

## **Appetite and growth compensation in the European minnow, *Phoxinus phoxinus* (Cyprinidae), following short periods of food restriction**

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### **Synopsis**

Changes in the daily appetite and weekly growth rates of individual adult minnows, *Phoxinus phoxinus*, on ad libitum rations were recorded before and after they had experienced 4 or 16 days of food restriction. Feeding levels during the restriction periods were either starvation or a maintenance ration. The latter was estimated from a previously determined regression model. Water temperature was 15°C and the photoperiod 9L15D in all experiments. The mean weight of fish used ranged from 1.06 to 2.15 g. The 4 day restriction had no detectable effects on appetite or growth. After the 16 day restriction, the minnows showed hyperphagia and had increased specific growth rates and growth efficiencies compared with control fish. The compensatory increases in appetite and growth were not sustained and within three weeks had declined to levels not significantly different from those of the control fish. At the end of the experiments, there were no significant differences between the mean weights or cumulative food consumption of the restricted and control groups. The results suggest that adult minnows regulate their appetite and growth rate in relation to their previous nutritional history.

### **Introduction**

The capacity of teleost fishes to regulate their appetite and growth is poorly understood. Evidence of regulation may be obtained from the responses of the appetite and growth of individual fish to changes in the availability of food. Compensatory growth (the ability of a dietary restricted animal to achieve its normal body weight and form by a growth spurt on realimentation) is well documented in the endothermic birds and mammals (e.g. Wilson & Osbourn 1960, Ledin 1984, Ashworth 1986). In fishes fecundity and often mortality rates are size-dependent (Wootton 1990), so the ability to show growth compensation is likely to be an advantage. It has been demonstrated in salmonid fishes (Bilton & Robins 1973, Weatherley & Gill 1981, Dobson &

Holmes 1984, Kindschi 1988, Miglavs & Jobling 1989, Quinton & Blake 1990). In Arctic charr, *Salvelinus alpinus*, the restoration of satiation feeding levels after a period of food restriction led to sustained hyperphagia (Miglavs & Jobling 1989). This increase in appetite, together with changes in growth efficiency, contributed to the compensatory growth shown by the charr.

Evidence for compensatory growth in cyprinids is equivocal. Schwarz et al. (1985) failed to demonstrate growth compensation in carp, *Cyprinus carpio*. However, Wieser et al. (1992) demonstrated growth compensation in juveniles of three other cyprinid species (*Leuciscus cephalus*, *Chalcalburnus chalcoides mento* and *Scardinius erythrophthalmus*). On the basis of a bioenergetic model of the growth of the European minnow, *Phoxinus phoxi-*

*nus*, Cui & Wootton (1989) suggested that evidence of the regulation of appetite in relation to growth rate would be observed in this cyprinid.

The purpose of this study was to determine the capacity for intrinsic appetite and growth regulation in adult European minnow. The feeding regimes of fish were manipulated and the consequent changes in appetite and growth rates monitored for evidence of compensatory changes in relation to recent nutritional histories. All the experiments used fish housed individually rather than in groups. This had the advantage that the appetites and growth of known individuals were measured before and after the period of restriction. It had the disadvantage that the number of replications per treatment was small.

### Materials and methods

Adult minnows were collected from Brays Pool, a small reservoir in mid-Wales. Dates of collection and the mean weights of the experimental fish are shown in Table 1. They were kept in stock tanks in a constant environment room at 15°C on a photoperiod of 9L15D. During an acclimation period of 26 days, the fish were fed commercial flake food made available for 2 min per day and live enchytraeid worms provided for 5 min per day. During the acclimation period, the fish were treated for 11 days with chloramine-T to prevent whitespot caused by *Ichthyophthirius multifiliis* (Cross & Hursey 1973). The standardized acclimation conditions were designed to bring individuals to a similar nutritional and reproductive status. The 9L15D photoperiod was chosen to maintain the gonads in a quiescent state. Outside the breeding season, males and females are difficult to distinguish on the basis of external features and there is no evidence that under the conditions used the sexes differ in their growth.

