COMPENSATORY GROWTH IN MOZAMBIQUE TILAPIA (*Oreochromis mossambicus*), FED A SUB–OPTIMAL DIET

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Summary

Mozambique tilapia, *Oreochromis mossambicus*, held in 30‰ seawater and at 29–30 °C, were divided into four groups (n = 50/group in replicate), and given one of four feed cycles: 1) control, with continuous feedind, 2) 5:5, 3) 10:10 and 4) 15:15, wherein fish were subjected to starvation and subsequent refeeding cycles of 5, 10 and 15 days respectively. All animals were fed a commercial diet containing 18.4% protein, 6.7% lipid, 58.6% carbohydrate and 7.2% ash, over a 60 day trial period. Growth compensation was observed in the feed cycled groups as increased (P<0.03) weight specific growth rates during refeeding. However, feed cycled groups were unable to achieve the weghts of control fish. Starvation reduced (P<0.01) haematocrit values when compared to control levels and, in the 15:15 cycled groups, elevated the testicular index (P<0.02). The results are considered with respect to the commercial application of compensatory growth during production of tilapia.

Key words: feed cycling, protein, tilapia, growth

INTRODUCTION

Over the past two decades global aquaculture has experienced a rapid expansion, by quantity, and since 1984 it has had an average annual increase of almost 10% compared with for terrestrial livestock and 1.6% for capture fisheries production. By 1992 global aquaculture contributed 23% of total world aquatic production of which more than 90% was acounted for by Asia (N e w and C s a v a s, 1995). Consensus indicates that the aquaculture sector will continue to grow, although it is likely that the rate of growth will

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eventually decline, as resources and markets become progressively saturated, and opportunities for expansion restricted. However, it is anticipated that growth in total aquaculture production will come from improving yields and operational efficiencies, and the trend towards intensification will continue in many parts of the sector. Global aquaculture is dominated by finfish culture, accounting for more than of production, by weight and value (FAO, 1992). The vast production of finfish isw situated in underdeveloped nations. On the cultured finfish species in these areas, 97% are non–carnivorous, with the most important species being cyprinidis, tilapias and milkfish (FAO, 1992).

The curent finfish culture systems in Asia consist mainly of extensive or semi–intensive ponds, with little or no supplementary fertilisation of feeding. These systems are thus at least partially dependent upon natural food (Yakupitiyage, 1993). In Asia in particular, the aquaculture industry is embarking on an increasing phase of intensification. This has been driven by multitude of economic forces, amongst which are an increasing need for even the small–scale farmer to transform from subsistence aquaculture to an income generating enteprise (De Silva, 1993). However, with an expected intensification of culture systems the use of supplementary feeding will become inevitable and increased costs of production along with environmental impacts must be evaluated for sustainability. The people most in need of supplemental aquafeeds for intensifying their culture operations are generally resource–poor farmers and their use of formulated feed will mainly be dependent upon the availability of feed ingredients (Yakupitiyage, 1993). A question that requires immediate attention is how to make best use of low quality feed ingredients available to resource–poor farmers.

As formulated feed for carnivorous species incorporates expensive high quality protein much research has been undertaken in the area of increasing feed utilisation. During the past two decades numerous studies have found that depriving certain temperate carnivorous species of food for several days, or even every alternate week, the refeeding to satiation, can result in little growth loss e. g. Arctic charr (Miglavs and Jobling, 1989), or no growth loss e. g., rainbow trout (Dobson and Holmes, 1984) when compared to fish fed daily to satiation. This phenomenon is termed 'compensatory growth' and it is defined as a phase of rapid growth, following a period of starvation. That is, compensatory growth is greater than control growth rates associated with continuous satiation feeding (Paul et al., 1995). The physiological basis of compensatory growth is incompletely understood but starved–refed animals may become hyperphagic and/or improve food conversion efficiency compared with animals reared continuously on liberal feeding regimes (Miglavs and Jobling, 1989). The improved food utilisation is an aspect frequently highlighted in studies of compensatory growth, and is often used to argue in favour of the exploitation of the response in the production of fish and domestic animals (Jobling et. al., 1994).

Compensatory growth responses have been reported in juvenile cyprinids at sub–tropical temperature fed artemia or enchytraeids (W e i s e r *et al.*, 1992; R u s s e l l and W o o t t o n, 1992). Thus, the phenomenon has been demonstrated in several species under both temperature and sub–tropical temperature. L u n q u e t *et al.* (1995), observed elevated specific growth rates with feed cycled African catfish upon satiation feeding, following a period food restriction. However, no study has examined compensatory growth, by applying a starvation/satiation feed cycle, in a species under tropical conditions. Accordingly the main objective of the present research was to determine whether tilapia, *Oreochromis mossambicus*, possess compensatory growth mechanisms when subjected to feed cycling under tropical conditions. The effects of subjecting this species to feed cycles, of different duration, upon the overall growth performance were investigated.

