La sélection sur la croissance de la truite fario (Salmo trutta) affecte la consommation mais pas l'efficacité alimentaire

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Aquat. Living Resour. 14 (2001) 41–48

S0990744000011037/FLA

Selection for growth of brown trout (*Salmo trutta*) affects feed intake but not feed efficiency

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Received 4 April 2000; accepted 4 December 2000

Abstract – Brown trout (*Salmo trutta*) were selected for growth for 4 generations. We tested the effects of selection on voluntary feed intake measured by self-feeders, feed efficiency and size variability. The specific effects of a slight feed restriction and of food deprivation were also investigated. Fish were issued from groups of eggs of selected females fertilised with sperm of selected (S group) or control males (S½ group). According to the growth rates expected for the selected and control lines, the S½ group was fertilised 12 days before the S group, so that all the fish reached 8 g at the same time. At 8 g, they were allotted to 8 tanks (500 fish per group) and 3 experimental periods followed. Fish were accustomed to self-feeders during a 28 days pre-experimental period. Then, half of the groups were fed ad libitum, and half were restricted (80% of the expected ad libitum level) for 171 days; growth and feed intake were recorded regularly and any uneaten food was weighed. Then followed a 56 days starvation period. At the end of the pre-experimental, feeding and starvation periods, individual weights and lengths were measured on 50 trout per tank. The response to selection at the end of the feeding period varied with the feeding level. In ad libitum fed groups, the mean final body weight of S was +6.1% higher than that of S½ and feed efficiency was similar (1.10 for S and S½). The higher growth of S compared to S½ was related to a higher feed intake of the S groups (+5.3%). When fish were restricted, the final body weight was lower in S (117.1 ± 2.1 g) than in S½ groups (123.8 ± 1.7 g). This was mainly related to a slightly lower feed efficiency of S compared to S½ at the beginning of the feeding period. Neither the group nor the feeding level affected the size variability of the fish. At the end of the starvation period, the relative loss of weight was equivalent for all the groups, and the variability of the weight was higher for S than for S½. The results highlight the fact that genetic gain can only be expressed when brown trout are fed ad libitum. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

brown trout / selection for growth / feed intake / feed efficiency / size variability / feed restriction

Résumé – La sélection sur la croissance de la truite fario (*Salmo trutta*) affecte la consommation mais pas l'efficacité alimentaire. Des truites fario (*Salmo trutta*) ont été sélectionnées selon leur croissance depuis 4 générations. Nous avons évalué les effets de cette sélection sur l'ingestion volontaire mesurée par des distributeurs d'aliment à la demande, l'efficacité alimentaire et la variabilité des poids et taille individuels. Les poissons sont issus de fécondations de femelles sélectionnées par des mâles sélectionnés (S) ou témoins (S½). Les fécondations des S½ ont été effectuées 12 jours avant celles des S pour que les poissons aient le même poids (8 g) au début de l'essai. Ils ont été répartis dans 8 bacs (500 par bac) et 3 périodes expérimentales se sont succédées. Les poissons ont été habitués à l'utilisation des distributeurs d'aliment pendant 28 jours. Les groupes ont ensuite été alimentés à volonté ou restreints (80% ad libitum) pendant 171 jours ; la croissance et la consommation ont été mesurées régulièrement. Un jeûne de 56 jours a ensuite suivi. A la fin de chaque période, les poids et longueurs individuels ont été mesurés (50 poissons par bac). La réponse à la sélection à la fin de la période d'alimentation a varié avec le niveau d'alimentation. Lorsque alimentés à volonté, le poids moyen final des S a été supérieur de 6,1% à celui des S½, alors que l'efficacité alimentaire était similaire (1.1). Ceci est expliqué par une ingestion plus importante des S (+5,3%). Lorsque les poissons étaient restreints, le poids moyen final des S (117,1 ± 1 g) a été inférieur à celui des S1/2 (123,8 ± 1,7 g), essentiellement parce que l'efficacité alimentaire des S a été plus faible au début de la période. Ni le groupe, ni le niveau d'alimentation n'ont affecté la variabilité des poids individuels. A la fin de la période de jeûne, la perte de poids relative a été équivalente pour tous les groupes. Ces résultats montrent que le progrès génétique des lignées de truites fario sélectionnées ne peut s'exprimer que lorsque les truites sont alimentées à volonté. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

truite fario / sélection pour la croissance / ingestion / efficacité alimentaire / variabilité de la taille / restriction alimentaire