To allow for measurements of individual rates of food consumption and growth the minnows were housed individually after the completion of the acclimation period in 131 tanks. Within an experiment, the food consisted solely of enchytraeid worms provided daily in rations measured to the

nearest 0.05 mg. Any uneaten worms were collected and weighed before the next ration was fed. Enchytraeids were readily taken by the fish. The mean energy content of the worms was 22.1 J g<sup>-1</sup> dry wt or 4.8 J g<sup>-1</sup> wet wt. Fish were measured to the nearest mm and weighed to the nearest 0.05 mg at the beginning of the experiment and then at weekly intervals. Before a fish was weighed, excess moisture was removed by careful blotting. No anaesthetic was used.

Each experiment used 20 acclimated fish. On the day preceeding an experiment, five of these fish were killed and their length and weight measured. The remaining fish were assigned at random to starvation (Group S, N = 5), maintenance (Group M, N = 5) and control (Group A, N = 5) treatments. For the first two weeks of the experiment fish in all three groups had unrestricted, ad libitum access to white worms. After this initial period the treatments (absolute or relative food deprivation), starvation or maintenance rations, were imposed for a fixed period of time. All fish from all groups were then fed ad libitum for a recovery period of three weeks. The control group received ad libitum rations throughout the experiment. At the end of the experiment all the remaining fish were killed. All fish were then dried to constant weight at 65°C and reweighed.

In two experiments, the treatment period was 16 days and in a third experiment it was 4 days. During the period of deprivation, Group S received no food. For fish in Group M, the daily maintenance ration as % body wt per day was calculated from the equation:  $C_{\text{main}} = \exp(0.5045 + 0.1735 \ln T) - 1$ , where  $C_{\text{main}}$  is maintenance ration and T is temperature (°C) (Cui & Wootton 1988). The periods of deprivation were chosen because 4 days were sufficient for the fish to have completely emptied their guts but too short for significant weight loss to be measured. After 16 days of starvation, statistically significant declines (compared to initial values) in wet weight, protein and lipid contents have been measured in adult minnows (Mehsin 1981). He had found that after 16 days of starvation, the fish weighed, on average, 90% of their initial wet weight.

The initial experiment with a 16 day deprivation

used static water in the individual tanks. Under these conditions water quality declined. In subsequent experiments with 16 and 4 days deprivation, a continuous flow of recirculated filtered water was maintained through the individual tanks providing a constant water quality throughout each experiment. A complete turnover of recirculated water took just over 1 hour. The results from both the static and flow-through conditions are presented.

Individual growth rates were expressed as specific growth rates (SGR) calculated as:

$$\text{SGR} = (\log_e W_t - \log_e W_o)/t,$$

where  $W_t$  and  $W_o$  are the final and initial weights of the fish and  $t$  is the interval in days between the weighings. Gross growth efficiency (GGE) was calculated as:

$$100 \cdot (\Delta B/C),$$

where  $\Delta B$  is the absolute change in wet body weight and  $C$  is the weight of food consumed.

ANOVA and ANCOVA were used in the statistical analysis. The covariance analysis was used to adjust for individual differences in the initial sizes of the fish. Unless otherwise stated, all comparisons were pre-planned orthogonal contrasts. Lengths, weights and rates of consumption were logarithmically transformed prior to analysis. The need to house and maintain the fish individually restricted the sample sizes in each treatment. Consequently, a significance level of  $p < 0.1$  was taken as indicating a result of biological interest rather than the more conventional level of  $p < 0.05$ .

## Results

In all three experiments, after the first day of individual housing and ad libitum feeding there was a significant decline in appetite (defined as daily food consumption) over the next 2 to 3 days. A similar decline also occurred on the restoration of ad libitum rations after the restriction period. This effect may reflect the effect of gut-filling on appetite

(Cole 1978). The short-term effects of gut filling on appetite will be the subject of a subsequent paper.

After the initial decline in appetite, daily variations in consumption at ad libitum rations were usually low with one exception. Appetite usually showed a sharp drop in the 24 h after a fish had been weighed.

