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Effect of past nutritional history and fasting on feed intake and growth in rainbow trout *Oncorhynchus mykiss*

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Abstract − Groups of juvenile rainbow trout were fed to satiation for 10 days after 1, 11 and 21 days of feed deprivation. These fish (initial body weight = 20 ± 2 g) were previously fed at different feeding levels (0.5 or 1.5 % initial body weight, to satiation) with a high (20.4 kJ·g^{-1}) or a low (16.2 kJ·g^{-1}) digestible energy diet content for 34 days. It is shown that past nutritional history affected growth performance: duration of feed deprivation has a major effect on intake and feed conversion efficiency; previous feeding level has an effect on intake; dietary energy content affected feed conversion efficiency. In addition, an attempt was made to identify some of the metabolic parameters that could be involved in the increase in growth performance during the 10-day feeding period (whole body and muscle protein and lipid, plasma glucose, free fatty acids and triglycerids). Feed intake after fasting does not appear to be driven by body composition but feed conversion efficiency was correlated with the plasma glucose and free fatty acids. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

aquaculture / compensatory growth / past nutritional history / appetite / feed efficiency

Résumé − Effet du passé nutritionnel et du jeûne sur l'ingestion et la croissance de la truite arc-en-ciel *Oncorhynchus mykiss*. Des groupes de truites arc-en-ciel juvéniles ont été nourris à satiété durant dix jours après 1, 11 ou 21 jours de jeûne. Au préalable, ces poissons (poids initial = 20 ± 2 g) étaient alimentés à différents taux de rationnement (0,5 ou 1,5 % du poids initial ou à satiété) avec un aliment à haute (20,4 kJ·g^{-1}) ou basse (16,2 kJ·g^{-1}) teneur en énergie digestible durant 34 jours. Cette étude montre que le passé nutritionnel affecte la performance de croissance des truites arc-en-ciel : le niveau d'ingestion volontaire est significativement différent selon la durée du jeûne et le taux de rationnement passé, tandis que l'efficacité alimentaire est significativement influencée par la durée du jeûne et le niveau d'énergie de l'aliment. On a aussi essayé d'identifier l'existence d'un lien entre la composition corporelle et musculaire, la concentration du plasma en glucose, acides gras libres et triglycérides en fin de période de jeune et les caractéristiques de la croissance au cours de la période de réalimentation. Aucun lien significatif entre la composition corporelle et le niveau d'ingestion volontaire n'a pu être mis en évidence. En revanche, l'efficacité alimentaire est corrélée avec la concentration en glucose et en acides gras libres du plasma. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

aquaculture / croissance compensatrice / passé nutritionnel / appétit / efficacité alimentaire

1. INTRODUCTION

Many fish species are subjected to a natural starvation period during part of the year. They have developed an impressive ability to withstand long periods of starvation during which they mobilise their body reserves to stay alive (Collins and Anderson, 1995; Paul et al., 1995). Starvation periods are followed by a short period of compensatory growth, this last notion being defined by Russel and Wootton (1992) as "the

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ability of a dietary restricted animal to achieve its normal body weight and form by a growth spurt on re-alimentation". It is known to occur in a range of birds and mammals (Wilson and Osbourne, 1960; Thornton et al., 1979). In fish, the effect of fasting on subsequent feeding and growth is the subject of an increasing body of literature and studies have been undertaken with *Oncorhynchus nerka* (Bilton and Robins, 1973), *Oncorhynchus mykiss* (Weatherley and Gill, 1981; Dobson and Holmes, 1984; Kindschi, 1988; Quinton and Blake, 1990), *Salvelinus alpinus* (Miglavs and Jobling, 1989) and cyprinids (Russel and Wootton, 1992; Wieser et al., 1992).

The physiological basis of compensatory growth is incompletely understood but appears to involve increased feed intake (hyperphagia) and improved conversion efficiency (Miglavs and Jobling, 1989; Russel and Wootton, 1992), and past nutritional history is suggested to modulate growth performance (Weatherley and Gill, 1987). A mechanism for this modulation would require some functional indicators of the physiological state of the fish in connection with a means of controlling growth. It has been observed by numerous authors that growth is influenced by a large number of nutritionally related factors. Among them, fatness and physiological mechanisms involved in the maintenance of overall energy status and in the control of body weight are often invoked in fish (Lee and Putnam, 1973; Jobling and Wandsvik, 1983; Fletcher, 1984; Kaushik and Luquet, 1984), as in mammalian studies (Burton-Freeman et al., 1997).