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1. INTRODUCTION

Selection for growth has been undertaken for many generations in farm animals and the other traits modified by selection, i.e. the correlated effects, have been characterized. Improved growth of selected lines is generally linked to higher feed intake and/or better feed efficiency (Dunnington and Siegel, 1996; Feki et al., 1996; Marks, 1996; Schadereit et al., 1998). In fish, selection for growth has been carried out more recently and on certain species (salmonid, carp, catfish and tilapia; Gjedrem, 1998). A genetic gain of 10 to 20% per generation has been achieved depending on the species and selection method. This genetic progress is large compared to what is usually observed in higher vertebrates, but the correlated responses have been seldom measured. Growth, feed intake and feed efficiency were compared between selected salmonid lines and wild populations. In rainbow trout (*Oncorhynchus mykiss*), selection for growth is accompanied by improved feed efficiency (Smith et al., 1988), while in Atlantic salmon (*Salmo salar*) it is accompanied by both higher feed intake and better feed efficiency (Thodesen et al., 1999). However, the comparison of selected lines to wild strains is biased, because it does not take into account possible effects of domestication that can result during the adaptation to farming conditions. The use of a control line, originating from the same population as the selected line and maintained under the same rearing conditions, is needed to provide an adequate test of the selection process' influence on feeding and other performance characters. The fact that improved growth rates are linked either to higher feed intake or to better feed efficiency may depend on the selection process, or on the species studied.

The results of experiments testing this link are also largely dependent on the way feed intake is measured. Feed intake has previously been measured on groups of fish indirectly, by oxygen consumption for example (Storebakken and Austreng, 1987), or by visual estimation of satiety during meals. In this latter case, groups of fish are generally hand fed to limit waste. This does not suit species that do not come to eat spontaneously when the meal is hand fed, such as brown trout (*Salmo trutta*) for example. Recent feeding devices have been developed, which allow fish to control feed by themselves (Boujard and Leatherland, 1992), hence there is less feed waste than with automatic feeding devices. If the species studied is well adapted to the feeder, feed waste is more easily measured, and relatively good estimates of the feed intake can be obtained at the group level (Boujard and Médale, 1994; Gélineau et al., 1998).

One other correlated response of the selection for growth can be the lowering of phenotypic variability of the weight. For fish farming, this can lead to a reduction in the number of sortings carried out regularly for homogeneous production. The evolution of this parameter with the selection process has seldom been described. But if the enhancement of growth is accompanied by modifications in the feed intake, it would be difficult to discriminate which factor may induce changes in the variability of the body weight, because in certain species, groups of fish fed ad libitum are more homogeneous than groups fed restricted rations (Davis and Olla, 1987). The separate effects of selection and feed intake on phenotypic variability of fish size can be accurately measured when selected and control lines are compared.

The objectives of the present study were to measure some of the correlated effects of selection for growth of brown trout. The lines used were selected on length by an individual selection process since 1987 (Chevassus et al., 1992), and were issued from the 4th generation of selection. A control line was maintained under the same rearing conditions. The genetic gain was estimated by comparing the growth rates of the selected and control lines: with a selection pressure of about 5%, the mean body weight of the selected lines was on average enhanced by 10% per generation. In the present experiment, the effect of half of the selection pressure was measured. Feed was delivered using self-feeders. To be sure to detect any effect of selection on feed utilisation, the performances of both lines were examined not only under ad libitum conditions, but also when fed restricted rations or fasted.