MATERIALS AND METHODS

Source and initial acclimatisation of fish

Approximately 3000 tilapia (weight: 5–80 g), *Oreochromis mossambicus* (Peters), were obtained from earthern ponds administered by Hasanuddin University, Ujung Pandang, Sulawesi, Indonesia. Fish were not provided with supplemental feed and the tambaks were untertilised. Ponds were flooded by tidal action. Temperature and salinity at collection was 30 °C and 27‰ respectively. Fish were transported to a Marine Field Station sited at Barang Lompo (Spermonde Archipelago an area between 4°07 S–5°09 S and 118°55 E–119°37 E). During transportation, which lasted approximately 2 hours, salinity was increased to that of 100% sea water (30‰). Fish were held in two outdoor concrete tanks (1.5 m x 8.0 m x 1.0 m) which contained 10 m^3 of water per tank, at ambient photoperiod, temperature (29–30 °C), and salinity with 90% daily batch water exchange. Dissolved oxygen, total ammonia (TAN) and pH in inlet seawater was measured to 6.0–7.0 mg O_2/L (Tetra Oxygen Kit), 0.2 mg TAN/L (Merck Total Ammonia Kit) and pH 8.0 (Merck Acilit® and Alkalit®). Fish were hand fed a locally produced commercial diet (Table 1), once a day until experimental start.

Experimental protocol

Fish were subjected to one of feed cycles, over an experimental period of 60 days. The feed cycles consisted of deprivation and feeding periods of different duration:

— continuous feeding (control)
— five days deprivation, five days feeding (5:5)
— ten days deprivation, ten days feeding (10:10)
— fifteen days deprivation, fifteen days feeding (15:15)

Four hunderd fish of mixed sex were anaesthetised (benzocain, 10% solution dissolved in 96% ethanol, 0.5 ml/L water; Sigma) and weighed to the nearest 0.1 g (mean: 15.9±3.8 g). Total lenght was measured to the nearest 0.1 cm (mean 9.7±0.9 cm). Animals were randomly distributed into eight blue fiberglass tanks (1.5 m x 1.2 m x 0.6 m) containing a water volume of approximately 0.8 m^3. Two tanks of fish were randomly allocated to each feed cycle by drawing of lots. Tanks were covered with fishing net (mesh size: 50 mm) and placed outdoors under a roof. Thus tanks were constantly in shade during hours of dayling. During periods of feeding, fish were hand fed *ad lib* three times a day (7.00 am, 12.00 am and 16.00 pm).

Water quality

Seawater was pumped to a header tank and filtered, through filter bags (retaining particles >10 µm), before entering experimental tanks, 90% water volume was exchanged once daily before noon to prevent algal blooms. Aeration of tanks was conducted by means of a blower (Sweetwater®, diaphragm type, RA–L70). Oxygen concentrations ranged from 2.0–6.0 mg O_2/L. Temperature range throughout the experiment was 28–30 °C, salinity 30–31‰, with no differences between experimental tanks. pH ranged between 7.5–8.5, TAN range 0.2–0.4 mg TAN/L, depending on feed cycle and time of day. Faecal matter and excess feed were siphoned from tanks twice daily (prior to morning and afternoon feeding).

Growth, haematocrit and somatic measurements and general observations

Fish were weighed (0.1 g) and measured (0.1 cm) every five days during the first 30 days. Thereafter, fish were measured at 15 day intervals. At each sampling, fry and eggs were removed and all tanks were thoroughly cleaned. Ten fish were removed from each tank at experimental end for haematocrit analyses. Following anaesthetisation the caudal peduncle was several and blood collected using microhaematocrit capillary tubes (I. D. 1.1–1.2 mm). Blood samples were immediately centrifuged (5 minutes at 5,000 rpm) and the division coinciding with the boundary line between red blood cell sediment and plasma recorded as haematocrit value in % volume (Sigma, Laborzentrifugen GmbH). All fish were deprived of food for two days post–termination of experiment. 20 fish from each tank were killed by anaesthetisation, dissected, and weight of liver, evacuated guts and gonads measured to the nearest 0.1 g. Sex was determined by visual inspection of gonads. Comparison of somatic indices for each sex according to feed cycles, is thus presented. Mortality was recorded daily. Feeding–, territorial— and breeding behaviour were recorded during periods of deprivation and refeeding and general observations made continuously.

Growth analyses

Average percentage changes in weight and lenght were calculated as:

$$\text{Average \% body weight change} = \frac{100 \cdot \left(\sum \frac{W_s - W_i}{W_i} \right)}{n}, \text{ (Quinton \& Blake, 1990)}$$

$$\text{Average \% body length change} = \frac{100 \cdot \left(\sum \frac{L_s - L_i}{L_i} \right)}{n}, \text{ (Quinton \& Blake, 1990)}$$

where W_s was sample weight, W_i initial weight, L_s sample lenght, L_i initial lenght and n the number of individual samples.

