

Voluntary feed intake, feed and nutrient utilisation in slow and fast growing rainbow trout strains

Luísa Maria Pinheiro Valente⁽¹⁾, Benoît Fauconneau⁽²⁾,
Emídio Ferreira dos Santos Gomes^(3*)

⁽¹⁾ *Secção de Engenharia Biológica e Ambiental, Universidade de Trás-os-Montes e Alto Douro, Apartado 202, 5001-Vila Real codex, Portugal*

⁽²⁾ *INRA, Laboratoire de Physiologie des poissons, Campus de Beaulieu, 35042 Rennes cedex, France.*

⁽³⁾ *Instituto Ciências Biomédicas 'Abel Salazar', Universidade do Porto, 4000-Porto, Portugal*

Received June 5, 1997; accepted February 20, 1998.

Abstract – Two rainbow trout strains differing in their growth performance were used to study possible interactions between genotype, dietary composition and feed level on their feed utilisation efficiency and voluntary feed intake. Two diets (35 and 45 % of crude protein) and two feeding levels (to satiation or at a restricted level of 2 % of body weight), were used. The two diets were distributed, in duplicate, for each strain, during a four month growth trial. At the end of the experiment the digestibility of the two diets was determined in each strain, using chromic oxide, as a marker, and an automatic system for the faecal collection. The body composition of both strains was also analysed. The final weight of fish of the fast growing strain, fed to satiation, was significantly higher than that observed for fish of the slow growing strain. No significant differences were found between the strains's body weights, when a dietary restriction was made. Results observed for the feed-gain ratio were also similar between the two strains. The apparent digestibility coefficient (ADC) of dry matter and energy were significantly different between the two diets but similar for both strains. Concerning protein digestibility no significant differences were observed for diets, although one of the strains appeared to show a higher ADC for protein. Body composition as well as nitrogen and energy retention were similar for both diets and strains. © Ifremer-Elsevier, Paris.

Nutrition / strain / growth efficiency / digestibility / *Oncorhynchus mykiss*

Résumé – Capacité d'ingestion et efficacité alimentaire de deux souches de truites arc-en-ciel à fort et faible potentiel de croissance. Deux souches de truites arc-en-ciel ayant des potentiels de croissance différents ont été étudiées pour les interactions possibles entre le génotype, la composition alimentaire et les quantités d'aliments sur leur capacité d'ingestion et d'utilisation des nutriments. Deux aliments (35 et 45 % de protéine brute) ont été distribués à deux niveaux d'alimentation (ad libitum ou restreint à 2 % du poids vif) sur une période expérimentale de quatre mois. La composition chimique de la carcasse des deux souches a été analysée en début et en fin d'expérience. En fin d'expérience, la digestibilité des deux aliments a été analysée pour les deux souches par la méthode indirecte de marquage de l'aliment avec l'oxyde de chrome et par la récolte en continu des feces. Les deux aliments utilisés induisent des croissances et des coefficients d'utilisation des nutriments différents. Le poids vif final des poissons alimentés ad libitum est significativement plus élevé dans la souche à forte croissance que dans la souche à faible croissance quel que soit l'aliment distribué. La capacité d'ingestion estimée par la quantité d'aliments distribués ad libitum est significativement plus élevée chez les poissons de la souche à forte croissance que chez ceux de la souche à faible croissance. Aucune différence de poids final n'est observée entre les deux souches nourries avec une alimentation restreinte à 2 % du poids vif. L'indice de consommation, les coefficients d'utilisation des nutriments et les coefficients d'utilisation digestive de la matière sèche et de l'énergie sont similaires pour les deux souches. La digestibilité des protéines n'est pas significativement différente entre les deux aliments testés. Une des souches tend à présenter un coefficient d'utilisation digestive des protéines plus élevé mais cette différence n'est pas significative. La composition de la carcasse ainsi que le bilan azoté et énergétique sont similaires pour les deux aliments et pour les deux souches de poissons. © Ifremer-Elsevier, Paris.

Nutrition / croissance / digestibilité / *Oncorhynchus mykiss*

1. INTRODUCTION

Many factors affect the rate of growth: environmental, nutritional, genetic and endogenous [27]. Differences in growth rate among strains have been reported for various salmonid species [2, 9, 12, 17, 18, 26, 28, 29], but it is not known how the increased growth obtained through genetic selection programmes is achieved. One of a very large number of possibilities is that a better efficiency of digestion and/or a subsequent better utilisation of the food is being achieved. Alternatively, perhaps higher quantities of ingested feed are being selected [27].

