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Digestibility in selected rainbow trout families and relation to growth and feed utilisation

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Abstract Experiments have been carried out aimed at clarifying variations in the digestibility of dietary nutrients in rainbow trout families and studying how differences in digestibility may be related to growth and feed utilisation at various growth rates. The digestibility of protein, lipid, carbohydrates (nitrogen-free extracts, NFE) and dry matter was analysed in two experiments involving eight rainbow trout families [Ab, Ba, Cd, Dc (first study); V, X, Y, Z (second study)]. In the first experiment rainbow trout were reared for 128 days at 13.0°C, and in the second experiment, they were reared for 84 days at 16.8°C. In both experiments, the fish were fed ad libitum and reared from an initial weight of 70–100 g to a final weight of 500–700 g. When the fish reached a weight of approximately 200 g, some individuals were moved to another experimental system in which the digestibility of protein, lipid, nitrogen-free extracts and dry matter was measured. Taken as a whole, our results indicate that selective breeding still offers a large potential for improved growth and feed utilisation in rainbow trout strains. In the first study, family Dc showed a higher specific growth rate (SGR) than the other three families ($P < 0.05$), and family Ba showed a lower feed conversion ratio (FCR) than family Ab ($P < 0.05$); there were no observed differences in digestibility despite some differences in growth. In the second study, family Y grew faster than all of the other families ($P < 0.05$), and family Z grew faster than families V and X ($P < 0.01$). A comparable pattern was seen for FCR, with family Y utilising feed better than family V ($P < 0.05$), and families V, Y and Z performing better than family X ($P < 0.001$). Protein digestibility was higher in the two fastest growing families (Y and Z) than in the slower growing family X ($P < 0.05$), while lipid digestion was higher in family Y than in family V ($P < 0.05$). A comparison of the results from both experiments revealed that protein digestibility in particular was closely

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related to the SGR and the FCR at high growth rates. However, despite the advantageous protein digestibility on fish growth, analysis of the protein retention efficiency (PRE) showed that when protein was ingested in relatively large amounts, as in the fastest growing families, the "excess" nitrogen was excreted and therefore did not contribute to protein deposition in the fish body. Hence, the potential weight gain offered by improved protein digestibility does not materialise when the protein intake is above a certain level. Other factors must therefore explain the positive relation between fast growth and high protein digestibility.

Keywords Rainbow trout · Digestibility · Selective breeding · Growth · Feed utilisation · Protein retention efficiency

Introduction

In a recent publication on aquaculture in a historical context, Duarte et al. (2007) described the extraordinary developments that have occurred in aquaculture—in specific fish species—compared to those in agriculture. The last 100 years have been particularly successful. One of the popular species, the rainbow trout (*Oncorhynchus mykiss* Walbaum), has been cultured for more than 100 years in Denmark, where selective breeding has been a main factor in the success of fish production. The importance of selective breeding in the success of salmonid aquaculture was highlighted by Gjedrem (2000), and the advantages of improving growth rate through selective breeding and the parallel response in improved feed conversion efficiency were reported by both Gjedrem (2000) and Henryon et al. (2002). Henryon et al. (2002) concluded that selection for growth characteristics among Danish trout strains remained a promising approach. It has been questioned to which degree the improved growth of salmonids is obtained by better feed and, more specifically, how this may be determined by the high digestibility of main nutrients in the diet (Valente et al. 1998; Sunde et al. 2001). With regard to lowering nitrogen discharge from fish farms, Halver and Hardy (2002) noted that an important strategy may be to focus on broodstock with high protein retention efficiencies.

The primary aim of the experiments reported here was to elucidate how the digestibility of protein, lipid, nitrogen-free extracts (NFE; carbohydrates) and dry matter varied among different families of rainbow trout from a brood stock that had already undergone selective breeding for decades. In contrast what has been reported in earlier publications (Austreng and Refstie 1979; Refstie and Austreng 1981; Valente et al. 1998), high-energy trout feed is now the standard feed of fish raised in fish farms (digestible energy: approx. 20 MJ kg^{-1}). We also examined how the digestibility of the main nutrients was associated with fish growth. To this end, two consecutive experiments were carried out that revealed growth variations in rainbow trout families with different feed intakes. Although the experimental design did not allow the use of the same families in both experiments, it did provide the opportunity to study the importance of growth rate on the ability to express phenotypic traits in a total of eight rainbow trout families.

Materials and methods

Fish husbandry

The Danish Trout Breeding programme has been carrying out selective breeding on rainbow trout (*Oncorhynchus mykiss* Walbaum) brood stock for several generations. The primary breeding objectives have been to improve growth and feed utilisation. The original brood stock for these particular studies were obtained from two Danish trout farms, Mark Mølle Dambrug and Fousing Dambrug, where fish have been kept as pure strains for at least 25 years. Prior to our experiments, the breeding strategy focused on families that had been originally selected from 50 families produced annually by mating 25 sires and 25 dams using a partly factorial design (Berg and Henryon 1998; Henryon et al. 2002). The eight experimental fish families used in our studies were selected based on the growth performance data of their parents. The trout families were studied in two successive experiments: the first involved families Ab, Ba, Cd and Dc; the second, families V, X, Y and Z. Families Ab and Ba were related as half-siblings so that Ab and Ba had the same mother but different fathers. The same relationship held for families C and D. Families V, X, Y and Z had no common parenthood, and each family consisted of full-siblings.