### *Differences in appetite before and after deprivation within groups*

For each group (A, S and M), ANCOVA was used to compare the mean daily rate of food consumption averaged over the 5 days immediately preceding deprivation with the mean daily consumption averaged over the 5 days following realimentation. Initial fork length was used as the covariate. Thus for each treatment, a direct comparison was made between pre- and post-deprivation appetites.

Food consumption was significantly higher in the post-deprivation period in fish starved for 16 days in both experiments (static-water,  $p = 0.003$ ; flowing-water,  $p = 0.018$ ). For Group M, on a maintenance ration for 16 days, the post-deprivation appetite was significantly higher in the static-water experiment ( $p = 0.061$ ), and approached significance in the flowing-water experiment ( $p = 0.131$ ). A deprivation period of 4 days had no significant effect.

### *Differences in appetite between groups before and after deprivation*

ANCOVA with initial length as the covariate was used to compare the effects of the treatments. Two orthogonal contrasts were made between group means. Consumption by control fish was compared with the mean consumption by deprived fish (Group A vs Group S and Group M) and the mean consumption by starved fish was compared with that by control fish (Group A vs Group S). In all cases, where one pre-planned contrast was significant, the other also was.

In each experiment there were no significant differences between the groups for the daily food

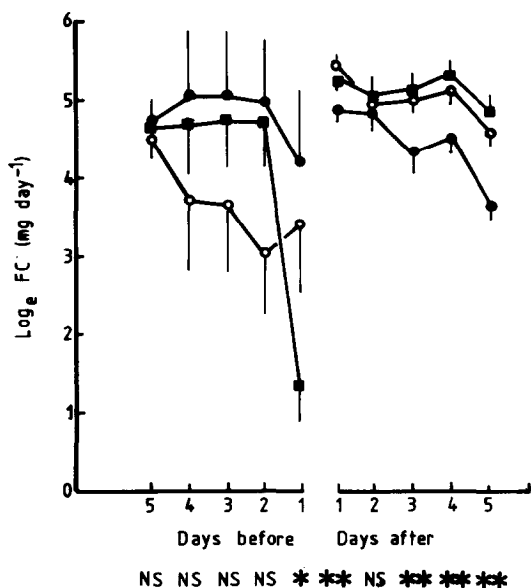


Fig. 1. Adjusted mean rates of food consumption (ad libitum ration) by minnows on the five days before and after 16 days food deprivation (flowing-water). Weight used as covariate and all data transformed logarithmically prior to analysis. Group A (controls) = ●; Group S (starved during deprivation period) = ■; Group M (maintenance ration during deprivation period) = ○. Vertical line indicates 1 S.E. Planned orthogonal contrast between control (Group A) and treatment groups (Group S and Group M): NS,  $p > 0.1$ ; \*,  $0.1 > p > 0.05$ ; \*\*,  $0.05 > p > 0.01$ .

consumption on any of the five days that preceded the onset of deprivation. The one exception was that on the day immediately prior to the imposition of the 16 day restriction period there was a significant difference in appetite between the designated control and treatment groups in the flowing-water experiment (Fig. 1). No obvious explanation of this is available.

The orthogonal contrasts showed that in the 16 day treatment (static-water), there was significant hyperphagia in the deprived fish compared with the controls on 3 of the 5 days following realimentation. In the 16 day deprivation (flowing-water), there was significant hyperphagia on 4 of the 5 days (Fig. 1). Deprivation for 4 days had no significant effects with one exception. Starved fish ate more than control fish on the fourth day of realimentation ( $p = 0.049$ ).

#### *Effects of treatments and realimentation on specific growth rates*

Growth rates did not differ significantly between the treatments groups during the initial two week period on ad libitum rations in the three experiments.