Specific growth rate (SGR) in weight and lenght were calculated as:

$$\text{SGR}_{\text{weight}} \left(\frac{\%}{\text{day}} \right) = 100 \cdot \left(\frac{\ln(W_2) - \ln(W_1)}{(t_2 - t_1)} \right), \text{ (Weatherly \& Gill, 1987)}$$

$$\text{SGR}_{\text{length}} \left(\frac{\%}{\text{day}} \right) = 100 \cdot \left(\frac{\ln(L_2) - \ln(L_1)}{(t_2 - t_1)} \right), \text{ (Weatherly \& Gill, 1987)}$$

where WMV was weight at time t_2, W_1 weight at time t_2, L_2 lenght at time t_2, L_1 lenght at time t_1.

Condition factor (CF) were calculated as:

$$CF = 100 \cdot \left(\frac{W}{L^3} \right), \text{ (Weatherley \& Gill, 1987)}$$

where W was weight (g) and L lenght (cm)

Somatic analyses

Hepato–(HSI), gastrointestinal–(GISI) and gonado–(GSI) somatic indices were calculated as:

$$\text{Somatic index (\% body weight)} = 100 \cdot \frac{\text{organ weight}}{\text{body weight}}, \text{ (McLean et al., 1994)}$$

where organ and body weight were measured wet weight.

Statistical analyse

The statistical analyses of growth, somatic and haematocrit data utilised SigmaStat computer packages (Jandel Scientific, version 1.0) for ANOVA and multiple comparison of means. Where significant differences were observed Student–Newman–Keul's procedure was used to determine multiple comparison of means. 95% confidence levels (P<0.05) were used unless otherwise stated.

Growth-, somatic— and haematocrit differences between the various experimental groups were compared by one way ANOVA, fixed effects model:

$$Y_{ij} = \mu + \tau_i + \varepsilon_{ij} (Montgomery, 1991)$$

Y_{ij} = actual observation

μ = overal mean

τ_i = treatment effect of ith treatment

ε_{ij} = random error component

RESULTS

The growth response of non–cycled and feed–cycled tilapia over the experimental period, on a percent body weight increase basis is summarised in Fig. 1. By day 5, weight increase was significantly higher for fish in the control group (3.5%) when compared to fish given feed cycling treatments (range: –4.8 to –5.1%). Control group fish maintained a significant weight advantage in terms of body weight increase throughout the experimential period when compared to feed cycled groups (Fig. 1.). Growth performance of tilapia was significantly impacted by feed cycling i. e. during periods of deprivations, fish lost body weight, and during refeeding, gained body weight. During refeeding periods fish were never able to recoup lost weight to achieve the size of controls.

By experimental end, significant differences in body weight gain were recorded when comparing fish from control groups with feed cycled groups and also amongst feed cycled groups (Table 2), with tilapia from the control group being heavier than animals subjected to feed cycling. Tilapia subjected to feed cycling regimes (10:10) and (15:15) were significantly heavier than tilapia from regime (5:5; Table 2). Weight SGR of tilapia from the control group varied little throughout the course of the 60 day experiment. However, within the first 15 days there was a slight increase, followed by a decrease over time. In contrast, SGRs of feed cycled fish displayed considerable changes
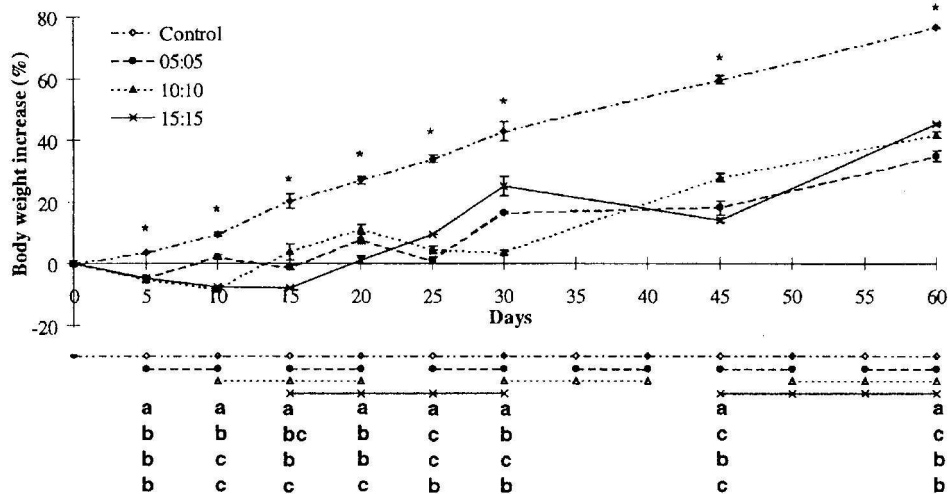
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Figure 1. Mean percent body weight increase at specific time points throughout
the experimental period for control and feed cycled groups. Bars represent
±SEM. Horizontal lines at the bottom of the figure represent periods of feeding.
Asterisks mark significant differences in weight at the P<0.01 level. Dissimilar
letters describe significant differences (P<0.05) between groups at specific time
points by Student–Newman–Keul's test. The letters are presented in relation to
the groups described in the key (i. e. top = control, bottom = 15:15).