The growing fish body can be regarded as consisting of two major components: water and dry matter, with the latter component further divisible into the (sub-) components of lipid, protein, carbohydrate and ash, i.e. mineral contents [30]. Concerning the genetic improvement of growth, results on the modifications of body composition and digestibility coefficients are controversial. While Austreng et al. [1] found no differences in fat, protein or moisture content between families of rainbow trout, others observed an influence of body composition by genotype [2, 17, 21, 22].

The aim of this work was to evaluate whether differences in performance due to genetic origin could be explained by differences in voluntary feed intake and/or feed efficiency or utilization of nutrients measured as nitrogen and energy budgets.

2. MATERIAL AND METHODS

2.1. Experimental animals

Two strains of rainbow trout (*Oncorhynchus mykiss*) were used in this study. Strain C, known to have high growth rates, was originally obtained from a French farm (Cornec 29) and had been raised in the INRA experimental facilities for six generations; strain M (Mirwart strain) obtained from a private farm in Belgium by the University of Louvain, had been raised in the INRA experimental facilities for three generations.

Eggs of the two rainbow trout strains were fertilized on the same day, and were transported to the experimental fish farm of Trás-os-Montes e Alto Douro University, in Vila Real, Portugal, at the eyed stage. The eggs were then incubated at 11 °C, and they hatched on January 1, 1996. The feeding regime was adjusted in order to start the experiment with fish of both strains having the same body weight. The experiment was carried out between April and July 1996, both strains being raised in the same experimental conditions.

Twelve groups of 135 fish, with an individual weight range of 3.5–4.5 g, were randomly distributed among 12 square fibre glass tanks (300 L), in duplicate groups for each treatment. The water temperature during the experiment ranged from 12 to 16 °C, depending on the

season; while the water flow was about 5 L·min⁻¹, in an open circuit system.

2.2. Feed and feeding

Four groups of fish of each strain were fed one of two diets, Diet 1 (D1) or Diet 2 (D2), containing 45 and 35 % of crude protein, respectively. The diets were prepared after grinding, and mixing the ingredients in a pelleting machine at 50 °C. Feed ingredients and diet composition are summarized in *table 1*. Fish were fed to satiation, by hand, three times a day at about 9.30, 14.00 and 18.30. The quantity of non-ingested food was negligible. The other two groups of each strain were fed diet D1 at a ration level of 2 % body weight/day (D1r). Data on distributed food and weight gain was collected every 3–4 weeks during the 4 month trial. Twenty fish from each tank were weighed individually, at each time, to the nearest 0.01 g.

Table 1. Ingredients and chemical composition of the two experimental diets.

	Diet 1	Diet 2
Ingredients (%)		
Fish oil	3.00	3.00
Wheat ¹	19.10	36.10
Fish meal ²	36.00	27.50
Full-fat soybean ¹	23.00	23.00
Meat meal ³	18.50	10.00
Binder ⁴	0.20	0.20
Vitamin premix ⁵	0.10	0.10
Mineral premix ⁶	0.10	0.10
Chemical composition		
Dry matter (%)	90.70	91.69
Protein (Nitrogen × 6.25) (%)	45.06	35.65
Fat (%)	10.45	9.79
Energy (kJ·g ⁻¹)	19.59	20.16

¹ Infrared micronized and flaked in a roller mill.

² Brown fish meal from Chile (Anchova).

³ Defatted meat meal from Portugal.

⁴ Lignino sulphate.

⁵ Vitamins (mg · kg⁻¹ diet): α -tocopherol, 20; menadione, 5; thiamine, 5; Ca panthothenate, 10; nicotinic acid, 100; pyridoxine, 5; folic acid, 2; cyanocobalamin, 0.05; biotin, 0.5; ascorbic acid, 200; paraminobenzoic acid, 50; inositol, 500; choline chloride, 500; (IU · kg⁻¹ diet) retinol, 10000; cholecalciferol, 2000.

Minerals (mg · kg⁻¹ diet): cobalt sulphate, 1.91; copper sulphate, 19.6; iron sulphate, 200; sodium fluoride, 2.21; potassium iodide, 0.78; magnesium oxide, 166; manganese oxide, 13; sodium selenite, 0.22; zinc oxide, 12.5; (g · kg⁻¹ diet) dicalcium phosphate, 5; sodium chloride, 0.4; potassium chloride, 1.

2.3. Digestibility

A digestibility trial was performed, with 40 fish (weight range 55–75 g) of each strain, fed once a day (1 % of body weight/day), and two experimental diets (D1 and D2) containing 1 % of chromic oxide as an

external marker. Faeces were collected over a 4 day period using a continuous automatic faeces collector [6]. After collection, faeces were stored at -18°C until they were analyzed. This procedure was repeated four times for each diet, each replicate being carried out in a different tank to reduce any tank effect.