2. MATERIAL AND METHODS

2.1. Animals

The selected and control lines of brown trout (*Salmo trutta*) had the same origin being made up of fish from various European populations to maximise genetic variability (Chevassus et al., 1992). The criterion for selection was length, mainly because it is easier to measure than weight in a wide range of conditions (Chevassus et al., 1992). The experiment was undertaken at the SEMII experimental fish farm (Sizun, France). Fish were produced by in vitro fertilisation of eggs of selected females by the sperm of control (S½ group) or selected males (S group). We chose to use the same group of females and to measure only half of the selection pressure, because the size of the egg can affect the initial growth of the fingerling, and depends on the size of the female. We wanted to initiate the experiment with fish reaching the same weight at the same time. Considering the growth curves obtained for the former generations of selected and control lines (B. Chevassus, unpublished data), we calculated that the S½ group had to be fertilised 12 days before the S group. After hatching, fingerlings were reared in 2 tanks per group supplied with flow through 11 °C water. They were fed ad libitum a commercial dry feed (Biomar Aqualife 17) containing 42% protein and 22% lipid (according to manufacturer) by automatic feeders delivering food 12 hours a day until the animals of both groups reached the same weight. At this time, individual weights and lengths were measured on 200

Table I. Protocol of food distribution with self-feeders during the pre-experimental and feeding periods.

Period	Feeding level	Meal without demand	Meal duration (s)	Number of trigger actuations to receive a meal	Latency time between 2 trigger actuations (s)	Inhibition period
Pre-experimental	restricted	every 30 min	3	1	45	22h00 – 5h30
Feeding	restricted	every 30 min	2	1	45	22h00 – 5h30
	ad libitum	5h30	2	2 if $D^a < R100^b$	35	22h00 – 5h30
				3 if $R100 < D < R140$	45	
				4 if $R140 < D < R160$	45	

[a] Delivered food, [b] *R100*, *R140* or *R160* (100, 140 or 160% of ad libitum ration predicted by the software '*Écureuil*')

fish per group (of approximately 6000 fish). To create homogeneous clusters, fish were sorted by length (range = mean ± SD). Each group was divided into 8 sets of 500 fish reared in 3 m^3 tanks supplied with flow through water from Lake Drennec (April to November, 9.6 to 17.7 °C).

2.2. Successive periods

A pre-experimental period of 28 days was initiated to accustom the fish to self-feeders (Imetronic). This was necessary because, to our knowledge, the utilisation of this feeding device with brown trout has not been described. Based on a pilot study it appeared that brown trout fingerlings needed time to become accustomed to this feeder. This period could induce growth divergence among the groups that could not be limited if selection affected feed efficiency. On the other hand, if selection affected feed intake, a slight food restriction may have limited the discrepancies among the groups. So, we chose to restrict the fish to 80% of their usual ad libitum ration (calculated using the prediction software '*Écureuil*' developed on the SEMII fish farm, taking into account the line, the water temperature, and the weight of the fish). The constraints in the food delivery by the self-feeders were as follows: one trigger actuation was sufficient to deliver a meal lasting for 3 s until all the ration was delivered, and self-feeders were stopped during the night to limit feed waste due to darkness (*table I*). The first experimental period, later referred to as feeding period, began when the fish were accustomed to the self-feeder, i.e. when the number of trigger actuations became regular and feed waste was no longer observed. It lasted for 173 days. During this period, 4 tanks per group were fed ad libitum and the other 4 tanks remained restricted to 80% of the expected ad libitum ration. Restricted tanks were fed by self-feeders as described in the pre-experimental period, except that each meal lasted for 2 seconds (*table I*). In the tanks where fish were fed ad libitum, access to the self-feeders was not totally free. It was restricted in order to limit feed waste because when there were larger amounts of feed in the faeces, the estimation of feed waste was further biased. Meals were delivered only during the photophase (5h30 to 22h00, *table I*). The trigger could be activated by the fish and the food not eaten. This behaviour is well described in rainbow trout (Gélineau et al., 1998), and the food delivery by self-feeders has to be limited. We used the recommendations published for rainbow trout (Gélineau et al., 1998). To avoid feed waste, the number of trigger actuations required to receive a meal was increased when fish had already eaten to the estimated satiation ration ('*Écureuil*' software, *table I*). These limitations were applied during the first 12 weeks of the feeding period. Then, because self-feeders did not seem fully adapted to brown trout, fish had free access to the devices during the photophase. The waste was weighed three times a week to calculate the real amount of feed intake. During the first week, feed and faeces were separated by hand and the respective percentages of uneaten feed and faeces were evaluated for each tank. After that, these percentages were used to estimate the amount of uneaten feed per tank.

