 ± 4.77	1.11	17.07 ± 8.86	16.30 ± 6.06	17.79 ± 8.40	17.30 ± 3.54	13.20 ± 7.15	13.05 ± 4.15	1.13
Crude Lipid	17.96	19.20 ± 9.44	14.11 ± 8.28	18.89[a] ± 6.86	18.28 ± 5.12	19.65 ± 5.95	21.66 ± 6.92	1.53	20.27 ± 7.63	21.07 ± 6.34	18.60 ± 5.32	18.86 ± 2.77	17.95 ± 8.26	21.71 ± 6.10	0.17

Note: The degree of freedom (d. f) is 5, 35. Values are mean ± SD of six replicates. Mean in the sane row in the same block with no superscript are not significantly different ($P > 0.05$).

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

6.3.7 Liver Composition

Data on liver composition of fish in an initial sample, at the end of phase I (weeks 0 -4) and at the termination of the experiment (weeks 0 - 8) are presented in Table 6.10. At the end of 1st phase liver moisture content did not show significant differences (P > 0.05) between groups. Significantly the lowest (P < 0.05) liver lipid content was shown in feeding schedule II in comparison with feeding schedule I (control) whereas no significant differences (P > 0.05) were seen among other groups. Liver protein did not differ significantly (P > 0.05) among feeding schedules.

At the end of the experiment (weeks 0 - 8) liver moisture did not differ significantly (P > 0.0.5). At the end of the experiment liver moisture and lipid contents in treatment I (control) and treatments III to VI did not show notable changes while treatment II showed considerable changes in comparison to phase I (weeks 0 - 4) (Table 6.10).

Table 6.10 Liver composition of *Clarias gariepinus* (% mean wet wt. basis) maintained mixed feeding schedules at the middle and at the end of the experiment

		Sampling time end of 4th week Middle of the experiment (0 – 4 week)							Sampling time end of 8th week End of the experiment (0- 8 week)						
Treatments	Initial	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM	T-I	T-II	T-III	T-IV	T-V	T-VI	± SEM
Parameters (%)															
Moisture	63.67	64.72[a] ± 4.55	66.66[a] ± 2.14	66.11[a] ± 2.11	65.00[a] ± 3.17	65.29[a] ± 1.88	65.23[a] ± 3.11	0.47	63.79[a] ± 3.87	65.28[a] ± 1.84	66.29[a] ± 3.82	64.71[a] ± 1.39	66.07[a] ± 1.61	66.20[a] ± 1.62	0.43
Crude Protein	14.55	10.56[a] ± 2.32	11.48[a] ± 2.02	11.94[a] ± 1.20	11.50[a] ± 1.51	11.44[a] ± 1.17	12.34[a] ± 1.87	0.28	11.14[a] ± 3.36	10.23[a] ± 2.15	10.06[a] ± 2.66	10.65[a] ± 1.95	9.69[a] ± 1.52	9.46[a] ± 1.53	0.37
Crude Lipid	14.09	11.58[b] ± 1.15	7.59[a] ± 2.06	9.99[ab] ± 2.09	8.97[ab] ± 2.49	8.91[ab] ± 1.39	8.60[ab] ± 1.96	0.40	10.07[a] ± 2.61	10.38[a] ± 3.28	8.63[a] ± 3.22	8.85[a] ± 1.89	9.30[a] ± 2.46	7.03[a] ± 1.01	0.43

Note: The degree of freedom (d. f) is 5, 35. Values are mean ± SD of six replicates. Mean in the same row in the same block having different superscript are significantly ($P < 0.05$) different and means in the same row in the same block with same superscript are not significantly different ($P > 0.05$).

The treatments (feeding schedules) were viz., T-I (control), T-II, T-III, T-IV, T-V and T-VI refers A56, R28 + 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.

6.4 DISCUSSION

6.4.1 Growth Performance and Feed Efficiency

The results of the current study demonstrate that the length of restricted feeding and subsequent appetite feeding periods influenced growth performance and feed efficiency in African catfish, *Clarias gariepinus*. Unsurprisingly during phase I, significantly the highest and lowest growth rates in terms of final body weight, % weight gain and SGR were observed in fish fed either to appetite (A28 + 0) or a restricted ration (R28 + 0) respectively. Groups III to VI, fish fed alternate periods restricted and appetite feeding, showed partial growth recovery. However, they did not fully compensate since these groups showed significantly lower growth rates than the control fed to appetite throughout (Table 6.3). Thus, it might be suggested that the 4-week period was not sufficient to induce any marked compensatory growth response in *Clarias gariepinus*. It has been reported that the hyperphagic response and compensatory growth are dependent upon the severity and duration of feed restriction (Jobling *et al.,* 1993; Jobling and Koskela, 1996).