2.4. Calculation

The daily growth coefficient (DGC), specific growth rate (SGR), feed gain ratio (FGR) and voluntary feed intake (VFI) were calculated using the following formulae:

$$\text{DGC} = 100 (W_f^{1/3} - W_i^{1/3})/\text{days } (\% \cdot \text{d}^{-1}),$$

$$\text{SGR} = 100 (\text{Ln } W_f - \text{Ln } W_i)/\text{days } (\% \cdot \text{d}^{-1}),$$

$$\text{FGR} = \text{feed intake (g dry matter)}/\text{weight gain (g)},$$

$$\text{VFI} = \text{feed intake}/\text{mean body weight}/\text{days } (\% \cdot \text{d}^{-1}).$$

The apparent digestibility coefficients (ADC) of dry matter and nutrients were calculated using the following formulae:

$$\text{ADC of dry matter } (\%) = 100 - [100 \times (\% \text{ chromic oxide in diet}/\% \text{ chromic oxide in faeces})],$$

$$\text{ADC of nutrients } (\%) = 100 - [100 \times (\% \text{ chromic oxide in diet}/\% \text{ chromic oxide in faeces}) \times (\text{nutrient or energy content in faeces}/\text{nutrient or energy content in diet})].$$

Metabolizable energy (ME) was estimated indirectly by carcass analysis and digestibility data, calculating total nonfaecal nitrogen losses, branchial and urinary, by the differences between digested nitrogen and recovered nitrogen as shown in the following expressions:

$$\text{Metabolizable energy (ME)} = \text{Digestible energy (DE)} - \text{Non faecal energetic losses (NFEL)},$$

$$\text{NFEL} = \text{Non faecal excreted Nitrogen (NFEN)} \times 25 \text{ kJ} \cdot \text{g}^{-1} \text{ N [7]},$$

$$\text{NFEN} = \text{Digestible Nitrogen (DN)} - \text{Retained Nitrogen (RN)}.$$

$$\text{Total heat loss} = \text{ME} - \text{Recovered energy (RE)}.$$

2.5. Analytical methods

Frozen whole body samples and faeces were lyophilized before analysis. Feed, whole body and faeces samples were analyzed for dry matter (104°C for 24 h), ash by calcination in a muffle furnace (600°C for 15 h), crude protein (Kjeldahl, total nitrogen $\times 6.25$) after acid digestion, fat content by petroleum ether $40\text{--}60^{\circ}\text{C}$ extraction (Soxhlet) and energy using an adiabatic bomb calorimeter (Parr).

2.6. Statistical analysis

Statistical analyses followed methods outlined by Sokal and Rohlf [23]. Data were subjected to analysis of variance with the Statistics 5.0 for Windows package. When F values indicated significance, individual means were compared by Tukey's Honest Significant Difference (HSD) test. All differences were considered significant at $P < 0.05$. Covariate models were performed in cases where a dependence between initial body weight and growth performance or/and feed intake could be expected.

3. RESULTS

3.1. Growth performance

Data on body weight was collected every 3–4 weeks during the trial (*figure 1*). A general analysis of variance showed significant differences between strains and feeding level: fish of strain C weighing more than those of strain M, and fish fed to satiation weighing more than those fed at a restricted level. When differences between groups were tested, significant differences were found, in body weight, between strains fed to satiation diet D1 or diet D2; after 7 weeks of treatment ($P < 0.05$) but no significant differences were observed between strains fed the restricted level, diet D1r ($P > 0.05$).

Results on weight gain, feed intake and efficiency are presented in *table II*. Concerning final weight gain, fish of strain C showed significantly higher values than fish of strain M ($P < 0.05$), when diets D1 or D2 were fed to satiation. No significant differences were found for fish fed the restricted level, diet D1r. The results observed for daily growth coefficient are in accordance with those obtained for weight gain. However, when the specific growth rate was used to characterise growth performance, no significant differences were found between strains fed either of the diets to satiation. Fish fed a restricted ration level, showed an overall SGR of 1.43 and 1.63, in the C and M strain fish, respectively.

The specific growth rate, for both strains, calculated for each of the five periods of the experiment, was plotted against body weight. For an 85 g fish, the estimated SGRs were 1.99 and 1.89 for fish of strains C and M fed diet D1, and 2.01 and 1.93 for fish of strains C and M fed diet D2.