In the 16 day deprivation experiments, the period of deprivation included the third and fourth weeks and the first two days of the fifth week. Consequently, the SGR for Week 5 resulted from 2 days deprivation and 5 days of ad libitum feeding. In Weeks 5 and 6, fish in Group S had a significantly higher mean SGR than the control fish in both the static and flowing-water experiments ( $p = 0.019$ ,  $0.011$  and  $p = 0.056$ ,  $0.024$  respectively). In Week 7, there were no significant differences. The orthogonal contrast of the mean growth of the treatment groups with the mean growth of control group (Group S and Group M vs Group A) showed that the differences were significant only in Weeks 5 and 6 (static-water) and Week 6 (flowing-water) (Fig. 2).

The 4 day deprivation failed to evoke a compensatory rise in SGR on subsequent realimentation.

#### *Effect of deprivation and realimentation on gross growth efficiency*

There were no significant differences in growth efficiencies in the first two weeks of any experiment.

On realimentation after a 16 day deprivation, the efficiency of treatment fish was significantly higher than that of control fish (Fig. 3). In the final week (Week 7), there were no significant differences. The contrast of starved fish with controls also showed that prior starvation was associated with significantly increased growth efficiencies in Weeks 5 and 6 of realimentation (Static-water: Week 5,  $p = 0.013$ ; Week 6,  $p = 0.014$ . Flowing-water: Week 5,  $p = 0.007$ ; Week 6,  $p = 0.071$ ).

The four day deprivation had no significant effect on growth efficiency after realimentation.

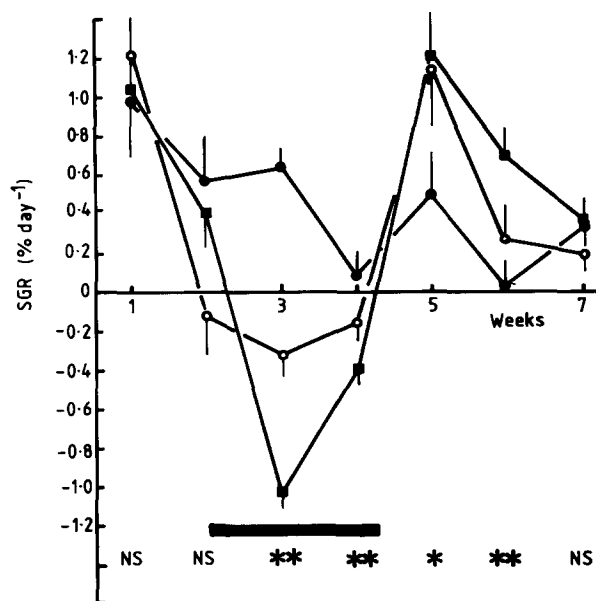


Fig. 2. Adjusted mean weekly specific growth rates in weeks before, during and after 16 day food deprivation period (flowing-water). Period of deprivation indicated by solid bar. Other details as in Figure 1.

#### Overall differences between groups in appetite and growth during three week realimentation period

The effects of the three week recovery period were analysed using ANCOVA to adjust the mean total food consumption, the mean final weights and the mean weight increment in the three week period to a mean common initial weight. This initial weight was taken as the weight of the fish at the end of the period of restriction.

Adjusted mean total food consumption did not differ significantly between groups in any of the experiments. Deprivation for 4 days had no significant effects on adjusted mean specific growth rate, weight increment or final weight. In the 16 day deprivation (static-water) experiment, treatment fish had significantly higher adjusted mean specific growth rates ( $p < 0.05$ ), absolute weight increments ( $p < 0.05$ ), and final weights ( $p < 0.05$ ) than control fish. Similar results were obtained in the 16 day deprivation (flowing-water) experiment: adjusted mean specific growth rate ( $p < 0.1$ ), absolute weight increment ( $p < 0.05$ ), final weight ( $p < 0.1$ ). Comparisons of the unadjusted means using