During phase II (weeks 4 - 8) fish fed feeding schedule II (that had suffered the greatest growth deprivation during 4 weeks feed restriction in phase I) became hyperphagic and the previously restricted feeding fish displayed markedly greater growth rates (Table 6.4, Figure 6.1 and Figure 6.2). This type of growth response is generally referred to as compensatory or catch-up growth as has been described previously for a variety of fish species and hyperphagia is often observed during the period of compensation (Dobson and Holmes, 1984; Miglavs and Jobling, 1989a; Jobling *et al.,* 1993; Russell and Wootton, 1994; Jobling *et al.,* 1994; Jobling and Koskela, 1996; Saether and Jobling, 1999). The physiological background to the response is not fully understood. The next major compensatory growth responses were for feeding schedule V (R3 + A4). Growth responses following a period of feed restriction may be more variable, possibly because of the inequalities that arise within groups (McCarthy *et al.,* 1992; Jobling and Koskela, 1996; Damsgaard *et al.,* 1997). Jobling and Koskela (1996) reported that compensatory growth responses were higher in those rainbow trout that had suffered the greatest growth deprivation during a period of feed restriction.

By the end of the experiment (weeks 0 - 8) partial growth recovery (in terms of final weight, % weight gain and SGR) was observed influenced by the length of restricted feeding and subsequent appetite feeding periods applied (Table 6.5 and Figure 6.2). Fish fed schedule II (R28 + A28) and III (R14 + A14) with relatively longer alternating periods of feeding grew more slowly than fish fed shorter cycles or the control. The differences between these groups are illustrated in different patterns of partial compensation of growth response. The results for *Clarias gariepinus* in this study are similar to those in Arctic charr, where alternating periods of feeding restricted and satiation rations did not induce complete compensatory growth in a 16-week experimental period (Miglavs and Jobling, 1989a,b). These authors concluded that the restricted – satiation feeding regime employed did not have any beneficial effect with regard to energetic efficiency or growth improvement. In contrast other studies reported for Atlantic cod, *Gadus morhua* L., and Arctic charr, *Salvelinus alpinus* L., that deprivation periods of up to 3 weeks in duration were not sufficient to induce compensatory growth (Jobling *et al.,* 1993; Jobling *et al.,* 1994). In these latter studies, Atlantic cod and Arctic charr were returned to adequate feeding conditions following 8 weeks and 24 weeks respectively of restricted feeding. This return to adequate feeding gave rise to a compensatory growth response, with the degree of compensation being directly related to the severity and duration of the food restriction previously imposed (Jobling *et al.*, 1993; Jobling *et al.,* 1994). Thus, larger fish may require longer periods of feeding restriction before the ‘nutritional stress’ becomes sufficiently severe to induce a compensatory growth response.

The findings of the current study with *Clarias gariepinus* also provide evidence that there might be complete recovery of growth response. In other words, *Clarias gariepinus* may have displayed a complete, rather than a partial, compensatory growth response if the duration of appetite feeding was applied for longer. Complete compensation of growth has been reported in red porgy, *Pagrus pagrus* L. which were fasted for 7, 14 or 28 days followed by full feeding of 84, 77 and 63 days respectively (Rueda *et al.*, 1998). The rapidly growing *Clarias gariepinus* on more severe feed restriction or under-nutrition may lead to increased aggressiveness and social interaction which may result in fish being unable to fully recover body weight, but tending to show a partial compensatory response.

Partial compensation for a previous period of food restriction can be said to have occurred when an animal display more rapid rates of weight gain than the controls when the feed restriction is removed but does not manage to fully restore body weight to the same levels as the control individuals. Partial compensation is the response most often recorded in both domestic animals (Wilson and Osbourn, 1960; O'Donovan, 1984;) and fish (Weatherley and Gill, 1981, 1987; Miglavs and Jobling 1989a; Jobling *et al.*, 1993; Jobling *et al.*, 1994), although complete compensation has previously been recorded in some studies carried out on fish (Bilton and Robins, 1973; Dobson and Holmes, 1984; Quinton and Blake, 1990; Rueda *et al.*, 1998; Saether and Jobling 1999).

The present experiment appears to disagree with the results reported by Bilton and Robins (1973) and Dobson and Holmes (1984) where salmonids showed marked improvement in growth efficiency during periods of recovery from feeding restriction or under nutrition. Bilton and Robins (1973) also found that sockeye salmon fry, *Oncorhynchus nerka* were capable of showing full recovery growth following 3 weeks, but not following longer periods, of restriction. In a similar experiment Dobson and Holmes (1984) reported that alternating 3-week periods of restriction and feeding in rainbow trout, *Orcorhynchus mykiss* resulted in the production of larger fish than did a continuous feeding regime.