3.2. Feed intake and efficiency

No significant differences were found in the feed gain ratio (FGR), between strains or diets; however,

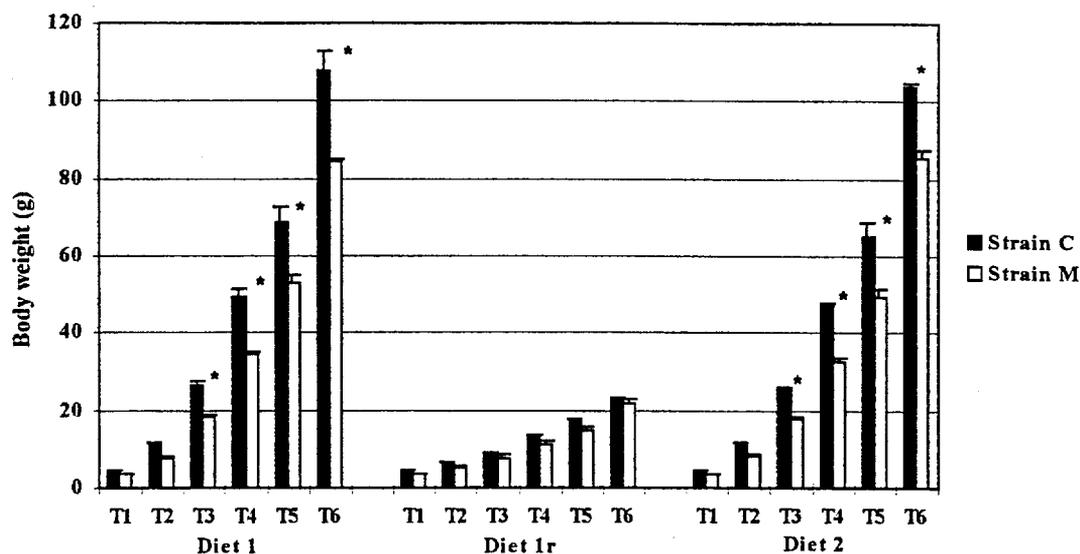


Figure 1. Body weight (g) of two rainbow trout strains, C and M, fed Diet 1 (D1) and Diet 2 (D2) to satiation, or Diet 1 at a restricted level of 2 % of body weight (D1r) in different periods of time (101, 123, 150, 170, 186 and 214 days after hatching). * ANOVA $P < 0.05$.

Table II. Growth performance and feed intake of two rainbow trout strains (C and M) fed diet D1 (45 % protein), diet D1r (D1 at 2 % body weight) and diet D2 (35 % protein). Means of duplicate groups \pm SD.

	D1		D1r		D2	
	C	M	C	M	C	M
<i>Growth performance</i>						
Weight gain (g)	103.40 \pm 4.67 ^a	80.91 \pm 0.73 ^b	18.60 \pm 0.08 ^c	18.26 \pm 1.12 ^c	99.40 \pm 0.78 ^a	82.12 \pm 2.05 ^b
Daily growth coefficient (% \cdot d ⁻¹)	2.75 \pm 0.05 ^a	2.55 \pm 0.02 ^b	1.06 \pm 0.01 ^c	1.13 \pm 0.04 ^c	2.70 \pm 0.02 ^a	2.56 \pm 0.04 ^b
Specific growth rate (% \cdot d ⁻¹)	2.80 \pm 0.03 ^a	2.84 \pm 0.03 ^a	1.43 \pm 0.01 ^b	1.63 \pm 0.04 ^c	2.77 \pm 0.02 ^a	2.83 \pm 0.04 ^a
Feed gain ratio	1.18 \pm 0.03 ^a	1.22 \pm 0.09 ^a	1.05 \pm 0.01 ^b	0.92 \pm 0.001 ^b	1.30 \pm 0.03 ^a	1.24 \pm 0.02 ^a
<i>Intake</i>						
Feed (% \cdot d ⁻¹)	2.11 \pm 0.06 ^a	2.18 \pm 0.16 ^a	1.37 \pm 0.01 ^b	1.29 \pm 0.02 ^b	2.30 \pm 0.0004 ^a	2.21 \pm 0.03 ^a
Crude protein (% \cdot d ⁻¹)	1.04 \pm 0.03 ^a	1.08 \pm 0.08 ^a	0.68 \pm 0.01 ^b	0.64 \pm 0.01 ^b	0.88 \pm 0.0002 ^c	0.84 \pm 0.01 ^c

Figures with different superscripts in the same line are significantly different from each other (ANCOVA, $P < 0.05$).

fish fed at a restricted ration level had the lowest FGR (table II).