The aim of the present experiment was to evaluate the importance of nutritional history on feed intake and growth. In addition, an attempt was made to identify some of the metabolic parameters that could be involved in the increase in growth performance during the re-alimentation period. For these purposes, we studied the growth performances of rainbow trout submitted to a 10-day re-alimentation challenge, in relation to their previous feeding level, duration of feed deprivation, and the state of the fish just prior to the re-alimentation challenge (body weight, body composition, muscle composition and plasma content of glucose, free fatty acids and triglycerids). This experiment was conducted in parallel with two diets of different energy level.

2. MATERIALS AND METHODS

2.1. Preparation of the feed

Two experimental diets, designated as HE (high energy) and LE (low energy) diets, were formulated to contain a constant protein level and different proportions of starch and fish oil. After pelleting, an aliquot of each diet was sampled for analyses. A digestibility trial was performed with fish fed twice a day with the experimental diets containing 1 % of chromic oxide as an inert marker. Faeces were collected over a 15-day period using a continuous automatic faeces collector (Choubert et al., 1982) and frozen (–20 °C) until estimation of chemical composition. The digestibility of the dietary nutrients were calculated as outlined by (Kim and Kaushik, 1992). Information concerning the ingredients, the chemical composition and the apparent digestibility coefficients of the experimental diets are summarised in *table I*.

Table I. Ingredients, chemical composition and apparent digestibility coefficients (ADC) of the experimental diets HE (high energy) and LE (low energy).

	HE	LE
Ingredients ($g \cdot kg^{-1}$)		
Fish meal	572	572
Gelatinised starch	202	136
Crude starch	0	237
Fish oil	186	15
Mineral mix[a]	10	10
Vitamin mix[b]	10	10
Na-alginate	10	10
Chemical composition		
Dry matter (%)	95.0	93.8
Protein ($N \times 6.25$)(% DM)[c]	40.6	40.5
Fat (% DM)[c]	22.9	6.6
Gross energy ($kJ \cdot gDM^{-1}$)[c]	22.6	18.9
ADC values (%)		
Dry matter	82.5	76.6
Protein	91.3	90.5
Fat	92.0	92.5
Energy	90.3	85.3
Digestible energy ($kJ \cdot gDM^{-1}$)[c]	20.4	16.2
Digestible protein (% DM)[c]	37.1	36.7
DP/DE ratio ($mg \cdot kJ^{-1}$)	18.2	22.7

[a] Luquet, 1971; [b] EIFAC, 1971; [c] DM, dry matter.

2.2. Preparation of the fish

Immature rainbow trout *(Oncorhynchus mykiss)* were raised at the experimental fish farm of Donzacq (Landes, France). Fish were randomly selected in order to make up six groups of 550 trout each (mean weight 20 ± 2 g). Each group of fish was maintained in 2-m^3 flow-through tanks (natural photoperiod) supplied with bore hole water (temperature range: 15–17 °C). Dissolved oxygen was higher than 90 % saturation. In order to achieve a range of different feeding histories, fish were fed by hand at 09:00 hours and 16:00 hours with high energy (HE) or low energy (LE) diets (*table I*) at three feeding regimes: to satiation, at 1.5 (about half the intake of fish fed to satiation) or 0.5 % (approximately the maintenance needs) of their initial body weight during 34 days. After day 34, fish were maintained without food in the same tanks.

After 1, 11 and 21 days of feed deprivation, ten fish from each of the six groups were removed from each tank by dipnet. Blood samples were rapidly taken by caudal puncture with previously rinsed (potassium

Table II. Effect of dietary treatment (HE or LE diet, fed to satiation, at 1.5 or 0.5 % of their body weight during 34 days, and subsequently feed deprived during 1, 11 or 21 days) on fish weight (Wi), body and muscle composition (protein [prot] and lipid [lip] expressed in % of fresh weight, energy [en] expressed as $kJ \cdot g^{-1}$ of fresh weight), and plasma concentrations of glucose (Glu, $g \cdot L^{-1}$), free fatty acid (FFA, $mmol \cdot L^{-1}$), and triglycerids (Trigly, $g \cdot L^{-1}$). Data are given as means of 5, 5 and 10 fish, respectively, for body and muscle composition and plasma concentrations.