Slika 1 Prosječni postotak porasta mase tilapija za vrijeme pokusa

depending upon food supply, with depressed growth during periods of food
deprivation returning negative SGRs. In marked contrast, following refeeding,
weight SGRs surpassed those of controls, at times by more than a factor 2
(Table 3).

Table 2 summarises the 60 day weight SGR response for each group. Peak
SGRs during periods of refeeding differed amongst feed cycled groups, with
peaks for (10: 10) being noted 5 days after refeeding followed by a decline 10
days after refeeding. The pattern of weight loss during food deprivations was
similar for all feed cycled groups, with greatest weight loss occurring during
the first 5 days of deprivation, followed by reduced rates of weight loss in
subsequent samplings (Fig. 1). Significant differences were observed in weight
SGR throughout the experimental period (Table 2). The weight SGRs during
periods of feeding and food deprivation over the first 30 days of experimen-
tation are presented in Table 3. SGRs during periods of feeding were
significantly higher for feed cycled groups than those of controls, with groups
(5:5) and (15:15) differing during food deprivation. Differences in lenght gain
amongst feed cycled tilapia were limited, even thought deprivation and feeding
sequences contrasted. Group (15:15) demonstrated a clear lenght–gain respon-
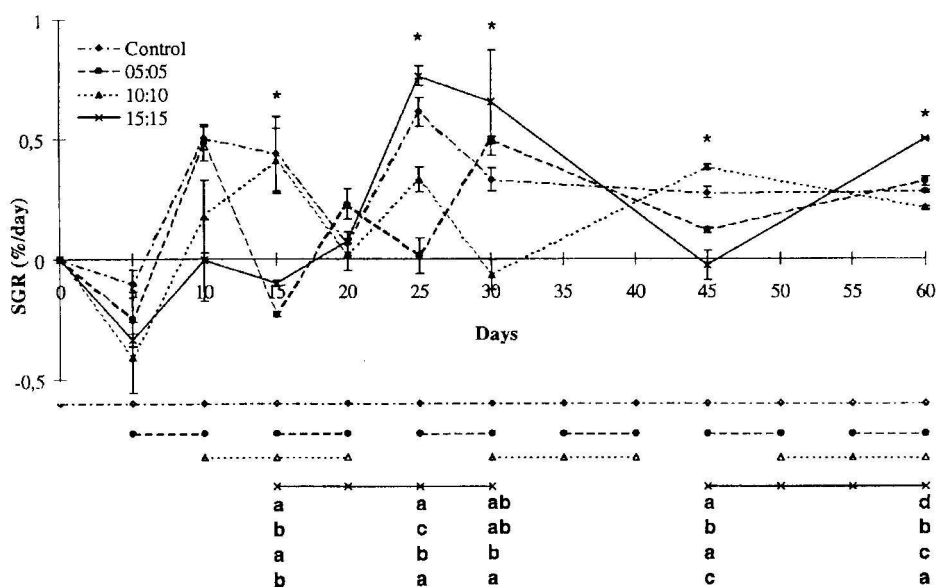
Figure 2. Mean specific growth rates (SGR%/day) related to lenght increase at each sampling interval during experimentation with control and feed cycled groups. Bars represent ±SEM. Horizontal lines at the bottom of the figure represent periods of feeding. Asterisks mark significant differences in weight at the P<0.01 level. Dissimilar letters describe significant differences (P<0.05) between groups at specific time points by Student–Newman–Keul's test. The letters are presented in relation to the groups described in the key (i. e. top = control, bottom = 15:15).

Slika 2 Prosječni specifični rast u odnosu na porast dužine za vrijeme pokusa

se–delay upon refeeding between day 15 and 20 (Fig. 2). An immediate lenght gain during the first 5 days of refeeding was recorded for (10:10), but by the 10th day of refeeding, this had regressed. By experiment end, the control group had a significantly greater body lenght increase than feed cycled groups (Table 2). No significant differences in lenght gain were recorded between feed cycled groups.