No significant differences were found in the voluntary feed intake (VFI) between strains (table II), however, and taking into account the general decrease of VFI with body weight, this means that the ingestion capacity of strain C was always higher than that observed in strain M. Although no effect of diet was observed, there was a slightly tendency for the fish fed diet D2 to show a higher voluntary feed intake than fish fed diet D1. Since diet D2 had a lower protein content, daily protein intake per unit body weight was lower in these groups. Plotting fish intake during each experimental period against body weight, strain C shows a higher intake for fish with a body weight lower than 40 g.

Table III. Apparent digestibility coefficients (%) of the experimental diets, D1 and D2, containing two protein levels 45 and 35 % respectively, in two rainbow trout strains C and M. Mean \pm SD; $n = 4$.

Strain	Diet	Dry matter	Energy	Protein
C	D1	72.7 \pm 1.3 ^a	82.0 \pm 1.7 ^a	86.2 \pm 0.6 ^{a,b}
C	D2	69.3 \pm 1.1 ^b	78.4 \pm 0.6 ^b	84.8 \pm 1.1 ^a
M	D1	71.6 \pm 3.1 ^a	81.5 \pm 3.1 ^a	86.8 \pm 1.6 ^{a,b}
M	D2	68.4 \pm 1.6 ^b	76.8 \pm 0.8 ^b	87.0 \pm 1.2 ^b

Figures with different superscripts in the same solution are significantly different from each other (ANOVA, $P < 0.05$).

3.3. Digestibility

The digestibility of the two diets (D1 and D2) was evaluated for each strain (table III). The apparent digestibility coefficients of dry matter and energy were

significantly different between the two diets and similar for both strains. Concerning protein digestibility, fish of strain M presented slightly higher values than fish of strain C, and no significant differences were observed between diets.

3.4. Body composition

The body compositions of the fish at the beginning and end of the experiment is presented in *table IV*. Fish fed to satiation contained more dry matter, ashes, energy and lipids than the initial sample. Concerning the feeding level, the amounts of dry matter, energy and lipids were significantly higher in fish fed to satiation, while the amount of ash was highest in the scantiest fed fish. No effect of diet or strain was however observed for any of the parameters analysed. The protein content of the whole fish was not significantly influenced by the ration level or type of diet.

3.5. Retention

No significant differences were observed between strains for nitrogen and energy retention (*table V*). Nitrogen retention efficiency was highest in fish fed diets D1r and D2. Only fish of strain C presented a significantly lower recovered energy than fish fed to satiation. The calculated heat increment was significantly lower for fish fed diet D1r compared with those fed diet D2.

4. DISCUSSION

The results obtained in this experiment demonstrated the higher growth potential of fish of strain C in comparison with fish of strain M and confirmed the previous data obtained by Valente et al. [24]. The methods used to characterise growth performance of the strains have a strong influence on the conclusion. In fact, results based on the specific growth rate (SGR) or on the daily growth coefficient (DGC) of strains were not equivalent. The decrease of SGR with increasing body weight does not allow the direct com-

parison of fish growth when one source of variation is the growth potential of the strains. The present results suggested that the DGC might be the best index to be used when fish growth capacities is being studied. Cho [5] has already suggested that the use of SGR presents a serious deficiency and that the DGC can be a more accurate and useful coefficient for growth prediction.

Food supply is probably the most important factor affecting the growth in fish, while other factors, either abiotic or biotic, only indirectly affect growth because they affect feeding and metabolism, and consequently the conversion of food into body materials and useful energy [13]. In this report the feed consumption of fish from strain C was higher than the feed consumption of fish from strain M throughout the experiment. Fish from either strain digested and retained similar amounts of nutrients, still the strains grew at different rates when fed *ad libitum*. On restricted feeding, fish from both strains grew at similar rates. This situation would effectively stop the fast growing fish to use its advantage in a larger capacity to ingest feed. When fed diet D1 *ad libitum*, fish from strain C gained 22 % more weight and consumed 19 % more feed (weight gain ÷ feed gain ratio) than fish from strain M. The corresponding numbers when fed diet D2 *ad libitum* were 17 % and 21 %. Thus, the growth differences appear to be well rationalised by the differences in the feed consumption. When calculated for the whole experimental period, the voluntary feed intake (VFI) was similar for fish of both strains when fed the diets *ad libitum*. As SGR, the feed intake will however decrease when the fish size increases. Considering the lower weight and the slower growth of fish from strain M, this fish may very well have consumed less feed than fish from strain C when related to fish size. Thus, although similar VFI, the feeding capacity of fish from population C appears to have been higher than the capacity of fish from population M throughout the experiment. Kinghorn [12] has already observed a genetic variation in feed consumption in rainbow trout; fish, which consume more feed, grow faster.