		Body composition			Muscle composition			Plasma concentrations		
	Wi	prot	lip	en	prot	lip	en	Glu	FFA	Trigly
HE										
ad libitum										
1	44.7	14.2	12.3	8.1	17.5	2.8	5.1	1.3	0.3	2.5
11	43.3	14.5	10.9	7.5	18.5	2.3	5.4	0.7	0.6	1.5
21	41.7	14.3	10.5	7.6	18.5	3.0	6.0	0.7	0.6	2.7
1.5 %BW										
1	30.7	15.1	9.3	7.1	17.0	2.3	4.9	1.4	0.4	1.7
11	27.7	14.5	10.5	7.2	18.0	2.0	5.1	0.6	0.5	2.4
21	26.3	13.8	8.2	6.5	18.1	2.1	6.5	0.6	0.6	2.2
0.5 %BW										
1	20.7	14.8	7.9	6.5	17.6	1.4	4.8	1.1	0.4	1.4
11	19.7	15.1	3.7	5.0	16.0	1.5	4.4	0.6	0.6	1.6
21	19.3	14.4	3.9	5.0	16.9	1.4	4.4	0.4	0.4	1.2
LE										
ad libitum										
1	36.3	15.4	6.4	6.2	18.9	1.6	5.0	1.1	0.4	2.2
11	33.0	15.7	5.6	6.0	17.7	1.6	5.1	0.6	0.5	0.8
21	32.3	15.4	3.9	5.2	18.1	1.2	4.6	0.6	0.6	1.1
1.5 %BW										
1	27.0	14.7	6.3	6.0	18.4	1.5	5.4	1.2	0.5	2.5
11	25.7	14.6	5.4	5.6	17.1	1.2	4.4	0.6	0.4	1.3
21	24.0	15.8	3.8	5.2	17.2	1.1	4.3	0.5	0.4	1.0
0.5 %BW										
1	20.0	15.5	5.0	5.5	17.9	1.2	4.7	1.0	0.4	1.2
11	18.3	14.5	3.5	4.9	16.1	1.4	4.3	0.5	0.3	1.3
21	17.7	13.9	3.4	4.9	16.9	1.1	4.3	0.5	0.5	1.0

oxalate and sodium fluorure) syringes. Fish were then killed by a knock on the head and weighed individually. Plasma was separated by centrifugation (5 000 rpm) and aliquoted for different assays (glucose, triglyceride, free fatty acid) and stored at –70 °C until analysis. Dorsal and ventral muscles were dissected and frozen at –20 °C for subsequent proximate composition analysis. A pool of five other fish per group was also killed by an excess of ethylene glycol-monophenyl ether and frozen (–20 °C) until estimation of the whole-body proximate composition. The mean weight (Wi), proximate composition and the plasma concentrations of the fish submitted to different feeding histories (diet, feeding level and duration of feed deprivation) are given in *table II*.

2.3. Re-alimentation challenges

From each of the six groups of fish and after 1, 11 and 21 days of feed deprivation, 150 trout were randomly selected in order to produce three replicates of 50 trout. These replicates were transferred into 0.25-m^3 tanks and submitted to a re-alimentation challenge for 10 days. Replicate groups were weighed at the beginning and at the end of the challenge, and they were fed the same diet they had previously been fed. Feed was distributed by hand to satiation twice daily at 09:00 hours and 16:00 hours, and intake was estimated by weighing the feed containers assigned to each replicate at the beginning and at the end of the challenge.

The growth performance during the re-alimentation challenge was described using the following parameters:

$$\text{mean weight gain (gain)} = \text{final mean weight} - \text{initial mean weight}$$

$$\text{feed conversion efficiency (FCE)} = \text{wet weight gain / dry feed consumption}$$

$$\text{digestible energy intake (DEI)} = \text{feed consumption} \times \text{gross energy of the diet} \times \text{ADC of the energy/number of fish}$$

At the end of the re-alimentation challenge made after 21 days of feed deprivation, a pool of five other fish per replicate was killed by an excess of ethylene glycol-monophenyl ether, and frozen (–20 °C) for estimation of the final whole-body proximate composition, in order to evaluate the nutrient gain, as well as the energy and protein retention of the fish.