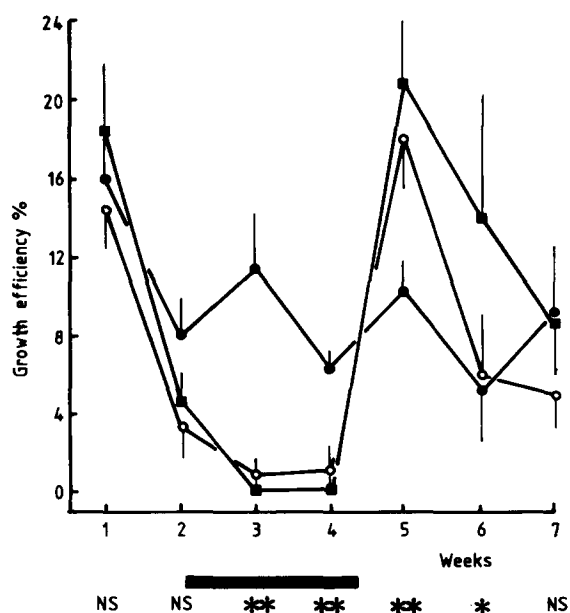


Fig. 3. Adjusted mean gross growth efficiencies based on fresh weight measurements in weeks before, during and after 16 day food deprivation period (flowing-water). Other details as in Figure 2.

ANOVA gave similar results except that the final weights did not differ significantly between groups (Table 2).

Thus, the brief hyperphagia noted in the first week of recovery did not lead to a significant increase in the total consumption over three weeks. The compensatory increase in specific growth rate following deprivation was sufficient to cause a significantly higher absolute weight increment.

A similar analysis using ANCOVA compared total growth and food consumption over the full 7 week experimental period. For the three experiments, there were no significant differences between the groups (Table 1). There were no significant differences between the groups in the final mean percentage dry weight of the fish nor between the final liver dry weights. Thus the effects of the 16 day restriction had been fully compensated for after three weeks of realimentation.

#### Discussion

The results suggest compensatory appetite and

growth changes after a 16 day period of food restriction in adult minnows. The comparison of the static and flowing-water experiments showed that the changes were not an artefact of the holding conditions. Wieser et al. (1992) have reported growth compensation in juvenile cyprinids. Of other studies reporting compensatory growth in fishes only Miglavs & Jobling (1989) have incorporated a parallel examination of adjustments in appetite and growth efficiency. They investigated the effect of an eight week deprivation period on the appetite and growth response during subsequent realimentation for eight weeks in juvenile Arctic charr, *Salvelinus alpinus*. Their fish weighed 5–10 g. In six of the eight weeks of realimentation, the deprived charr had significantly higher specific growth rates than control fish fed ad libitum continuously. The deprived fish were hyperphagic in six of the eight weeks of the realimentation period when compared with the controls. In the minnows the effect of deprivation beyond 16 days has not been examined, but the study of the charr demonstrates more persistent compensatory adjustments, particularly in appetite, to a longer term deprivation (eight weeks). The differences in responses of

juvenile Arctic charr and adult minnows are likely to result from differences in the severity and duration of restriction, age, species-specific differences, and differences in nutritional history prior to the restriction period.

The hyperphagia and compensatory growth in the minnows allowed the food-restricted fish to achieve the same size and cumulative food intake as the fish fed ad libitum throughout the experiment. Quinton & Blake (1990) found no significant differences in the overall change in weight, length nor specific growth rate between rainbow trout, *Oncorhynchus mykiss*, which had been cycled for 3 weeks of starvation and 3 weeks of feeding and continuously fed controls. However, their study did not measure individual food consumption. It was not known whether the compensatory growth was accompanied by hyperphagia and if the similar weight gains observed in fish fed on the cyclic schedule were achieved by consuming similar total weights of food to the controls. The study of the minnow is unique in measuring the individual rates of consumption both prior to and after the period of food restriction and so allowing total food consumption to be measured.

Table 1. Dates of collections, mean initial body weights, total food consumption, total growth increment, overall gross growth efficiency and final % water content of body for minnows, *Phoxinus phoxinus*, held for seven weeks including 4 or 16 days food restriction (standard error of the mean given in parentheses). Differences between treatment means tested by ANCOVA with initial fork length as covariate: NS,  $p > 0.1$ .