After the feeding period, a starvation period of 56 days was implemented.

2.3. Measurements and calculations

Mortality was recorded throughout the experiment. At the end of the 4-week pre-experimental period, and every third week during the feeding period, the groups of fish were counted (n_i and n_f for the initial and final number of fish, respectively) and weighed (W_i and W_f, for initial and final weights per tank, respectively) after 1 day of fasting. Growth performance and food utilisation were described using the following parameters:

– daily growth coefficient (*DGC* in %·day^{-1}),

$$DGC = 100(\, W_f^{1/3} - W_i^{1/3}\,) \times \text{days}^{-1} \qquad (1)$$

– feed intake (in g·100 g^{-1}·day^{-1}):

$$\textit{Feed intake} = 100\,(\,\textit{distributed food} - \textit{feed waste}\,) \times (\, W_i\, n_i \times \text{days}\,)^{-1} \qquad (2)$$

– feed efficiency:

$$\textit{Feed efficiency} = (\, W_f\, n_f - W_i\, n_i\,) \times (\,\textit{distributed food} - \textit{feed waste}\,)^{-1} \qquad (3)$$

During the starvation period, fish were weighed every third week and of course, only W_f was measured and *DGC* calculated.

At the end of each period (pre-experimental, feeding, and starvation periods), individual weights (in grams, non-eviscerated) and fork lengths (in centimetres) were recorded for 50 fish per tank, and the condition factor ($K = 100 \times weight \times L^{-3}$) was calculated. The coefficients of variation ($CV = 100 \times standard\ deviation \times mean^{-1}$) were evaluated within each tank for weight (*W*), fork length (*L*) and *K*-factor.

2.4. Statistical analysis

The statistical analysis for the experiment was based on a completely random design. Growth data, feed intake and feed efficiency were compared with an analysis of covariance including the effects of group, feeding level and interaction between these two factors, which were tested using the tanks as the experimental unit (4 replicates per treatment). The covariate was different for each period. For the feeding period, the initial body weight was taken into account because of a slight discrepancy between the two groups (see results). For the starvation period, the mean body weight at the end of the feeding period was taken as a covariate, to test the proper effects of starvation.

Individual data were compared with an analysis of variance taking into account the effects of group, feeding level and the interaction between these two factors, and the effect of the tank nested into this interaction (50 replicates per tank, 4 replicates per treatment).

Probabilities of differences between treatments were generated using the General Linear Model procedure of SAS (1996). When the interaction was significant, separate analyses of variance were performed to test the effect of the group for each feeding level and the effect of feeding level for each group. The means were subsequently compared using the test of Newman and Keul (significance level $P < 0.05$).

To compare the extent of the variation for each individual variable (*W*, *L*, *K*-factor), they were transformed to logarithms and the equality of the absolute deviates in each class was controlled. The absolute deviate was calculated ($|\ln Y_{ij} - \ln \tilde{Y}_j|$, where Y_{ij} is the *j*th term in the *i*th sample, and $\ln \tilde{Y}_i$ is the mean logarithm of the *i*th sample. The scatter of the absolute deviates was markedly unequal, indicating that a non-parametric test has to be applied (Sokal and Braumann, 1980). The coefficients of variation were thus compared with the non-parametric test of Kruskal-Wallis using the NPAR1WAY procedure of SAS (1996). The global effects of group (8 replicates per treatment) and feeding level (8 replicates per treatment) were tested. Separate analyses were carried out to test the effect of the line for each feeding level (4 replicates per treatment) and the effect of the feeding level for each line (4 replicates per treatment).

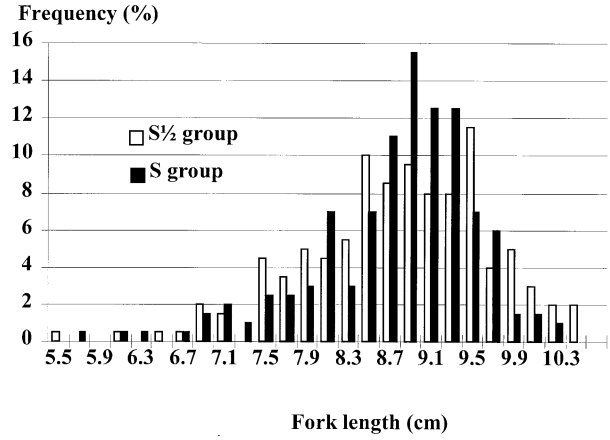

Figure 1. Distribution of fork length before sorting and the beginning of the pre-experimental period of brown trout selected for growth (S) or selected × control (S½); $n = 200$ for each group.