Feed again ratio, a trait of major importance in any animal production system, did not show significant

Table IV. Whole body composition of fish at the beginning and end of the experiment. Mean values (% wet weight) of duplicate groups of 5 pooled fish ± SD.

		Dry matter	Ash	Energy	Protein	Lipids
C	Initial	24.5	2.3	6.2	14.7	5.7
M	Initial	24.6	2.4	5.7	15.5	5.4
C	D1	26.9 ± 0.9 ^a	2.6 ± 0.06 ^a	7.2 ± 0.02 ^a	15.1 ± 0.01 ^a	8.3 ± 1.1 ^{a,c}
M	D1	25.7 ± 1.3 ^a	2.5 ± 0.03 ^a	7.1 ± 0.6 ^a	13.7 ± 0.001 ^a	7.5 ± 0.8 ^{a,c}
C	D1r	29.9 ± 1.7 ^b	2.9 ± 0.1 ^a	4.5 ± 0.6 ^b	13.4 ± 0.6 ^a	3.1 ± 1.0 ^b
M	D1r	24.2 ± 3.2 ^{a,b}	2.9 ± 0.4 ^a	6.0 ± 0.6 ^{a,b}	15.6 ± 1.9 ^a	5.5 ± 0.1 ^{a,b}
C	D2	27.2 ± 0.2 ^a	2.5 ± 0.1 ^a	7.3 ± 0.1 ^a	14.8 ± 0.2 ^a	8.6 ± 0.1 ^c
M	D2	26.5 ± 0.1 ^a	2.6 ± 0.1 ^a	6.7 ± 0.5 ^a	14.8 ± 1.0 ^a	7.8 ± 0.1 ^{a,c}

Figures with different superscripts in the same column are significantly different from each other (ANOVA, $P < 0.05$).

Table V. Retention of nitrogen ($\text{g N}\cdot\text{kg}^{-1}$) and energy ($\text{kJ}\cdot\text{g}^{-1}$) in two rainbow trout strains, C and M, fed diet D1, diet 1r or diet D2. Mean values of duplicate groups \pm SD.

	D1		D1r		D2	
	C	M	C	M	C	M
Crude Nitrogen intake	116.4 \pm 0.6 ^a	109.01 \pm 9.9 ^a	90.7 \pm 6.0 ^b	90.5 \pm 1.8 ^b	98.2 \pm 2.9 ^b	90.2 \pm 1.2 ^b
Digestible Nitrogen intake	100.3 \pm 0.5 ^a	94.6 \pm 8.5 ^a	78.2 \pm 5.1 ^b	78.5 \pm 1.6 ^b	83.3 \pm 2.4 ^b	78.4 \pm 1.1 ^b
Recovered Nitrogen	24.3 \pm 0.01 ^a	21.9 \pm 0.003 ^a	20.9 \pm 1.2 ^a	25.0 \pm 3.7 ^a	23.7 \pm 0.4 ^a	23.6 \pm 1.7 ^a
Non faecal excreted Nitrogen	76.0 \pm 0.5 ^a	72.7 \pm 8.5 ^a	57.3 \pm 6.4 ^b	53.5 \pm 2.2 ^b	59.6 \pm 2.0 ^b	54.8 \pm 2.7 ^b
Nitrogen retention efficiency (% digestible nitrogen intake)	24.2 \pm 0.1 ^a	23.2 \pm 2.09 ^a	26.8 \pm 3.3 ^b	31.8 \pm 4.1 ^b	28.5 \pm 0.4 ^b	30.2 \pm 2.5 ^b
Gross energy intake	28.7 \pm 0.2 ^a	26.9 \pm 2.4 ^a	22.4 \pm 1.5 ^b	22.3 \pm 0.4 ^b	31.8 \pm 0.9 ^c	29.2 \pm 0.4 ^c
Digestible energy intake	23.5 \pm 0.1 ^a	21.9 \pm 2.0 ^a	18.3 \pm 1.2 ^b	18.2 \pm 0.4 ^b	25.0 \pm 0.7 ^a	22.5 \pm 0.3 ^a
Recovered energy	7.2 \pm 0.02 ^a	7.1 \pm 0.6 ^a	4.0 \pm 0.8 ^b	6.1 \pm 0.7 ^{a,b}	7.3 \pm 0.1 ^a	6.8 \pm 0.5 ^a
Non faecal excreted energy	1.9 \pm 0.01 ^a	1.8 \pm 0.2 ^a	1.4 \pm 0.2 ^b	1.3 \pm 0.1 ^b	1.5 \pm 0.1 ^b	1.4 \pm 0.07 ^b
Metabolizable energy	21.6 \pm 0.1 ^a	20.1 \pm 1.8 ^a	16.9 \pm 1.0 ^b	16.9 \pm 0.4 ^b	23.5 \pm 0.7 ^a	21.1 \pm 0.2 ^a
Total heat loss	14.4 \pm 0.1 ^{a,b}	13.0 \pm 2.4 ^{a,b}	13.0 \pm 1.8 ^b	10.7 \pm 0.3 ^b	16.1 \pm 0.6 ^a	14.3 \pm 0.7 ^a
Energetic retention efficiency (% digestible intake)	30.7 \pm 0.1 ^a	32.8 \pm 5.7 ^a	21.8 \pm 5.7 ^a	33.6 \pm 3.1 ^a	29.4 \pm 0.4 ^a	30.3 \pm 2.6 ^a