2.4. Assays

The different whole-body and faeces samples, which were freeze-dried, and feed samples were analysed for chemical composition following usual procedures: dry matter (110 °C for 24 h), crude protein (Kjeldahl, total nitrogen × 6.25) after acid digestion, lipid extraction by petroleum ether in a Soxhlet apparatus after acid hydrolysis, energy using a Gallenkamp adiabatic calorimeter and chromic oxide according to Bolin and co-workers (1952).

Plasma glucose was analysed using a glucose analyser (Beckman II, USA). Plasma triglyceride and free fatty acid were measured by enzymatic colorimetric methods using commercial kits (triglycerids N Wako and NEFA C Wako, Unipath, France).

2.5. Statistical analysis

All statistical analyses were performed using the Splus 3.2 package (Sigma). The effects of nutritional history on the different variables were tested using a 2 × 3 × 3 (diet × ration level × fasting duration) factorial analysis of variance (ANOVA), and when necessary by analysis of co-variance (ANCOVA) using the initial mean body fish weight at the beginning of each re-alimentation challenge, as a co-factor. Regression analysis was also performed for each variable using parameters selected with leaps and bound procedure. The significance of the regressions was tested with ANCOVA using the tested nutritional factors as co-variables. Results were controlled by performing a series of ANOVAs with permutations of the different regressors using Type I SS.

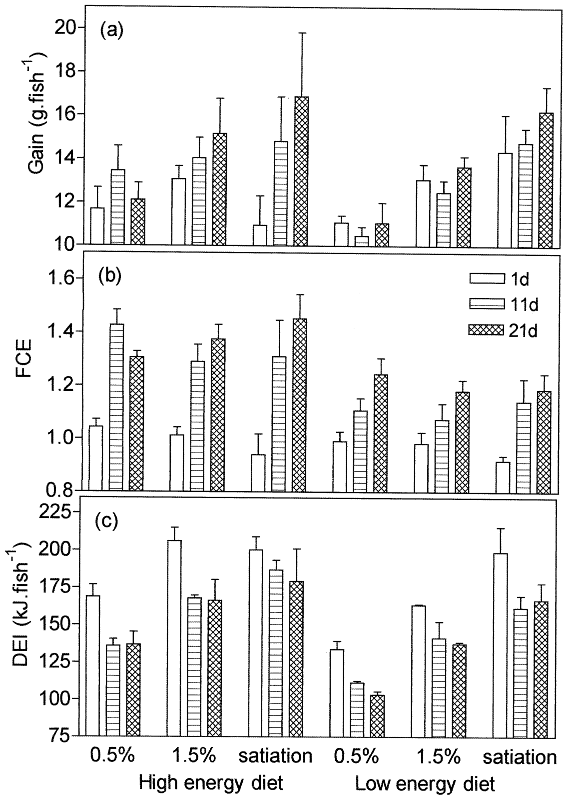

Figure 1. Histogram representations of (a) mean individual weight gain (gain); (b) feed conversion efficiency (FCE); and (c) digestible energy intake (DEI) of groups of rainbow trout fed to satiation for 10 days with high or low energy diets, after different feeding histories (previous feeding level of 0.5 %, 1.5 % or to satiation [satiation], and a duration of feed deprivation of 1, 11 or 21 days [1d, 11d, 21d]). Bars indicate mean values of triplicate groups and one standard deviation is represented.

3. RESULTS

3.1. Effect of nutritional history on growth performances during re-alimentation challenges

The effects of nutritional history on the different variables (gain, FCE, DEI) are presented in *figure 1a, b, c*. Results of ANCOVA are given in *table III*.

It can be seen that weight gain during the re-alimentation challenge is positively affected by the previous feeding level: it is higher in fish previously fed to satiation than in previously restricted fish (*figure 1a*). Weight gain is also affected by the duration of feed deprivation, but not by the diet composition. Nevertheless, the positive effect of feed deprivation on weight gain seems to be stronger in fish fed HE diet than in fish fed LE diet. This is probably the explanation of the significant effects, revealed by the co-variance analysis, of the interactions between the diet and the two other factors (feeding level and feed deprivation).

Feed conversion efficiency (FCE) was not affected by the previous feeding level, but was affected both by diet and the duration of feed deprivation. The increase in FCE in fish previously deprived of food for 11 or 21 days was higher when diet HE was used (*figure 1b*), and this interaction between diet and feed deprivation was significant.

Digestible energy intake (DEI) is significantly affected by previous feeding level (positive effect) and duration of feed deprivation (negative effect), but not by the diet according to the covariance analysis. There is also a significant effect of the interaction feeding level/diet. It is interesting to note here that the decrease in DE intake reached a maximum after 11 days of feed deprivation (*figure 1c*).