4. RESULTS

No significant mortality was observed during the experiment. Before the pre-experimental period, the individual weights and lengths were controlled. We checked that the two groups had comparable weights (8.4 and 8.3 g for S½ and S, respectively, $P > 0.91$) and lengths (8.7 cm for S½ and S, $P > 0.66$). However, the individual *K*-factors were slightly higher ($P < 0.04$) for S (1.25) than for S½ (1.22). The distributions of the lengths were taken into account for the sorting (*figure 1*); animals measuring 8.7 ± 2.0 cm were kept and distributed in 8 tanks per group. Within groups, the mean body weights of the different tanks were comparable; however, they were higher for S½ than for S groups (*table II*).

4.1. Pre-experimental period

At the end of the pre-experimental period, all tanks were accustomed to the use of the self-feeders. The final body weight of the S½ group remained significantly higher than that of the S group but the growth was similar between the two groups (*table II*). This initial difference was taken into account in further analyses (covariance analyses). The individual body weight values were consistent with the mean body weight calculated for each tank (*table II*). The S trout were shorter but had a higher K-factor than the S½ trout. Variability of individual weights and lengths was similar among the groups, but the K-factor was more variable in the S groups.

4.2. Feeding period

When fish were fed ad libitum, feed intake and growth rates were higher and feed efficiency lower than when they were restricted (*table III*). Feeding level affected individual body weights, lengths and

Table II. Growth, feed intake, and individual weights and lengths of brown trout selected or half selected for growth*.

	S½ group	S group	Probability associated to group
Global data			
Initial body weight (g)	9.2 ± 0.1^a	8.90 ± 1^b	0.0003
Final body weight (g)	16.4 ± 0.3^a	15.9 ± 0.3^b	0.0052
Daily growth coefficient (%·day^{-1})	1.59 ± 0.04	1.57 ± 0.05	0.3778
Voluntary feed intake (%·day^{-1})	1.94 ± 0.02	1.97 ± 0.03	0.0157
Feed efficiency	1.43 ± 0.05	1.39 ± 0.07	0.1477
Individual data			
Means			
Final body weight (g)	16.2^a	15.6^b	0.0371
Fork-length (cm)	10.8^a	10.6^b	0.0001
K-factor (g·cm^{-3})	1.25^a	1.29^b	0.0001
Coefficients of variation (%)			
Final body weight	23.7	21.9	0.1722
Fork-length	7.4	7.0	0.5995
K-factor	7.1	8.3	0.0063

* Brown trout selected (S) or half selected for growth (selected × control, S½) were fed 80% of the ad libitum ration by self-feeder during the pre-experimental period lasting for 28 days. Global data are means ± SD of 4 tanks (500 trout per tank) and individual data are means or coefficient of variation of 50 individuals per tank (4 tanks per group). For the same feeding level and for each variable, means with different superscripts are significantly different ($P < 0.05$), when the interaction between the group and the feeding level was significant, the difference was tested after an analysis of (co)variance testing the effect of the group within a feeding level.

K-factors, which were higher for fish fed ad libitum. But it did not influence the variability of individual measurements (*table III*).

The effect of the group varied with the feeding level, as shown by the significant interaction between these two variables (*table III*). When fish were fed ad libitum, at the end of the feeding period, the weight of S was slightly higher than that of S½. This difference was significant when measured on individual data ($P < 0.03$) but not when the mean body weights were measured within the tanks ($P > 0.09$). Feed efficiencies were not significantly different ($P > 0.25$) among the groups. Intake was on average 5% higher (not significant) for S than for S½ group. At the end of this period,

Table III. Growth, feed intake and individual weights and lengths of brown trout selected for growth or control*.