SGR in relation to lenght revealed that compensatory growth responses from feed cycling, in general, did not elevate growth rates significantly above those of controls during periods of refeeding. Positive lenght SGRs during periods of food deprivation were recorded, at times, for all feed cycled groups. However there were no specific patterns of occurrence i. e. positive SGRs were recorded both at the beginning and end of a deprivation period. At experimental end, after a period in which all groups had been feeding, no differences were recorded between feed cycled groups for lenght SGR (Table 2). From day 10 to 45 significant differences in CF values were observed (Table 4). During

Table 1. Chemical composition of experimental diet as percentage wet weight. Analyses were conducted on triplicate samples of feed. Protein concent was determined according to the Kjeldahl method (AOAC, 1975), lipid by chloroform–methanol extraction (B l i g h & D y e r, 1959). Dry weight and ash content were quantified following drying at 105 °C for 24 hours and incineration at 590 °C for 12 hours respectively. Carbohydrate level was calculated as: carbohydrates = dry matter–protein–lipid–ash.

Tablica 1 kemijski sastav pokusne hrane

	Dry matter [%]	Protein [%]	Lipid [%]	Ash [%]	Carbohydrates [%]	Pellet size [ø, mm]
Feed	90.9	18.4	6.7	7.2	58.6	6.0

Table 2. Mean±SEM percent body weight (% BW) and length (% BL) increase at experimental end for control and feed cycled groups (5:5), (10:10) and (15:15). SGR (%/day) values are calculated as an average for the entire study. Significance level denotes differences in responses to treatments. Different letters, in rows, indicate significant (P<0.05) differences between group means.

Tablica 2 Prosječni postotak porasta mase i dužine ribe za vrijeme pokusa

Indices	Treatment				Significance
	Control	5:5	10:10	15:15	level
% BW	76.4 ± 0.1^a	34.8 ± 1.7^c	41.8 ± 1.0^b	45.3 ± 0.4^b	P<0.01
% BL	19.2 ± 0.8^a	11.0 ± 0.2^b	11.9 ± 0.5^b	13.1 ± 0.2^b	P<0.01
$SGR_{weight,\ 0-60}$	0.95 ± 0.00^a	0.50 ± 0.02^d	0.58 ± 0.01^c	0.63 ± 0.01^b	P<0.01
$SGR_{len,\ 0-60}$	0.29 ± 0.01^a	0.18 ± 0.01^b	0.19 ± 0.01^b	0.21 ± 0.01^b	P<0.01

Table 3. Mean±SEM of average SGRs (%/day) related to weight in periods of feeding and non–feeding for the first 30 days of the study. Significance level denotes differences in responses to treatments. Different letters, in rows, indicate significant (P<0.05) differences between group means.

Tablica 3 Prosječni specifični rast (%/dan) u odnosu na masu

SGR_{weight} Days 0–30	Treatment				Significance
	Control	5:5	10:10	15:15	level
Feeding	1.19 ± 0.08^b	1.99 ± 0.13^1	1.95 ± 0.12^a	2.05 ± 0.20^a	P<0.03
Deprivation	–	-0.99 ± 0.15^1	-0.80 ± 0.03^{ab}	-0.56 ± 0.03^b	P<0.04

periods of food deprivation CFs generally decreased, and upon refeeding rose, often above initial levels. By the end of the experiment however, CFs were identical to those recorded for start values for all groups.

Haematocrit levels different among groups at experimental end (Table 5), with highest values being recorded for the control group and lowest in the (15:15) group. No differences in gastrointestinal, liver and female ganadsomatic indices were observed amongst treatments (Table 5). However a significant difference in male testicular gonadosomatic index was observed between groups, with group (15:15), (GSI of 0.85%) being higher than that of all others (range: 0.60–0.65%). Significant differences (P<0.03) were observed in morta-

Table 4. Mean±SEM for CF increase at each experimental date for control and feed cycled groups (5:5), (10:10) and (15:15). Significance level denotes differences in response to treatments. Different lettere, in rows, indicate significant (P<0.05) differences between group means.

Tablica 4 Prosječni porast faktora kondicije (CF)

| Day | Treatment | | | | Significance |
	Control	5:5	10:10	15:5	level
0	1.70±0.00	1.72±0.02	1.74±0.02	1.72±0.03	
5	1.78±0.01	1.69±0.01	1.75±0.02	1.72±0.03	
10	1.75±0.01[a]	1.69±0.02[b]	1.65±0.01[b]	1.66±0.00[b]	P<0.02
15	1.80±0.01[a]	1.69±0.01[b]	1.75±0.03[ab]	1.68±0.00[b]	P<0.02
20	1.89±0.01[a]	1.78±0.01[b]	1.88±0.01[a]	1.83±0.02[ab]	P<0.02
25	1.81±0.03[a]	1.67±0.01[b]	1.67±0.00[b]	1.77±0.00[b]	P<0.01
30	1.83±0.02[a]	1.78±0.00[a]	1.68±0.01[b]	1.83±0.01[a]	P<0.01
45	1.80±0.02[a]	1.71±0.02[b]	1.74±0.01[b]	1.69±0.00[b]	P<0.02
60	1.73±0.02	1.72±0.03	1.76±0.01	1.70±0.00	

Table 5. Mean±SEM hepato— (HSI), gastrointestinal— (GSI) and gonado— (GSI) somatic indices measured two days post–experimental end for control and feed cycled groups (5:5), (10:10) and (15:15). Values are given in percent body experiment. Haematocrit values were measured at experiment end and values were recorded as % volume. Significance level denotes differences in response to treatments. Different letters, in rows, indicate significant (P<0.05) differences between group means.