Figures with different superscripts in the same line are significantly different from each other (ANOVA, $P < 0.05$).

genetic variation, in the present study. This is consistent with earlier results [12, 17]. An effect of feeding level was, however, observed in the present study fish fed to satiation showing a higher FGR than fish fed a restricted ration. Similar results have been reported previously by Markert et al. [15], in coho salmon.

Although protein digestibility was equivalent in both diets, dry matter and energy ADC were lower in fish fed diet D2 (35 % protein). This can be explained by a greater inclusion of micronized wheat meal with a relatively higher level of fibre and consequently a poor digestion of the carbohydrate portion of this dietary component and/or by the relative larger inclusion of starch with a low digestibility [4]. Médale [17] observed a higher protein digestibility in a fast growing strain. However these results were not confirmed by the present work.

Body composition did not seem to be influenced by the genetic origin of the fishes. This is consistent with the findings of Austreng et al. [1] who found no differences in fat, protein or moisture content, between families of rainbow trout. Some studies have however shown a correlation between lipid content of carcass and growth rate [3, 9, 12], whereas other authors found a higher body fat and lower protein content in slow growing rainbow trout strains than in fast growing fish [17, 22].

The proportion of dietary protein did not appear to affect body composition significantly, which is in general accord with earlier observations by Reinitz and Hitzel [20]. The results concerning the feeding level correspond with previous findings [10, 19, 24] that reported an increase in the percentage fat and dry matter and a decrease in the percentage of ash with increasing rations. Protein appeared to be the only body component that was not affected by ration level or diets. This has already been observed in trout [10, 20, 25].

Concerning protein or energy retention, our results are in general accord with earlier observations by Médale [17], who also found no significant differences between rainbow trout strains for these two parameters.

In conclusion, our results suggest that the two rainbow trout strains demonstrated different capacity for feed consumption. This was the main cause of the higher weight gain of the strain with the highest feeding capacity, as the fast growing strain did not demonstrate more efficient nitrogen or energy retention than the slow growing one. Whether the difference in feeding capacity was due to faster absorption and metabolism of nutrients or a more aggressive feeding behaviour remains an open issue.

Acknowledgements

We thank Jorge Filipe and Tiago Aires for performing analytical work and António Júlio Pinto for his technical assistance during the growth trial. We also thank Dr S.J. Kaushik for his critical reading of the manuscript.