Feeding level	Ad libitum		Restricted 80%		Probability associated to:		
	S½	S	S½	S	Group	Feeding Level	Interaction
Global data							
Initial body weight (g)	16.4 ± 0.5	16 ± 0.2	16.3 ± 0.1	15.8 ± 0.5	0.0340	0.2472	0.7733
Final body weight (g)	148.5 ± 7.4	157.6 ± 8.0	123.8 ± 1.7^a	117.1 ± 2.1^b	0.9343	0.0001	0.0171
Daily growth coefficient (%·day^{-1})	1.59 ± 0.06	1.66 ± 0.06	1.42 ± 0.02^a	1.38 ± 0.01^b	0.8265	0.0001	0.0133
Voluntary feed intake (%·day^{-1})	4.19 ± 0.40	4.41 ± 0.17	3.27 ± 0.04	3.15 ± 0.10	0.4662	0.0001	0.0978
Feed efficiency	1.09 ± 0.03	1.12 ± 0.03	1.14 ± 0.02	1.13 ± 0.02	0.5166	0.0178	0.1643
Individual data							
Means							
Final body weight (g)	151.9^a	159.9^b	123.1^a	115.9^b	0.8572	0.0001	0.0011
Fork-length (cm)	22.1	22.3	21.0	20.6	0.3416	0.0001	0.0083
K-factor (g·cm^{-3})	1.39^b	1.41^a	1.31	1.31	0.0140	0.0001	0.0139
Coefficients of variation (%)							
Final body weight	21.0	24.4	22.0		0.2936	0.5286	
Fork-length	7.0	8.2	7.2	7.9	0.1415	0.9164	
K-factor	7.5	9.0	6.7	8.6	0.0117	0.4622	

* Brown trout selected for growth (S) or control (selected × control, S½) were fed ad libitum or at 80% of the ad libitum ration by self-feeder for 173 days. Global data are means ± SD of 4 tanks (500 trout per tank), and individual data are means or coefficient of variation of 50 individuals per tank (4 tanks per group). For the same feeding level and for each variable, means with different superscripts are significantly different ($P < 0.05$), when the interaction between the group and the feeding level was significant, the difference was tested after an analysis of (co)variance testing the effect of the group within a feeding level.

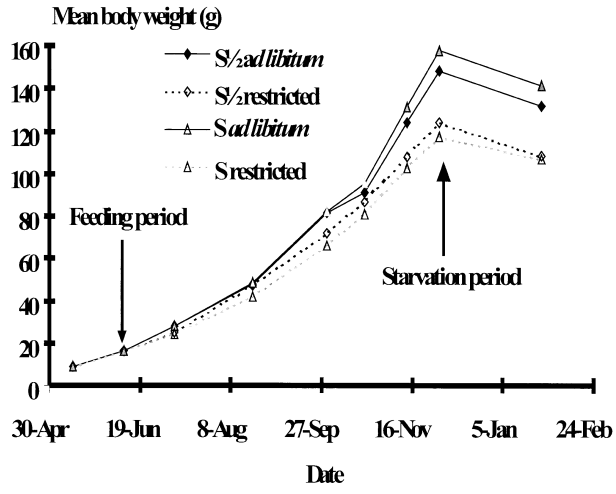

Figure 2. Mean body weight (g) of brown trout selected for growth (S) or selected × control (S½) fed ad libitum or at 80% of the ad libitum ration by self-feeder during a pre-experimental period of 28 days, a feeding period of 173 days and a starvation period of 56 days.

lengths of the fish were similar, but the K-factor was higher and more variable for S than for S½ group. Individual variability of the final body weight and length was not different between S and S½ groups.

When fish were restricted, the final weight (mean and individual data) and the daily growth coefficients of S were significantly lower than those of S½. Considering the data collected every 3 weeks, the main difference of growth between the groups occurred during the first six weeks ($P < 0.0001$, *figure 2*). Thereafter growth was comparable. Over the whole period, feed efficiency was similar between the two groups ($P > 0.62$), even if during the first six weeks of the experiment, feed efficiency was higher for S½ than for S groups (1.20 and 1.08, for S½ and S respectively, $P < 0.0002$). Lengths and K-factors were similar between the two groups, as was the individual variability of final body weight and length. Again K-factors were more variable in S than in S½ groups.

