Journal of Fish Biology (2000) **56,** 228–232
Article No. jfbi.1999.1154, available online at http://www.idealibrary.com on IDEAL®

Compensatory growth, feed utilization and activity in gibel carp, following feed deprivation

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(*Received 5 May 1999, Accepted 8 October 1999*)

Following a period of food deprivation, gibel carp compensated for growth through increased feed intake and conversion efficiency, but increased conversion efficiency was not achieved by increasing digestibility or reducing activity.

Key words: compensatory growth; feed utilization; activity; *Carassius auratus gibelio*.

Compensatory growth following food restriction occurs in many fishes (Russell & Wootton, 1992; Jobling *et al*., 1993; Kim & Lovell, 1995; Hayward *et al*., 1997), but was absent in the common carp, *Cyprinus carpio* L. (Schwarz *et al*., 1985). Usually food intake, and sometimes conversion efficiency, increases during compensatory growth (Russell & Wootton, 1992; Jobling *et al*., 1993; Hayward *et al*., 1997). In roach *Rutilis rutilus* (L.), reduced activity during maturation may save energy during gonad growth (Koch & Wieser, 1983). It is of interest to know whether reduced activity accompanies increased conversion efficiency during compensatory growth.

The present study examined whether the gibel carp *Carassius auratus gibelio* showed compensatory growth following food deprivation, and whether the growth responses were accompanied by changes in activity.

In a constant temperature room, fluorescent lights (105 lux) beneath 16 Plexiglas tanks (40 × 20 × 20 cm; water 10–12 cm deep) were used between 0800 and 2000 hours, and red lights (0·5 lux) used from 2000 to 0800 hours. Activity was recorded by videocamera mounted above the tanks (Videomex V Activity Monitoring System, Columbus Corporation, Ohio, U.S.A.). Horizontal distance swum per unit time and per cent time moving were monitored continuously for four fish each day from 0900 to 2000 and 2100 to 0800 hours and the camera was moved to record another four fish the next day.

Hatchery produced gibel carp were transferred to a holding tank in a constant temperature room 2 weeks prior to the trial. Water temperature was adjusted gradually to 25° C (1–2° C day^{-1}), and the fish were held at this temperature for 10 days. During this period, the fish were fed to satiation twice a day at 0900 and 1600 hours on a dry pellet diet containing 45% fish meal, 10% soybean cake, 34% wheat, 5% oil (50% lard + 50% soya oil), 5% vitamin and mineral premix (formulations for warmwater fish in National Research Council (1977)), 1% carboxymethylcellulose as binder and 0·1% yttrium oxide (Y_2O_3) as inert marker for digestibility measurement. Analysed composition of the diet was 92·2% dry matter, 34·9% protein, 7·8% lipid and 15·4 kJ g^{-1} energy (as fed).

The experiment, which lasted for 8 weeks, was divided into two phases, involving food restriction followed by re-alimentation. Following 2 days of food deprivation, 32 fish

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0022–1112/00/010228+05 $35.00/0

TABLE I. Body weights at different stages of the experiment in gibel carp deprived of food for different periods during weeks 1–4 and refed to satiation during weeks 5–8 of the experiment (mean ± S.E.)

Duration of deprivation (weeks)	*n*	Initial weight (g)	Weight before re-alimentation (g)	Final weight (g)
0	3	3·6 ± 0·0	6·2 ± 0·2a	7·7 ± 1·0a
1	4	3·7 ± 0·0	5·1 ± 0·1b	8·4 ± 0·4a
2	4	3·7 ± 0·1	4·8 ± 0·1c	8·4 ± 0·4a
4	4	3·8 ± 0·1	3·6 ± 0·0d	6·0 ± 0·5b

Letters after each value indicate results of Duncan's multiple range test; means with different letters were significantly different from each other ($P<0·05$).

were weighed individually and distributed at random among the 16 tanks. Four tanks were assigned to each treatment. Controls were fed to satiation twice a day throughout the experiment. Treatments S1, S2 and S4 were deprived of food during week 4, weeks 3 and 4, and weeks 1–4, respectively, and fed to satiation twice a day at 0900 and 1600 hours throughout the remainder of the experiment. At each feeding, a known amount of feed was added to each tank. Uneaten feed was collected 1 h later by siphoning, dried at 70° C and weighed. Loss rate of uneaten feed due to leaching (11·2 ± 0·5%; $n=8$) was assessed by placing a weighed amount of feed in tanks without fish for 1 h and then collecting, drying and reweighing. Weekly measurements of water quality gave dissolved oxygen 6–9 mg l^{-1}, pH 7–9 and $NH_4-N<0·5$ mg l^{-1}.