Date of collection	28.5.1988			10.2.1988			16.9.1988		
period of food restriction (days)	4			16 (static-water)			16 (flowing-water)		
Ration	Ad lib	Starv	Main	Ad lib	Starv	Main	Ad lib	Starv	Main
Mean initial wet wt (g)	1.973 (0.072)	1.969 NS (0.129)	2.154 (0.156)	1.064 (0.107)	1.261 NS (0.088)	1.299 (0.127)	2.067 (0.112)	2.086 NS (0.156)	1.928 (0.092)
Total food consumption (g wet wt)	3.844 (0.619)	4.595 NS (0.730)	3.693 (0.165)	4.614 (0.609)	3.941 NS (0.319)	4.336 (0.654)	5.583 (0.900)	4.703 NS (0.610)	4.719 (0.600)
Gross growth efficiency (wet wt basis)	11.94 (1.73)	11.94 NS (2.22)	12.87 (0.99)	10.04 (1.22)	10.96 NS (1.61)	11.59 (1.14)	9.28 (1.11)	8.87 NS (1.89)	7.10 (1.34)
Final water content of body (%)	69.04 (0.59)	69.84 NS (0.57)	69.73 (0.51)	70.28 (0.44)	70.14 NS (0.46)	70.59 (0.50)	69.12 (0.57)	69.52 NS (0.87)	71.04 (0.66)

Growth compensation may be a result of hyperphagia, or enhanced food conversion efficiency or both (Wilson & Osbourn 1960, Greeff et al. 1986, Mersmann et al. 1987, Williams & Sheedy 1987). In the minnows, a transitory growth spurt was associated with a brief elevation of appetite and an improved growth efficiency. In the more sustained growth compensation in the charr, growth efficiency was not increased throughout the compensatory growth phase, although the hyperphagia was more sustained (Miglav & Jobling 1989). Improved growth efficiency during re-alimentation after a period of starvation has also been suggested for sockeye salmon, *Oncorhynchus nerka* (Bilton & Robins 1973) and rainbow trout (Dobson & Holmes 1984).

The possibility that metabolic regulation is also a contributory factor in growth compensation cannot be excluded from the results obtained by Miglav & Jobling (1989) or from the present study. Reductions in standard metabolism during starvation have been reported in fishes (Jobling 1980). Some

mammals also reduce their metabolic rate during starvation (Apfelbaum 1978, Elliot et al. 1989). In rats, a reduction in basal metabolism extends into the initial stages of re-alimentation (Boyle et al. 1981). This may contribute to the enhanced efficiency of food utilization reported in food-restricted animals during recovery.

Compensatory growth provides support for the hypothesis that growth rates are optimized rather than maximized by fish with free access to food. The hypothesis of growth maximization assumes that organisms grow as fast as physiological and developmental constraints allow. Compensatory growth spurts are hard to explain on this hypothesis because it predicts that growth rates are always maximized by animals feeding ad libitum. If continuously fed animals grow less quickly than previously-deprived animals, the former must be growing at less than the maximum possible rate.

When minnows were provided for 21 days with ad libitum access to whiteworms, Cui & Wootton (1988) observed a progressive decrease in daily

Table 2. Unadjusted mean specific growth rate and consumption in the three week recovery period after 4 or 16 days of food deprivation (standard error of the mean given in parentheses). Effect of treatment (deprivation) tested by ANOVA; NS,  $p > 0.1$ ; \*,  $0.1 > p > 0.05$ ; \*\*,  $0.05 > p > 0.01$ .