Tablica 5 Prosječni hepato–(HIS); gastrointestinalno–(GIS) i gonadosomatski (GSI) indeksi

| Day | Treatment | | | | Significance |
	Control	5:5	10:10	15:5	level
Haematocrit	76.9±0.7[a]	64.5±0.1[b]	64.1±0.3[b]	61.4±0.6[c]	(P<0.01)
GISI	3.55±0.15	3.50±0.40	3.95±0.25	3.80±0.20	
HIS female	2.15±0.15	3.50±0.40	3.95±0.25	3.80±0.20	
HIS male	1.95±0.15	1.90±0.10	1.85±0.15	2.20±0.50	
GSI female	1.75±0.65	2.25±0.55	2.75±1.05	1.35±0.35	
GSI male	0.60±0.00[b]	0.65±0.05[b]	0.60±0.00[b]	0.85±0.05[a]	(P<0.02)

lity rate between the (15:15) group (24%) and groups (5:5) (11%) and group (10:10) (10%). During periods of feeding a territorial behaviour was observed in all tanks. Males became darker, and defended corners of tanks from intruders. One male would usually dominate one tank corner and beneath him one or two presumed females would well on the tank botton. Males in corners were also aggressive during the first days after refeeding (i. e. dominant males ate first). However, this behaviour decrease over time, as long as ample feed was present. During periods of starvation territorial behaviour was reduced. Upon refeeding, feed cycled tilapia were observed to have an

elevated appetite compared to continuously fed fish over first 2–3 days. Thereafter appetite decreased and stabilised to that of control.

DISCUSSION

While the phenomenon of compensatory growth has been demonstrated in a number of temperate and sub–tropical fish, including salmonids (J o b l i n g and K o s k e l a, 1996; R e i m e r s et al., 1993; Q u i n t o n and B l a k e, 1990; S k i l b r e i, 1990; M i g l a v s and J o b l i n g, 1989), Alaska yellowfin sole (P a u l et al., 1995), cod (J o b l i n g et al., 1994) and cyprinidis (W e i s e r et al., 1992; R u s s e l l and W o o t t o n, 1992), the present study provides the first evidence for compensatory growth in a tropical species. Alternating periods of food deprivation with those of unlimited provision of food depressed the growth of tilapia, below that of continuously fed controls. These findings are in accordance with results obtained for three species of cyprinid, Leuciscus cephalus, Chalcalburnus chalcoides mento and Scardinius erythrophthalmus (W e i s e r et al., 1992), Artic charr, Salvelinus alpinus (J o b l i n g et al., 1993) and cod, Gadus morhua (J o b l i n g et al., 1994). However, the results contrast to the findings of R u s s e l l and W o o t t o n (1992) for the cyprinid, Phoxinus phoxinus.

Fish fed on a 15 day off–on regimen (15:15) were larger at experiment end than those exposed to cycles of 5–, or 10–days deprivation and feeding. A number of animal species adapt to food deprivation and reduced levels of energy intake by reducing metabolic expenditure, probablu via reductions in physical activity and basal metabolic rate (W i l s o n and O s b o u r n, 1960). It has been suggested that in the period following transfer from restricted to satiation feeding, metabolic rates may not re–adapt to high levels of food availabity immediately, but that low rates of energy expenditure may be maintained for a short time, even thought animals are not food restricted (M i g l a v s and J o b l i n g, 1989). In the present study this may have been the case for (15:15), resulting in animals utilising more energy for growth rather than for basal metabolism, with a concomitant increase in size.

The pattern of growth in the refeeding period of (15:15) indicated that one of the highest growth rates appeared during the last 5 days (Figure 2). This is in accordance with results obtained for feed cycled trout Q u i n t o n and B l a k e, 1990). These authors reported that the pattern of growth during refeeding favoured compensation during the last week of a 3 week feed cycling. One explanation for this phenomenon may be that metabolic changes which occur during starvation are restored to normal during the first period of refeeding, and once restored, growth occurs at a greater rate. In tilapia, weight losses, during periods of fasting, were however, never recouped, relative to that of controls, following feeding, irrespective of protocol employed. This

tendency has also been observed in temperate and sub-tropical species (P a u l
et al., 1995; W e i s e r et al. (1992).

Upon refeeding of three species of juvenile cyprinidis, W e i s e r et al.
(1992) observed that relative growth rates increased rapidly and that the peaks
of this increase were directly proportional to the lenght of the starvation
period. Observations of SGR peaks amongst feed cycled groups, upon refee-
ding, in the present study, did not indicate a proportionality in SGRs due to
the lenght of starvation. Interestingly average SGRs in feed cycled animals
during periods of feeding were approximately twice that of controls (Table 3),
indicating that food deprived tilapia undoubtedly express growth compensa-
tion.