Similarly, the findings of this study also appear to differ from some other studies reported for fish (Wieser *et al.,* 1992; Russell and Wootton, 1992) and homeotherms (Plavnik and Hurwitz, 1985; Jones and Farrell, 1992). In these cases the feed restriction periods ranged between a few days and 2 - 3 weeks and were shown to be sufficient to induce a compensatory growth response. Most studies have, however, been carried out on the young, rapidly growing stages of fish and domestic animals in which a restriction of food supply of short duration may impose the 'nutritional stress' required to induce a compensatory growth response. To what extent animals show complete or partial recovery following return from restricted to appetite feeding seems to depend upon the age at which the restriction is applied, and upon the severity and duration of restricted feeding (Summers *et al*., 1990; Yu *et al*., 1990; Leeson *et al.,* 1991; Jones and Farrell, 1992; Jobling *et al.,* 1993; Jobling *et al.,* 1994).

In restricted groups, reduction of food supply usually results in greater increase in CV of final weight. However, this differs from the results of the present study. There was little evidence that *Clarias gariepinus* showed any change in CV with respect to the imposition of different feeding cycles. This is in marked contrast to observations made on rainbow trout, *Oncorhynchus mykiss* (Walbaum) where restricted feeding led to an increase in inter-individual variations in feeding that persisted over time, and this resulted in highly disparate growth amongst fish held on reduced rations (Jobling and Koskela, 1996). Depensatory growth is common among many fish species (Davis and Olla, 1987; Grant, 1993; Jobling, 1995) when groups of fish are subjected to alternating periods of restricted and appetite feeding. It is thought to be the result of dominant individuals consuming more food and growing faster. These inequalities result in an increase in variation in size with time. The results of the above studies appear contradictory to those of the present findings with African catfish, *Clarias gariepinus*.

During phase II (weeks 4 - 8) fish in treatment group II to VI showed a degree of compensatory growth resulting in improved FCE in comparison with phase I (weeks 0 - 4). Changing fish from restricted to appetite feeding increased feed consumption and fish became hyperphagic to their counterparts fed to appetite throughout (control). Thus, compensatory growth was accompanied by a high rate of food intake and the hyperphagic response was of major importance in permitting the growth spurt shown by these fish. *Clarias gariepinus* showing partial compensatory growth at the termination of the experiment (weeks 0 - 8) displayed better food conversion efficiency (FCE) in comparison to feeding to appetite throughout (Table 6.5). In periods following transfer from restricted to appetite feeding, metabolic rates may not re-adapt to high levels of food immediately, but low rates of energy expenditure might be maintained for a short time. Low metabolic expenditure during the period of recovery would ensure greater growth per unit food intake than observed in control individuals. In other words, greater energetic efficiency would occur during recovery resulting in improved FCE. Improved food conversion efficiency (FCE) has been reported for some mammalian species during recovery from nutritional restriction (Szepsi and Epstein, 1976; Ozelci *et al.*, 1978; Williams and Sheedy, 1987). 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, but this was only evident for a short period following the transfer from restricted to satiation feeding. Dobson and Holmes

(1984) and Bilton and Robins (1973) have suggest that salmonid fishes also show improved food conversion efficiency (FCE) during recovery from a period of starvation.

6.4.2 Apparent Nutrient and Energy Utilisation

Fish fed shorter alternating schedules (groups V and VI) in phase I (weeks 0 - 4) showed comparatively better PER and ANPU whereas in phase II (weeks 4 - 8) groups II to VI displayed improved PER and ANPU compared to fish fed to appetite throughout (control). Over the 8-week experimental period fish fed alternating feeding schedules exhibited higher PER and ANPU than the control. This may be due to the low metabolic expenditure, which possibly occurred during the period of recovery.

During phase I (weeks 0 – 4) feeding schedule II displayed marked decreases in ANLU and ANEU (Table 6.3). Miglavs and Jobling (1989b) reported that the weight gained in Arctic charr fed on a restricted feeding regime for 8 weeks throughout was in the form of comparatively low-energy carcass tissue comprised mostly of moisture and protein, whilst there was a decrease in high-energy lipid stores. Thus, FCE was relatively higher during the period of food restriction but ANEU was poor. During phase II ANLU and ANEU were higher in the alternating schedule groups than the control. Over the 8-week experimental period fish fed alternating feeding schedules exhibited greater lipid (ANLU) and energy (ANEU) utilisation than the control. This enhanced nutrient and energy utilisation efficiency probably was due to greater energetic efficiency, which would have occurred during recovery, resulting in improved growth rates. However, comparable results on nutrient and energy utilisation efficiency of fish species with similar alternating feeding with respect to compensatory growth are currently very limited.