REFERENCES

- [1] Austreng E., Risa S., Edwards D.J., Hvidsten H., Carbohydrate in rainbow trout diets. II. Influence of carbohydrate levels on chemical composition and feeding utilization of fish from different families, *Aquaculture* 11 (1977) 39–50.
- [2] Austreng E., Refstie T., Effect of varying dietary protein level in different families of rainbow trout, *Aquaculture* 18 (1979) 145–156.
- [3] Ayles G.B., Bernard D., Hendzel M., Genetic differences in lipid and dry matter content between strains of rainbow trout (*Salmo gairdneri*) and their hybrids, *Aquaculture* 18 (1979) 253–262.
- [4] Bergot F., Brèque J., Digestibility of starch by rainbow trout: effects of the physical state of starch and of the intake level, *Aquaculture* 34 (1983) 203–212.
- [5] Cho C.Y., Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirement, *Aquaculture* 100 (1992) 107–123.
- [6] Choubert G., De la Noüe J., Luquet P., Digestibility in fish: improved device for the automatic collection of faeces, *Aquaculture* 29 (1982) 185–189.
- [7] Elliot J.M., Davison W., Energy equivalents of oxygen consumption in animal energetics, *Oecologia* 19 (1975) 195–201.
- [8] Elvingston P., Johansson K., Genetic and environmental components of variation in body traits of rainbow trout (*Oncorhynchus mykiss*) in relation to age, *Aquaculture* 118 (1993) 191–204.
- [9] Gjerde B., Schaeffer L.R., Body traits in rainbow trout. II. Estimates of heritabilities and of phenotypic and genetic correlations, *Aquaculture* 80 (1989) 25–44.
- [10] Grayton B.D., Beamish F.W.H., Effects of feeding frequency on food intake, growth and body composition of rainbow trout (*Salmo gairdneri*), *Aquaculture* 11 (1977) 159–172.
- [11] Gunnes K., Gjerdrem T., A genetic analysis of body weight and length in rainbow trout reared in seawater for 18 months, *Aquaculture* 24 (1981) 161–174.
- [12] Kinghorn B., Genetic variation in food conversion efficiency and growth in rainbow trout, *Aquaculture* 32 (1983) 141–155.
- [13] Klaudatos S., Apostolopoulos J., Food intake, growth maintenance and food conversion efficiency in the gilt-head sea bream (*Sparus auratus*), *Aquaculture* 51 (1986) 217–224.
- [14] Linder D., Sumari O., Nyholm K., Sirkkomaa S., Genetic and phenotypic variation in production traits in rainbow trout strains and strains crosses in Finland, *Aquaculture* 33 (1983) 129–134.
- [15] Markert J.R., Higgs D.A., Dye H.M., MacQuarrie D.W., Influence of bovine growth hormone on growth rate, appetite, and food conversion of yearling coho salmon (*Oncorhynchus kisutch*) fed two diets of different composition, *Can. J. Zool.* 55 (1977) 74–83.
- [16] Morkramer S., Hörstgen-Schwark G., Langholz H.J., Comparison of different European rainbow trout populations under intensive production conditions, *Aquaculture* 44 (1985) 303–320.
- [17] Médale F., Relation between growth and utilization of energy substrates in three rainbow trout strains, in: *Fish Nutrition in Practice*, S.J. Kaushik, P. Luquet (eds), INRA, Paris, 1993 pp. 37–48.
- [18] Refstie T., Genetic and environmental sources of variation in body weight and length of rainbow trout fingerlings, *Aquaculture* 19 (1980) 351–357.
- [19] Reinitz G., Relative effect of age, diet, and feeding rate on the body composition of young rainbow trout (*Salmo gairdneri*), *Aquaculture* 35 (1983) 19–27.
- [20] Reinitz G., Hitzel F., Formulation of practical diets for rainbow trout based on desired performance and body composition, *Aquaculture* 19 (1980) 243–252.
- [21] Reinitz G.L., Orme L.E., Hitzel F.N., Variations of body composition and growth among strains of rainbow trout, *Trans. Am. Fish. Soc.* 108 (1979) 204–207.
- [22] Smith R.R., Kincaid H.L., Regenstein J.M., Rumsey G.L., Growth, carcass composition, and taste of rainbow trout of different strains fed diets containing primarily plant or animal protein, *Aquaculture* 70 (1988) 309–321.
- [23] Sokal R.R., Rohlf F.J., *Introduction to Biostatistics*, 2nd ed. W.H. Freeman Company, New York, 1987.
- [24] Storebakken T., Austreng E., Ration level for salmonids. I. Growth, survival, body composition, and feed conversion in Atlantic salmon fry and fingerlings, *Aquaculture* 60 (1987) 189–206.
- [25] Storebakken T., Austreng E., Ration level for salmonids. II. Growth, feed intake, protein digestibility, body composition, and feed conversion in rainbow trout weighing 0.5–1.0 kg, *Aquaculture* 60 (1987) 207–221.
- [26] Su G.-S., Liljedahl L.-E., Gall G.A.E., Genetic and environmental variations of body weight in rainbow trout (*Oncorhynchus mykiss*), *Aquaculture* 144 (1996) 71–80.
- [27] Sumpter J.P., Control of growth of rainbow trout (*Oncorhynchus mykiss*), *Aquaculture* 92 (1992) 299–320.
- [28] Sylven S., Elvingston P., Comparison of rainbow trout (*Oncorhynchus mykiss*) strains for body weight, length and age at maturity in different Swedish production systems, *Aquaculture* 104 (1992) 37–50.
- [29] Valente L.M.P., Gomes E.F.S., Fauconneau B., Biochemical growth characterization of fast and slow growing rainbow trout strains: effect of cell proliferation and size, *Fish Physiol. Biochem.*, 1997 (in press).
- [30] Weatherley A.H., Gill H.S., Protein, lipid, water and caloric contents of immature rainbow trout, *Salmo gairdneri* Richardson, growing at different rates, *J. Fish Biol.* 23 (1983) 653–673.