The experimental animals inability to ingest pellets before they had been
softened by water, led to food being given in excess, to ensure maximum
intake. This procedure negated calculation of food conversion ratios. It was
observed that after refeeding, fish from feed cycled groups exibited hyperpha-
gia compared to continuously fed fish. However, hyperphagia was not sustai-
ned and ceased after a few days of refeeding. Similarly, R u s s e l l and
W o o t t o n (1992), found a decline in appetite of Phoxinus phoxinus after the
first day of refeeding which they explained by the effect of gut–filling.
R e i m e r s et al. (1993), found that starved salmon expressed higher SGRs
than controls following refeeding, even though identical rations were presen-
ted. This finding indicates that starved fish utilise feed more efficiently,
resulting in better growth rates for feed cycled animals when compared
controls. Food intake for cycled animals in the present experiment were
estimated to be a little over half than taken by controls. But during periods
of refeeding SGRs were twice as high for cycled groups compared to that of
controls. Thus, periods of food deprivation in tilapia improves food conversion
efficiencies, supporting the statement of Miglavs and Jobling (1989): 'Low
metabolic expenditure during a period of recovery would ensure greater growth
per unit food intake than observed in continuously fed control individuals; in
other words, greater energetic efficiency would occur during recovery resulting
in improved conversion efficiency in restricted–satiation animals'.

N o e l and L e B a i l (1997), highlighted the cyclic nature of growth in
rainbow trout. They found a short increase in SGR followed by a continuous
decrease. This was also noted in the present study for the continuously feed
cycled groups. In feed cycled fish however, SGR did not follow the control
pattern. Rather, SGRs oscillated between low and hight. As growth rates
decrease over time for continuously fed groups there may be chance for feed
cycled groups to 'catch–up' with controls althought this can only be ascertai-
ned with longer duration studies than that undertaken herein.

During the first 5 days of experimentation fish in all groups expressed
degrowth in lenght. This phenomenon may have resulted from a long term
food restriction prior to experimental start, causing a response delay in lenght
increment for the control group. This delay in lenght increase was also noted

in refeeding periods for (10:10) and (15:15). At times, experimental animals exhibited positive SGRs during periods of starvation and thereby increased skeletal lenght during starvation. This supports the findings of Quinton and Blake (1990) with rainbow trout, indicating preferential lenght growth during starvation. CF in feed cycled groups decreased during periods of starvation, mainly due to weight loss. During periods of refeeding CF rose significantly as a result of weight gain. This response was cyclid in feed cycled groups. Rao et al. (1987) found that following short–term starvation (5 days) of tilapia no changes occurred in white muscle composition other than for protein. After refeeding of 5 day starved fish, protein content remained lower than controls. Long–term starvation (30 days), reduced dry matter, protein, carbohydrate and lipid levels. After refeeding Rao et al. (1987) observed an accumulation of protein, carbohydrate and lipid levels in the white muscle, althought total protein and lipid were lower than that of controls. Total carbohydrates were elevated above that of controls indicating active synthesis of carbohydrates in the muscle tissue following refeeding (Rao et al., 1987). These experiments indicate that even short–term starvation of tilapia results in depletion in protein, lipid and carbohydrate levels that cannot be recouped as seen in rainbow trout (Quinton and Blake, 1990). This difference may result due to temperature effects. Higher temperatures raise standard metabolic rates (SMR) (Weatherley and Gill, 1987), which in turn increases total energy demand (SMR and growth). It is possible therefore, that growth compensation in tropical species is les pronounced than, for example, in rainbow triut, due to temperature effects (e. g., higher SMR under food deprivation would result in greater weight loss), although further insights into this phenomenon can only be gained with analyses of proxinate compositions which was not possible during the present trial. By experimental end there were no differences in CF between treatments, which is in accordance with results obtained by Jobling et al. (1993) for Arctic charr.

Haematocrit levels in feed cycled tilapia were significantly reduced when compared to controls, which mimics the observations for rainbow trout and pike during starvation (Kawatsu, 1966; Ince and Thorpe, 1976). Anaemia might have resulted due to a reduced ability of fish to produce new red blood cells (Love, 1970). Ince and Thorpe (1976), report that pike haematocrit values returned to normal after a period of refeeding, which contrasts to the results for tilapia. These differences may have resulted due to the cycling periods employed, which may have been too long for the fish to recover, or simply reflect species differences.