3.2. Relationships between previous dietary treatment, growth performance and nutrient retention during the re-alimentation challenge after 21 days of feed deprivation

The influence of the previous dietary treatment (diet, feeding level) on nutrient intake, gain and retention during the re-alimentation challenge performed after

Table III. Influence of the previous dietary treatment (feeding level and diet) and the duration of feed deprivation on weight gain (Gain), feed conversion efficiency (FCE) and digestible energy intake (DEI) in trout fed to satiation during 10 days. The influence of the three factors and their interactions was tested by ANCOVA with Wi as co-factor for each variable (Splus 3.2, Sigma+, 1993). The F value and the *P* levels are indicated. ** and *** indicate when *P* levels are ≤ 0.01 and ≤ 0.001 %, respectively.

	Gain		FCE		DEI	
	F	*P*	F	*P*	F	*P*
Diet	3.9	0.055	6.2	**	0.0	0.957
Previous feeding level	5.2	**	1.13	0.332	13.6	***
Duration of feed deprivation	12.6	***	42.6	***	8.4	***
Feeding level/diet	8.6	***	0.1	0.916	14.9	***
Diet/duration of feed deprivation	5.8	***	10.9	***	0.4	0.706
Feeding level/duration of feed deprivation	5.9	***	2.9	0.036	0.7	0.610
Diet:duration of feed deprivation/feeding level	1.2	0.323	3.3	0.022	1.1	0.357
Cofactor (Wi)	7.8	**	0.29	0.590	17.4	***

21 days of feed deprivation was tested by ANOVA (*table IV*). It can be seen that no significant interaction between diet and previous feeding level was found, and nutrient retention was not affected by either of the two factors tested. Nevertheless, previous feeding level significantly affected all nutrient intakes and nutrient gains (which were highest in fish previously fed to satiation), and diet significantly affected energy and lipid intake, and energy and lipid gain.

Because a strong correlation is observed between previous feeding level and body weight at the beginning of the re-alimentation challenge (Wi), an ANCOVA was made using Wi as a co-factor, in order to test the robustness of diet effect on energy and lipid intake, and on energy and lipid gain. With this additional statistical analysis, the effect of diet remains significant only for lipid intake and gain, which were higher in trout previously fed the HE diet. Energy and protein retention is still unaffected by diet and previous feeding level.

3.3. Relationships between the state of the fish at the beginning of the challenge and growth performance during the re-alimentation challenge

In order to test the hypothesis that growth performances during re-alimentation challenges, described by the variables gain, FCE and DEI could have been predicted by the initial weight and the biological state of the fish, an attempt was made to explain the observed results using the values of the following parameters at the beginning of the challenges: body weight, body weight^2, whole body composition (protein, lipids, energy), muscle composition (protein, lipids, energy), and plasma concentration of glucose,

Table IV. Effect of previous dietary treatment (HE or LE diet, fed to satiation, at 1.5 or 0.5 % of their body weight during 34 days, and subsequently feed deprived during 21 days) on energy, lipid and protein intake, energy, lipid and protein gain, and energy and protein retention. Energy is expressed in kJ, lipid and protein in g of individual intake or gain during the re-alimentation challenge. Data are given as means ± s.d., $n = 3$. The influence of the previous dietary treatment (diet and previous feeding level) and the interactions was tested by ANOVA (Splus 3.2, Sigma+, 1993) for each variable. The results of ANCOVA (factor = diet; cofactor = Wi) is also given for each variable. The F value and the *P* levels are indicated for the two statistical treatments. ** and *** indicate when *P* levels are ≤ 0.01 and ≤ 0.001 %, respectively.