At the start, 10 fish from the stock tank, subjected to the same pre-experimental procedures as the experimental fish, were killed and frozen at −20° C for later analysis of body composition. After 4 weeks, all the test fish were deprived of food for 1 day, and weighed. One fish from each tank was killed for analysis of body composition and the other was returned to the tank. At the end of the experiment, all the fish were deprived of food for 2 days, weighed and killed for body composition analysis.

Faeces were collected for digestibility analysis by siphoning twice a day, faeces that remained intact being dried at 70° C and then frozen at −20° C until analysed. Activity was monitored during the refeeding period on 5 days in each tank.

Concentrations of dry matter, protein, lipid and gross energy were determined for samples of feed, faeces and fish as described in Fu *et al.* (1998), omitting lipid concentration in faeces. Concentration of Y_2O_3 in feed and faeces was determined by inductively coupled plasma atomic emission spectrometry (JY38S, Jobin Yvon, France). All analyses were carried out at least in duplicate.

Feed intake, conversion efficiency, and protein and energy retention efficiencies were calculated as described in Fu *et al.* (1998). Digestibilities of dry matter, protein and energy were estimated using Y_2O_3 as marker. Averages of the daily measurements of distance swum and time spent swimming for each fish over 5 days were used to represent activity level.

Differences between treatments were tested by analysis of variance. Proportions were arcsine transformed prior to analysis. Duncan's multiple range test was used for multiple comparisons. Differences were regarded as significant when $P<0·05$.

One fish in the control group developed fin erosion during the re-alimentation period, and so was excluded from analysis. There was no significant difference in initial body weight of fish among treatment groups ($P>0·05$), but after 4 weeks, differences became significant. At the end of the experiment, weights of S1, S2 and control fish did not differ, but S4 fish were significantly smaller than others (Table I).

During re-alimentation, weight-specific feed intake, conversion efficiency and protein and energy retention efficiencies were significantly higher in groups S1–S4 than in the controls, but did not differ among groups S1–S4 (Fig. 1, Table II). Protein digestibility

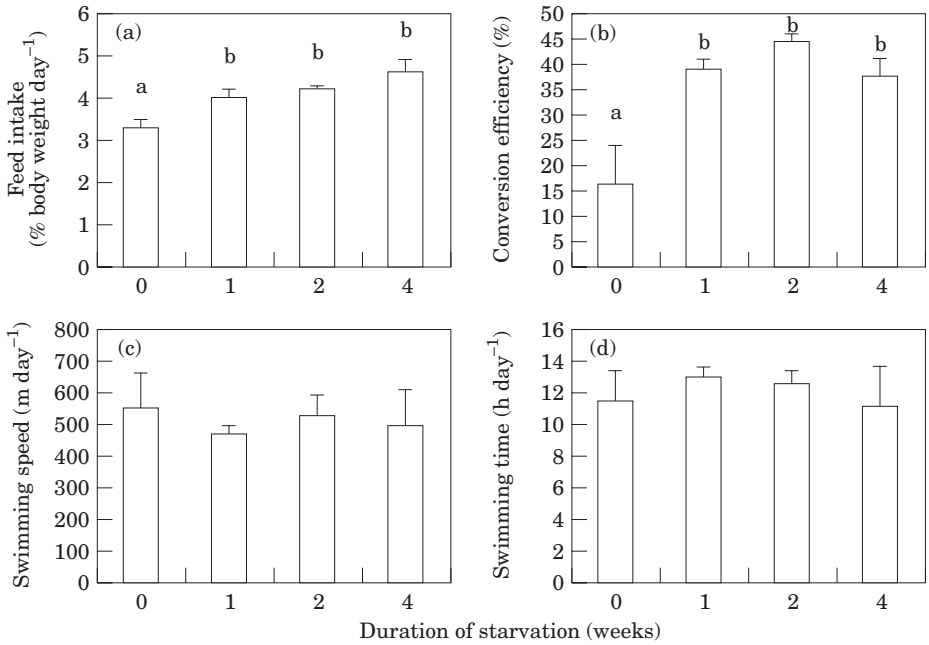

FIG. 1. Feed intake (a), conversion efficiency (b) and swimming activity (c) and (d) during the re-alimentation period in gibel carp deprived of food for different periods. Error bars represent +S.E. Values not sharing the same letter are significantly different from each other ($P<0{\cdot}05$).

TABLE II. Digestibilities of dry matter, protein and energy, and protein and energy retention efficiencies during the re-alimentation period in gibel carp deprived of food for different periods (mean ± S.E.)