GSI values for both males and females obtained in this experiment indicated that fish were generally breeding at experimental end when compared to values obtained by Cornish et al. (1996). However, Cornish et al. stated that male to female GSI ratio outside the breeding cycle was 1:2; whereas during the breeding period it may vary from 1:4 to 1:10. This is in contrast to the ratios found in this experiment which varied from 1:2 to 1:5,

but this may be due to animal size variation between experiments; C o r n i s h
et al. used tilapia almost ten times the size of those used herein. Females
reached reproductive maturity (increased GSI) prior to males, and therefore,
in addition to environmental cues such as temperature, photoperiod and
rainfall (C o r n i s h and S m i t, 1995), female maturity may be a stimulus for
the commencement of male gonadal development C o r n i s h et al., 1996).

Dominant males were found to defend tank corners and turn dark in
colour in agreement with the observations by C o r n i s h et al. (1996) who
found that breeding males changed colour to a deeper greyish black with a
white lower head and throat. When held together, male tilapia establish a
hierarchial system of dominance in which only some of the males exhibit
sexual activity and full testicular development (M e l a m e d et al., 199%). It
is possible that this was the case in the present study. However, autopsy at
experiment end did not reveal large differences in GSI for males within a
group giving no indication of differences of breeding status other than colour.

Breeding males from feed cycled groups displayed dominant feeding
behaviour after periods of deprivation. This feeding hierarchy became more
relaxed after a few days of excess food supply, opservations of which are in
accordance with results of J o b l i n g and K o s k e l a (1996), for rainbow trout.
However in group (5:5), five days seemed too short a period for the feeding
hierarchy to descend, thus these animals may have experienced excess stress
from dominant males. This stressor would result in decreased food availability
for suppressed animals which may have be one explanation underlying the
poorest overall growth performance displayed by this group.

The present studies demonstrate that tilapia posses compensatory growth
mechanisms which are reflected in elevated growth rates upon refeeding. The
best growth performance for a feed cycled groups was achieved by (15:15),
although weight gain for the continuously fed group was almost twice as large.
Thus, it is clear that feed cycled groups are not able to 'catch up' with
controls. The increased response in growth rates in periods of refeeding after
a period of food deprivation are short–term. Thus, fed cycling may prove a
good alternative to 'boost' growth rates up regularly in the practical setting.
The main problem encountered in feed cycling seems to be the loss weight
during starvation periods. This may be overcome if feed administration was
undertaken at a restricted, but high enough level, to maintain basal metabolic
functions, but low enough to trigger the compensatory growth effect during
periods of refeeding. Findings by R u s s e l l and W o o t t o n (1992) on a
cyprinid species, and L u q u e t et al. (1995), on African catfish, supports this
theory.

Farming of tilapia is often undertaken in ponds. Ponds have a primary
production from which O. mossambicus can benefit due its omnivorous feeding
behaviour and ability to filter feed (T r e w a v a s, 1983). The natural produc-
tion in ponds may be elevated by fertilisation. However, in intensive and
semi–intensive fish culture systems supplementary feed is given in order to

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enable increased densities and decrease production time. According to S e h - g a l and T o o r (1994), the cost of supplementary feed is approximately half of the total fish farming costs. One can speculate on the possibility of transferring the technology of 'compensatory growth' into the pond production area. In periods of starvation fish may be able to utilise pond primary production to uphold the basal metabolic functions and thereby avoid weight loss. In turn when supplementary feed is given a higher degree of utilisation may be exhibition by the compensatory growth mechanisms resulting in reduced production costs and a decrease in non–utilised nutrients in the water column. However, further research is needed in the area of compensatory growth to explain the relationship between feeding rates in deprivation and refeeding periods.

Sažetak

KOMPENZACIJSKI RAST MOZAMBIČKE TILAPIJE (Oreochromis mossambicus) HRANJENE SUBOPTIMALNOM HRANOM

Mozambičke tilapije, Oreochromis mossambicus, držane su u morskoj vodi s 30% o i na temperaturi od 29 do 30 °C. Podijeljene su u četiri grupe (50 jedinki po grupi u ponavljanju), od kojih je svaka izložena jednom od ciklusa dana gladovanja i dana ponovnog hranjenja: 1) kontrola, sa stalnom hranidbom, 2) 5:5, 3) 10:10 i 4) 15:15. Sve su ribe u pokusnom razdoblju od preko 60 dana hranjene komercijalnom hranom koja sadrži 18,4% bjelančevina, 6,7% masti, 58,6% ugljikohidrata i 7,2% pepela. Kompenzacijski je rast registriran kod ciklično hranjenih grupa kao porast (p<0,03) specifičnog rasta mase za vrijeme ponovnoga hranjenja. Ipak, ove ribe nisu bile u mogućnosti dostići mase kontrolnih riba. Gladovanje je smanjilo (p<0,01) vrijednost hematokrita u usporedbi s kontrolom, a kod skupine 15:15 i povećalo je testikularni indeks (p<0,02). Rezultati su promatrani u odnosu na komercijalnu primjenu kompenzacijskog rasta za vrijeme proizvodnje tilapija.

Ključne riječi: hranidbeni ciklusi, bjelamčevine, tilapija, rast

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