	Wi	Energy intake		Lipid intake		Protein intake		Energy gain		Lipid gain		Protein gain		Energy retention		Protein retention	
HE																	
ad libitum	41.8 ± 1.1	228 ± 26		2.4 ± 0.3		4.2 ± 0.5		173 ± 13		2.4 ± 0.2		3.3 ± 0.1		0.76 ± 0.09		0.79 ± 0.09	
1.5 % BW	26.5 ± 0.9	213 ± 22		2.2 ± 0.2		3.9 ± 0.4		127 ± 13		1.3 ± 0.2		2.7 ± 0.6		0.60 ± 0.08		0.68 ± 0.13	
0.5 % BW	19.2 ± 0.4	180 ± 13		1.9 ± 0.1		3.3 ± 0.3		117 ± 7		1.4 ± 0.4		2.3 ± 0.2		0.66 ± 0.09		0.70 ± 0.05	
LE																	
ad libitum	32.5 ± 0.6	207 ± 16		0.8 ± 0.1		4.7 ± 0.4		145 ± 28		1.1 ± 0.1		3.2 ± 0.9		0.69 ± 0.09		0.68 ± 0.14	
1.5 % BW	24.2 ± 0.9	175 ± 0		0.7 ± 0.0		4.0 ± 0.0		102 ± 6		0.8 ± 0.2		2.4 ± 0.0		0.58 ± 0.04		0.60 ± 0.01	
0.5 % BW	17.6 ± 0.2	135 ± 5		0.5 ± 0.0		3.1 ± 0.1		77 ± 7		0.5 ± 0.1		2.0 ± 0.3		0.58 ± 0.05		0.67 ± 0.09	
ANOVA		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Diet		19	***	423	***	1.1	0.345	19	***	67	***	0.6	0.461	2.3	0.158	2.4	0.148
Previous feeding level		20	***	10	***	25	***	17	***	24	***	8.7	**	5.3	0.022	1.4	0.288
Previous feeding level/diet		0.8	0.470	0.9	0.430	2.3	0.146	0.4	0.669	3.9	0.049	0.1	0.912	0.2	0.787	0.3	0.774
ANCOVA		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Diet		5.2	0.028	347	***	4.0	0.064	4.8	0.044	29	***	0.1	0.753	0.5	0.486	1.5	0.238
Cofactor (Wi)		24	***	18	***	21	***	43	***	40	***	16	***	6.7	0.021	1.4	0.260

Table V. Results of linear regression analysis for weight gain (Gain), feed conversion efficiency (FCE) and digestible energy intake (DEI) in trout fed to satiation during 10 days. Significant variables were selected with leaps and bound procedure (Splus 3.2, Sigma+, 1993. ** and *** indicate when *P* levels are ≤ 0.01 and ≤ 0.001 %, respectively. The influence of the three factors and their interactions were subsequently tested by ANCOVA (Splus 3.2, Sigma+, 1993) for each variable. The F value and the *P* levels indicate that with the exception of DEI, the influence of the factors (diet, previous feed level and duration of feed deprivation) is already included in the selected variables.

	Gain		FCE		DEI	
	coeff.	*P* > |t|	coeff.	*P* > |t|	coeff.	*P* > |t|
Body weight						
Initial weight	0.117	***	– 0.0077	***	7.19	***
Initial weight^2	– 0.002	***			– 0.090	**
Body composition						
Protein						
Lipids					2.36	0.023
Energy						
Muscle composition						
Protein						
Lipids			0.2062	***		
Energy			– 0.0652	**		
Plasma concentration						
Glucose	– 0.292	***	– 0.31	***	35.98	***
Free fatty acids	1.243	***	0.99	***	25.88	0.250
Triglycerids						
Overall ANOVA for the regression						
	R^2	*P*	R^2	*P*	R^2	*P*
	0.74	***	0.86	***	0.84	***
Covariance analysis of the same models + co-factor 'Diet-feed deprivation-feeding level'						
	F	*P*	F	*P*	F	*P*
	1.22	0.302	1.58	0.135	4.77	***

free fatty acids (FFA) and triglycerids. In order to achieve this analysis, the significant parameters were selected with leaps and bound procedures (Splus) and in a second step, a linear regression was made for each variable using the selected parameters (*table V*). The overall analysis of variance is significant at the 1 % level with coefficients of correlation between 0.74 and 0.86 for the three variables tested. It can be observed that body weight participated in the regression for gain, FCE and DEI. Among the parameters describing the initial body composition, only the muscle lipid content affected FCE. Among the plasma metabolites, glucose (*figure 2a, b*) and FFA (*figure 2c, d*) contributed significantly to the model, and especially when using high energy diet, but not the triglycerids.

Co-variance analysis of the same models (*table V*) did not improve the significance for gain and FCE, demonstrating that the influences of the three factors describing the nutritional history are already included in the effects of the selected variables. This is not the case for DEI, where the addition of these factors into the model significantly reduced (at the 1 % level) its variability.