4.3. Starvation period

After 56 days of food deprivation, the animals that were previously restricted had lost less weight than those previously fed ad libitum, but when the weight at the beginning of the starvation period was taken into account by the analysis of covariance, the difference was not significant (*table IV*). Neither the group nor the previous feeding level influenced the loss of weight. Mean length of the groups remained constant throughout the period but the K-factor decreased during the starvation period. The three variables measured on individuals were not influenced by the group or the former feeding level. The *CV* of the individual body weights, lengths and K-factors were higher in the S than in the S½ groups, but were not influenced by their previous feeding level.

5. DISCUSSION

In the present experiment, the weight of S group was higher than that of S½ only when fish were fed ad libitum. Under these conditions, the weight of S group was 6.1% higher than that of S½ group. This selection program has enabled a genetic gain of about 10% per

Table IV. Loss of weight, individual weights and lengths after starvation of brown trout selected or half selected for growth*.

Previous feeding level	Ad libitum		Restricted 80%		Probability associated to:		
	S½	S	S½	S	Group	Feeding Level	Interaction
Global data							
Final body weight (g)	134.6 ± 7.7	141.1 ± 7.8	112.6 ± 1.3	107.0 ± 1.0	0.3071	0.9153	0.1829
Daily growth coefficient (%·day^{-1})	–0.31 ± 0.05	–0.36 ± 0.03	–0.29 ± 0.02	–0.27 ± 0.02	0.3984	0.8563	0.1734
Individual data							
Means							
Final body weight (g)	132.0	134.9	110.1	105.7	0.6226	0.3257	0.7235
Fork-length (cm)	22.4	22.5	21.4	21.0	0.6361	0.0785	0.6186
K-factor (g·cm^{-3})	1.16	1.16	1.11^{b}	1.12^{a}	0.7227	0.4441	0.0390
Coefficients of variation (%)							
Final body weight	20.7	25.0	21.1	23.9	0.0078	0.7285	
Fork-length	6.5	7.8	6.5	7.9	0.0018	1.0000	
K-factor	5.7	6.6	6.5	7.9	0.0641	0.1649	

* Brown trout selected (S) or half selected for growth (selected × control, S½) were starved for 56 days after being fed ad libitum or at 80% of the ad libitum ration by self-feeder for 173 days. Group data are means ± SD of 4 tanks (500 trout per tank) and individual data are means or coefficient of variation of 50 individuals per tank (4 tanks per group). For the same feeding level and for each variable, means with different superscripts are significantly different ($P < 0.05$), when the interaction between the group and the feeding level was significant, the difference was tested after an analysis of (co)variance testing the effect of the group within a feeding level.

generation (Chevassus et al., 1992; B. Chevassus, unpublished data). Although we have measured only half of the genetic progress, a 20% difference at least should thus be expected. Several reasons may explain this limited response. First, fertilisations in the S½ group were performed 12 days before those of the S group. The S group hatched after and was thus younger than the S½ group throughout the experiment, while the response to selection has previously been measured on animals at the same age. Taking into account the difference of age in putative growth curves of S and control lines, genetic gain is lower (estimated at 16.8%). Secondly, the sorting performed at the beginning of the experiment may have influenced the results differently according to the groups: the mean body weight was higher after the sorting than before, and even higher in the S½ group. This initial difference was slight and may have no incidence on the results, but was taken into account in the analyses. However it must be mentioned that in brown trout the higher the weight at the beginning of the experiment, the better growth (Wohlfarth, 1992). Thirdly, and more importantly, in the present experiment, the real ad libitum level was perhaps not reached because access to self-feeders was restricted. Since brown trout do not come freely to feed when they are hand-fed, this device seemed to us the most suitable to correctly measure intake, and thus feed efficiency. However, in absence of published data on the behaviour of this species with self-feeders, and according to the recommendations for rainbow trout (Gélineau et al., 1998), food delivery was limited when the demands were too frequent to limit feed waste. This was done during the first 12 weeks of the feeding period and the initial limitations to deliver the food may have resulted in some restriction, which could have been more detrimental to fish exhibiting the highest voluntary intake. As soon as the access to food was no longer restricted, S ate and grew more than S½. So we cannot exclude that S did not express their growth potential fully when they were fed at the expected ad libitum level, because they were in fact slightly restricted. Feed efficiency was similar between the two groups, and this strongly suggests that the main difference between the two lines resides in their feed intake.