6.4.3 Whole Body Carcass Composition

Fish fed alternating schedules contained less fat (and more water) after 4 weeks, especially fish fed a restricted ration for 4 weeks (treatment II). During periods of restricted feeding, fish utilise stored energy supplies for metabolic processes. After 8 weeks fish fed alternating schedules showed similar whole body lipid and whole body water to the control. There was thus no indication, especially in treatment II, that growth compensation involved just fat or water deposition.

The results obtained in this study are similar to those reported from previous experiments in which fish were fed alternating periods of food restriction or deprivation and re-feeding. Quinton and Blake (1990) showed that carcass lipid decreased and moisture increased in rainbow trout after 3 weeks starvation. They suggested that in short-time starvation visceral fats and muscle fats are utilised as the energy source (Parker and Vanstone, 1966; Smith, 1981; Weatherly and Gill, 1981) and replacement of the muscle lipids with water occurs (Idler and Bitterns, 1959). After 6 weeks they observed that there were no significant differences between alternating periods restricted feeding and feeding continuously throughout. 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 did not vary much at either 4 or 8 weeks. Phillips *et al.*, (1960) reported that whole body protein levels in brook trout *Salvelinis 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. Similar results were reported for white sturgeon *Acipenser transmontanus* (Hung *et al.*, 1997). Whole body ash also did not vary after 4 or 8 weeks compared to the control. Quinton and Blake (1990) also reported that alternating bouts of 3 weeks fasting and 3 weeks feeding in rainbow trout showed compensatory growth and resulted in no significant differences in body protein and body ash content in comparison to continuously fed control fish.

6.4.4 Organ Indices

After 4 weeks the eviscerosomatic index (EVSI) of fish fed alternating schedules was reduced whereas treatment II showed an increase compared to the control. After 8 weeks, EVSI values were similar to continuously fed fish (control). In contrast, Miglavs and Jobling (1989b) reported that 8 weeks fasting in Arctic charr resulted in a reduction in EVSI compared to feeding continuously throughout. However, after 16 weeks, by the end of the experiment, they found that the EVSI values were similar to those of continuously fed controls.

After 4 weeks the VSI and HSI of fish fed alternating schedules increased whilst treatment II showed reduced values compared to the control. After 8 weeks VSI and HSI values in fish fed different feeding schedules were similar to those of continuously fed controls. This observation is in accordance with observations in several fish species (Weatherley and Gill, 1987; Miglavs and Jobling, 1989b; Collins and Anderson, 1995; Rueda *et al.*, 1998).

6.4.5 Eviscerated Carcass Composition

Starvation or restricted feeding generally leads to a reduction in the percentage lipid content and an increase in the water content of fish tissue (Jobling, 1980; Love, 1980; Black and Love, 1986). The major body lipid may be located in eviscerated carcass (muscle) tissue (Miglavs and Jobling, 1989b). In the present study at 4 weeks fish fed-alternating schedules exhibited reduced fat and increased water in comparison to the control. This reduction in EV lipid was higher in group II. This might be due to short-term restriction of feeding when muscle fat is used as the energy source (Weatherley and Gill, 1981) and replacement of the muscle fats with water occurs (Idler and Bitterns, 1959). After 8 weeks the lipid and water content of eviscerated carcasses of fish mixed schedules were similar to the control. The growth occurring during the 'rapid growth phase' of compensatory growth appears to be due to protein synthesis, not just increase in fat deposition or water uptake.

The EV protein and EV ash in fish groups fed mixed feeding schedules were similar to the control group after 4 weeks and after 8 weeks. Similar observations for body protein have been reported in eviscerated carcass composition for Arctic charr fed alternating fasting and re-feeding for 16 weeks (Miglavs and Jobling, 1989b).

6.4.6 Viscera Composition

After 4 weeks fish fed schedule II (restricted ration) showed reduced visceral lipid. Probably because in short-term restricted feeding, visceral fats are utilised as the principal energy source (Smith, 1981; Weatherley and Gill, 1981) and replacement of the viscera fat component with water occurs (Idler and Bitterns, 1959). After 8 weeks, at the end of the study, visceral fat in fish fed alternating feeding schedules showed similar values to the control (Table 6.9). Love (1980) and Weatherley and Gill (1987) also 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.

6.4.7 Liver Composition

Similarly to viscera composition, after 4 weeks fish fed alternating schedules showed a decrease in liver lipid and increased in liver moisture percentage in comparison with the control group for the reasons stated previously. After 8 weeks the difference was no longer detectable. Similar observations have been reported in liver lipid and liver water composition for Arctic charr during alternating feeding to fasting and re-feeding for 16 weeks periods (Miglavs and Jobling, 1989b).

In conclusion, African catfish, *Clarias gariepinus* display a partial compensatory growth response. These observations also suggest that alternating days of restricted and appetite such as schedule V (R3 + A4) would be a plausible way to maintain good growth and reduce feed input cost.