Duration of deprivation (weeks)	*n*	Apparent digestibility (%)			Retention efficiency (%)	
		Dry matter	Protein	Energy	Protein	Energy
0	3	68·8 ± 1·2a	91·0 ± 0·2	85·1 ± 0·2a	7·7 ± 3·0a	11·0 ± 3·0a
1	4	71·1 ± 0·5a	91·7 ± 0·2	86·0 ± 0·4a	22·9 ± 1·0b	19·2 ± 1·3b
2	4	66·7 ± 2·0ab	91·6 ± 0·3	85·0 ± 0·9a	20·4 ± 1·1b	21·1 ± 0·9b
4	4	63·2 ± 1·5b	90·6 ± 0·9	82·9 ± 0·6b	20·0 ± 1·4b	18·1 ± 1·6b

Letters after each value indicate results of Duncan's multiple range test; means with different letters were significantly different from each other ($P<0{\cdot}05$).

did not differ significantly among groups, but a significant reduction in digestibilities of dry matter and energy was observed in group S4 (Table II).

The ratio of protein gain to lipid gain in the control fish was >1 during weeks 1–4, but <1 during weeks 5–8. This ratio was >1 during re-alimentation in the S1–S4 groups (Table III).

There were no significant differences in distance swum or time spent swimming among fish in the different treatment groups (Fig. 1).

Compensatory growth of warmwater fishes was reported only in channel catfish, *Ictalurus punctatus* (Rafinesque) (Kim & Lovell, 1995), and hybrid sunfish, *Lepomis cyanellus* Rafinesque × *L. macrochirus* Rafinesque (Hayward *et al.*, 1997), but not in carp (Schwarz *et al.*, 1985). The present study confirmed the existence of compensatory growth in the warmwater omnivorous gibel carp.

TABLE III. Protein and lipid gains during feed deprivation and re-alimentation in gibel carp deprived of food for different periods (mean ± S.E.)

Duration of deprivation (weeks)	0	1	2	4
Feed deprivation period				
Protein gain (g)	0·31 ± 0·03	− 0·03 ± 0·01	0·11 ± 0·01	− 0·18 ± 0·02
Lipid gain (g)	0·12 ± 0·01	0·07 ± 0·01	0·01 ± 0·00	− 0·09 ± 0·00
Protein gain : lipid gain	2·64 ± 0·03	− 0·43 ± 0·20	12·09 ± 1·21	1·98 ± 0·07
Re-alimentation period				
Protein gain (g)	0·23 ± 0·14	0·69 ± 0·07	0·49 ± 0·13	0·48 ± 0·08
Lipid gain (g)	0·36 ± 0·14	0·33 ± 0·03	0·35 ± 0·02	0·22 ± 0·03
Protein gain : lipid gain	0·53 ± 0·19	2·09 ± 0·04	1·37 ± 0·35	2·18 ± 0·03

Growth in gibel carp controls was much slower during weeks 5–8 than 1–4. Water quality was adequate throughout the experiment. Though the fish were switched from pair-rearing to individual rearing, previous experiments suggested that gibel carp showed good growth performance when transferred from group rearing in stock tanks to individual rearing (Qian, 1998; Zhu *et al*., 2000). Cui & Wootton (1988) reported that absolute daily intake in the minnow *Phoxinus phoxinus* (L.) declined progressively during 3-week experiments, though the fish were fed *ad libitum* and gained substantial weights, as found in minnows in recirculation systems over 7-week experiments (Russell & Wootton, 1992). From Russell & Wootton's figure, growth rates upon re-alimentation were significantly higher in the food deprived fish than in the controls, but the values were actually close to the level in the controls at the start of the experiment. Alternating phases of rapid and slow growth were reported in rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Wagner & McKeown, 1985) and coho salmon, *O. kisutch* (Walbaum) (Farbridge & Leatherland, 1987). Thus, the decreased growth in the control fish during the latter part of the present study may have been a slow phase caused by endogenous factors.

This slowed growth was associated with a decrease in protein, but not lipid growth. During re-alimentation period, though the groups previously deprived of food started with a much smaller body size, the absolute protein gain was greater than in the controls. The result supported the argument that protein deposition takes precedence during compensatory growth (Jobling *et al*., 1995).

Compensatory growth in the gibel carp was accompanied by improved efficiency and protein and energy retention, but such improvements were not caused by a higher digestibility or reduced activity.

We thank S. Xie and X. Zhu for help during the experiment, and R. J. Wootton and two anonymous referees for comments on earlier drafts of the manuscript. This work was supported by the National Natural Science Foundation of China (No. 39625006), the Chinese Academy of Sciences (No. KZ951-A_1-102-01), the Ministry of Sciences and Technology of China (No. 96-008-02-03) and the State Key Laboratory for Freshwater Ecology and Biotechnology of China (FEBL).

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