Indeed, restricting to 80% of the usual ration had a more detrimental impact on growth in S than in S½ lines. This was mainly due to the lower feed efficiency that S fish exhibited during the first weeks of the feed restriction and could indicate that selected fish need more time to get used to a feed restriction. All these results show that the trout selected for growth can express their growth potential only when fed ad libitum.

The selection procedure seems to have favoured fish exhibiting higher feed intakes while maintaining the same abilities of converting feed into body mass. It may be partly explained by the fact that fish have always been fed in excess during the selection procedure. Moreover, after the fast, fish from both lines lost the same amount of weight. This suggests that their abilities to mobilise their energy reserves and maybe their carcass composition and adipose mass are similar (Médale et al., 1999). These latter assumptions have to be confirmed.

The present study highlights a link between the growth potential and feed intake. Selected fish tend to eat more than controls while maintaining the same feed efficiency, and this suggests a genetic determinism of feed intake capacities. Actually, this trait seems to be more heritable than feed efficiency. In rainbow trout, the few estimates of heritabilities published for this trait vary between 0.15 ± 0.30 (Gjoen et al., 1991) and 0.41 ± 0.13 (Kinghorn, 1983, where feed intake was estimated indirectly by oxygen consumption). Estimates of heritabilities of feed efficiency do not differ from zero in brown trout (Rab and Kalal, 1984) as well as in rainbow trout (Kinghorn, 1983).

On the other hand, feed efficiency is linked to the feeding level because in different species of fish it decreases with higher feed intake (Valente et al., 1998; Storebakken and Austreng, 1987; Silverstein et al., 1999; results of the present study). It is thus remarkable that selected fish eat more than controls, when feed efficiency is not affected. The difference in intake observed here was surely too small to induce any divergence in feed efficiency, but this remains to be investigated by measuring the effect of the whole selection pressure.

In higher vertebrates, and namely chicken, enhancement of growth due to selection has led to higher feed intake (Dunnington and Siegel, 1996). The physiological mechanisms have been studied. In broilers, selection for increased body weight has affected the hypothalamic satiety mechanisms leading to overconsumption (Burkhart et al., 1983). In fish, little is known about the satiety mechanisms and the selected and control lines of brown trout used in this study appear to be good experimental models for this purpose.

In the present study, neither selection nor the feeding level influenced the phenotypic variability of body weight. This is not in agreement with the results previously observed in these lines, weight variability being generally lower in selected lines (B. Chevassus, unpublished data). This was the case in the present experiment before fish had been sorted to begin the pre-experimental period (results not shown). On the other hand, it seems that in fish, the feeding level interacts with body weight variability. Lowering the ration generally leads to higher body weight variability (Davis and Olla, 1987; Gélineau et al., 1998) because aggressions and competition increase (Davis and Olla, 1987). The fact that, as already mentioned, fish that should have been fed ad libitum were slightly restricted may also have affected more strongly the selected line. We thus cannot come to any conclusion on the evolution of the phenotypic variability of the weight and the length with the selection process or the feeding level from the present results.

In conclusion, the genetic gain observed in the present study is explained by the higher intake of the fish selected for growth. This kind of selection did not affect feed efficiency. The implication is that the genetic progress can be expressed only when the selected fish are fed ad libitum. The physiological impact of this kind of selection has to be studied and it would be important to measure other correlated responses (e.g. nutrient requirements, digestive transit, satiety factors). The results imply that selected and control lines may be useful for studying the control of feed intake in fish.

Acknowledgements. The authors thank all the team of the SEMII fish farm which participated in the experiment, and in particular H. Barone for daily care of the fish and improving the use of the self-feeders, I. Queau and L. Lebrun for all their spontaneous help. We thank also J.B. Denis for his expert advice in statistics. Constructive comments from referees were greatly appreciated.

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