Because several of the variables are correlated, the results mentioned above have been determined by performing a series of ANOVAs with permutations of the different regressors, including the more significant combinations of the three factors describing the nutritional history and taking into account only the type I

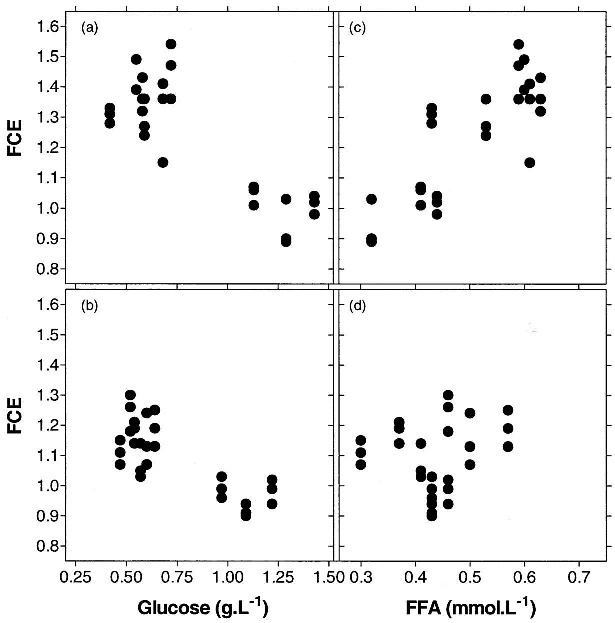

Figure 2. Scatterplots showing relationships between initial plasma glucose concentration and feed conversion efficiency (FCE) in rainbow trout fed high (a) or low (b) energy diets, and between initial plasma free fatty acid concentration and feed conversion efficiency in rainbow trout fed high (c) or low (d) energy diets, after being submitted to different past nutritional histories.

SS. The only difference was that plasma glucose was no longer significant for gain and FCE, but remained significant in the DEI model (results not shown).

4. DISCUSSION

Past nutritional history affected growth during re-alimentation. Nevertheless, it can be seen that the dietary energy content, the previous feeding level and the duration of feed deprivation did not equally affect the different parameters tested. Among these three factors, duration of feed deprivation had a major effect on weight gain, FCE and DEI. Previous feeding level had an effect only on gain and DEI, while dietary energy mainly affected FCE. Strong interactions between the factors were noted.

Because fish continue to be fed two different diets during re-alimentation the diet effect cannot be fully considered as a past nutritional effect. The only way to differentiate the specific effect of the diets taken apart from the 'history' would have been to use both diets on each treatment using a $2 \times 2 \times 3 \times 3$ factorial design (diet during the re-alimentation $\times$ diet during the preparation of the fish $\times$ ration level $\times$ fasting duration). Therefore, the design of this experiment can be considered as incomplete. Nevertheless, the fact that weight gain during the re-alimentation challenge was not affected by the dietary energy content is of particular interest. With the exception of Talbot (1993), evidence for a growth potential that is not related to dietary energy content has been found with rainbow trout by several authors (Grove et al., 1978; Takeuchi et al., 1978; Boujard and Médale, 1994). This experiment was the first to suggest that the lack of influence of dietary energy on growth when fish are fed to satiation is not masked by the past nutritional history such as several days of starvation.

The fact that FCE was not affected by the previous feeding level should also to be mentioned. This result suggests that even a severe restriction in feeding level is not similar to a period of food deprivation in the preparation for a compensatory growth process. Kim and Lovell (1995) failed to demonstrate any effect of a temporarily restricted feeding on subsequent FCE in *Ictalurus punctatus*. Jobling and Koskela (1996) observed that rainbow trout display compensatory growth following a period of under-nutrition by increasing feed intake. The response was strongest amongst those individuals that previously suffered the greatest growth limitation but no effect on FCE was observed.

Increased feed intake during growth compensation following a period of food deprivation has been reported for Arctic charr *Salvelinus alpinus* (Miglavs and Jobling, 1989), Atlantic cod *Godus morhua* (Jobling et al., 1994), Atlantic salmon *Salmo salar* (Metcalfe and Thorpe, 1992; Bull et al., 1996; Bull and Metcalfe, 1997), and European minnow *Phoxinus phoxinus* (Russel and Wootton, 1992, 1993). Unlike most other studies, no increase in appetite (DEI) related to the duration of feed deprivation could be shown in our experiment. This discrepancy could be species specific, or linked to an experimental artefact that limited the appetite of the fish, but it should also be remembered that our experiment was conducted with small, fast-growing rainbow trout, raised at optimal temperature for growth. So, feed intake might have already been optimum in our control groups (fish submitted to 1 day of feed deprivation only). Moreover, in most studies with rainbow trout that demonstrate growth compensation after short periods of food deprivation, food intake is not monitored so hyperphagia is suspected but not demonstrated (Weatherley and Gill, 1981; Quinton and Blake, 1990).