Duration (days)	Restriction ration	Initial wt (g)	Final wt (g)	Increment (g)	SGR	Consumption (g)
4	Ad lib	2.3014 (0.1377)	2.4450 (0.1271)	0.1436 (0.0456)	0.0626 (0.0228)	2.2228 (0.2222)
	Starv	2.3364 (0.0914)	2.5680 (0.0916)	0.2316 (0.0576)	0.0950 (0.0244)	2.9342 (0.4337)
	Main	2.4940 (0.1938)	2.6324 (0.1428)	0.1384 (0.0585)	0.0602 (0.0254)	2.4148 (0.0852)
		NS	NS	NS	NS	NS
	Ad lib	1.4099 (0.1313)	1.5090 (0.1365)	0.0991 (0.0200)	0.0685 (0.0130)	2.1006 (0.2992)
	Starv	1.3906 (0.0803)	1.7002 (0.1112)	0.3097 (0.0674)	0.1989 (0.0382)	2.3645 (0.2066)
16 (static-water)	Main	1.5149 (0.1297)	1.8161 (0.1849)	0.3012 (0.0674)	0.1762 (0.0280)	2.5268 (0.4592)
		NS	NS	**	**	NS
	Ad lib	2.4300 (0.1392)	2.5899 (0.1668)	0.1599 (0.0349)	0.0621 (0.0112)	1.9327 (0.2135)
	Starv	2.1432 (0.1616)	2.5175 (0.1965)	0.3742 (0.0711)	0.1606 (0.0251)	2.8022 (0.2770)
	Main	2.0459 (0.1134)	2.2870 (0.1177)	0.2411 (0.0580)	0.1123 (0.0275)	2.4802 (0.4370)
		NS	NS	*	**	NS
16 (flowing-water)	Starv	2.1432 (0.1616)	2.5175 (0.1965)	0.3742 (0.0711)	0.1606 (0.0251)	2.8022 (0.2770)
	Main	2.0459 (0.1134)	2.2870 (0.1177)	0.2411 (0.0580)	0.1123 (0.0275)	2.4802 (0.4370)
		NS	NS	*	**	NS

consumption. On the basis of these short-term studies, a bioenergetics model of growth of *P. phoxinus* was formulated (Cui & Wootton 1989). The model overestimated long-term growth at high rations. Cui & Wootton (1989) postulated that the decline in consumption was a symptom of active control to reduce the growth rate to a 'desired' level. In the present study, growth and gross growth efficiency of unrestricted controls during the seven week experiments showed a significant decline, whilst consumption showed a more moderate reduction. Several explanations for these observations are possible. Firstly, they may be a consequence of the monotony of the diet. Secondly, decline in performance may result from a nutritional inadequacy in whiteworms as a food resource. Lastly, the response may reflect active control of growth. Reduced palatability or nutritional inadequacy are considered the weakest explanations because of the ability of the diet to support a compensatory response. Additional studies on *P. phoxinus* have revealed a progressive rise in SGR under a different feeding regime with the same diet (unpublished). Therefore, it is proposed that growth is controlled by adjustments of consumption and gross growth efficiency.

The active control of appetite and growth have already been implicated in the 'set-point' theory of weight regulation in mammals (Le Magnen 1985). This theory suggests that adult mammals 'remember' their nutritional history and compensate for it with modifications in appetites (hypo- or hyperphagia) so that a 'set-point' adult body weight is achieved. Fish growth is usually indeterminate, consequently modifications of appetite to compensate for nutritional history probably involve compensation in relation to a 'set-point' growth rate rather than a 'set-point' weight. A model proposed for the regulation of indeterminate growth in invertebrates by Hubbell (1971) and Calow (1973, 1976) can also be applied to fish. It assumes that there is an intrinsic capacity for the regulation of appetite and growth which functions as a homeostatic mechanism to achieve a genetically predetermined growth trajectory. Temporary deflections from this trajectory caused by poor feeding conditions lead to a readjustment of appetite or

metabolic rate, or more probably both. These adjustments tend to minimize the discrepancy between the achieved growth trajectory and the predetermined trajectory. Fish may monitor their achieved growth rate indirectly by monitoring the specific metabolites or fat reserves (Thorpe 1986). A comparison of this achieved rate with the 'desired' rate would stimulate any compensatory adjustments required. It is assumed that the genetically determined growth trajectory is shaped by natural selection. It is the trajectory which tends to maximise the lifetime production of offspring. Studies are now in progress on the effect of food restriction on metabolic rate, levels of activity and fat reserves in minnows.

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