In our study, the increase in gain during the growth spurt is clearly caused by a FCE increase regardless of the dietary energy content. The enhanced feed conversion efficiency following periods of food deprivation in rainbow trout has been suggested by several authors (Dobson and Holmes, 1984; Kindschi, 1988; Quinton and Blake, 1990). One might hypothesise that this phenomenon is due to a preferential accretion of lean body mass. But this assumption is not supported by our data, since lipid gain was high in all fish fed after 21 days of fasting, regardless of the previous dietary treatment. In addition, both protein and energy retention was found to be high, the highest values of retention being ca. 0.8 in fish fed previously to satiation, with the HE diet [protein and energy retention were 0.45 and 0.50, respectively, in rainbow trout of the same strain, same size, fed near satiation during a 3-month growth trial performed at the same farm with similar diets (Brauge et al., 1995)]. According to Russel and Wootton (1992), the enhanced efficiency of feed utilisation during the re-alimentation challenge might be caused in part by a reduction in basal metabolism which takes place during the feed deprivation period, and extends into the initial stages of re-alimentation.

The influence of the size of lipid depots on feed intake during compensatory growth has been demonstrated in Arctic charr (Jobling and Miglavs, 1993) and Atlantic salmon (Bull and Metcalfe, 1997). From our set of data an effect of internal lipid stores on feed intake of rainbow trout was not evident. Fish body and muscle composition at the beginning of the challenges did not affect growth performance and feed intake, nor protein and energy retention after 21 days of feed deprivation, despite the fact that past nutritional history induced a large variation in body lipid content (3.4 to 12.3 % wet weight). Only the proportion of lipids in the muscle and FCE were correlated, but this is not surprising since FCE and muscle adiposity are both closely related to the dietary energy content. The fact that body and muscle composition participated so weakly to the regression analysis for gain, FCE and DEI suggests that if lipid stores are contributing to the regulation of compensatory growth response, it is not by means of increased feed conversion efficiency.

During the re-alimentation challenges FCE was highest in groups of fish that had the lowest plasma glucose content. This is an effect of the fasting duration, plasma glucose being lower after 11 and 21 days fasting than after a 1-day fast. However, one might suppose that glucose enters more easily into the cells to be used as an energy source when the levels of circulating glucose are low and the cells' energy demands are high. Increasing the energy supply to cells would thus contribute to the improvement of FCE.

FCE was also affected by the initial plasma free fatty acids concentration in trout previously fed the high lipid diet. The level of circulating free fatty acids generally reflects the mobilisation of body lipid reserves. In mammals, β oxidation is stimulated by food deprivation (Yu et al., 1997). In fish, oxidation of body lipids is also a major pathway to meet the energy requirements during fasting (Kaushik and Médale, 1994). The data obtained in the present study suggest an inhibition of fatty acid β oxidation during the re-alimentation challenge in order to restore body lipid reserves. This hypothesis is supported by the high lipid gain observed in fish fed the HE diet to satiation before the 21 days fasting. Consequently the enhanced FCE would result from the improved lipid gain.

5. CONCLUSION

This experiment is the first to consider both feed intake and feed efficiency during compensatory growth with rainbow trout submitted to different past nutritional histories. The effect of feed deprivation does not seem to be the same as the effect of feed restriction: from our set of data and the information available in the literature, it can be seen that the former is responsible for an increase in feed efficiency, and the latter induces hyperphagia. In addition, the compensatory growth response is affected by the dietary energy content of the diet, with the highest increase in growth performance in fish previously fed with high energy diet. So, past nutritional history has to be considered with caution during compensatory growth experiments. The strongest response was observed when fish were previously fed to satiation with diets of high energy content, and submitted to 3 weeks of feed deprivation. This suggests a kind of 'memory' of metabolic pathways in relation to the previous dietary treatment. Feed intake during the re-alimentation challenge does not appear to be driven by body lipid content.

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