Before the start of both experiments, the fish were left to acclimatise in the rearing tanks for 14 days. The fish were starved for 48 h before being weighed. Prior to all measurements, the fish were anaesthetised in tricaine methane sulphonate (MS-222).

In the first experiment, each fish of families Ab, Ba, Cd and Dc initially weighed 70–73 g (150 fish per tank). They reached a final weight of 591–662 g after a rearing period of 128 days. In the second experiment, families V, X, Y and Z were reared for 84 days from an initial weight of 85–99 g per fish (140 fish per tank) to final weight of 482–672 g. Both experiments were run in triplicate in tanks of approximately 1000 l each (i.e. 12 tanks per experiment). The room containing the tanks was illuminated from 7.50 a.m. to 22.30 p.m. Water temperature was 13.0 ± 1.2°C in the first experiment and 16.8 ± 0.8°C in the second experiment. Pure oxygen was automatically added whenever

Table 1 Main components of the fish feed based on chemical analyses of the diets used in the two experiments

Main components of the fish feed	Composition of the fish feed	
	Experiment 1	Experiment 2
Crude protein (g 100 g^{-1})	42.6	42.0
Crude lipid (g 100 g^{-1})	26.4	27.4
Crude fibre (g 100 g^{-1})	1.91	0.82
Ash (g 100 g^{-1})	6.32	7.32
Nitrogen-free extracts (g 100 g^{-1})	15.9	18.1
Dry matter (g 100 g^{-1})	93.1	95.6
Phosphorous (g 100 g^{-1})	0.9[a]	0.9[a]
Digestible energy (MJ kg^{-1})	19.8[a]	19.8[a]
Gross energy (MJ kg^{-1})	23.9[a]	23.9[a]
Vitamin A (IU kg^{-1})	2500[a]	2500[a]
Vitamin D_3 (IU kg^{-1})	500[a]	500[a]
Vitamin E (IU kg^{-1})	150[a]	150[a]
Etoxyquine (mg kg^{-1})	100[a]	100[a]

[a] Values declared by the feed producer

the water oxygen concentration fell to below 7 mg O_2 l^{-1}. The pH was in the range 7.2–7.6 and was regulated by the addition of sodium bicarbonate. For the control and optimisation of water quality, measurements of unionised and ionised ammonia (NH_3/NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) were carried out every second day.

All of the fish in both experiments were fed the same commercial feed type (GEP 576 Export; Aller Aqua, Christiansfeld, Denmark), but two different feed batches were provided in the two studies that varied only slightly with respect to their main ingredients (Table 1). During the growth experiments, the rainbow trout were fed ad libitum using pendulum demand feeders from 8.15 a.m. to 3.00 p.m.; uneaten pellets were removed just after feeding. In order to calculate precisely the daily amount of feed ingested, removed pellets were counted and their total weight calculated from the number of pellets and average pellet weight before distribution in the tanks.

Fish growth was calculated as specific growth rate, $SGR = (\ln W_2 - \ln W_1) \times 100\% \times \text{experimental days}^{-1}$, where W_2 is the weight of the fish at the end of the experiment, and W_1 is the weight at the start of the experiment. The feed conversion ratio (FCR) was calculated as the ratio between the amount of feed ingested and the fish weight gain according to the formula: FCR = feed ingested (g) × fish weight gain $(g)^{-1}$. Protein retention efficiency (PRE) was calculated as PRE (%) = (g protein in fish at experimental termination − g protein in fish at experimental start) × 100% × (g protein intake during experiment)$^{-1}$. The protein content in fish was analysed according to McKenzie et al. (2007).

Digestibility measurements

When fish from each family reached about 200 g, sub-samples of ten (first experiment) or 15 (second experiment) fish from each family were transferred to separate 150-l tanks for digestibility measurements. The bottom of each tank was conical with a ball-valve and a bottom grate at the outlet, where a box for the collection of faeces and uneaten feed pellets was mounted. The collectors were submerged into ice-water (0°C) to minimise bacterial catabolism of the faeces during collection.

The fish were acclimated for 1 week before the start of the experiment. Both experiments were run in triplicate, i.e. three tanks per family. In each of the two experiments, the digestibility measurements were carried out for three consecutive periods of 3 days each, i.e. 9 days in total. Throughout the experiments the water temperature in the tanks was 10.0 ± 0.9°C and the oxygen saturation was at least 70%.

During the experiments, fish were fed twice daily to apparent satiation at 10 a.m. and again at 2 p.m. Feed waste was observed in all tanks in both experiments, with the total weight percentage of uneaten pellets being 6.0% in the first experiment and 7.4% in the second experiment. During the relative short periods of feeding, faeces collection was halted, and uneaten pellets flushed out of tanks when feeding was completed. The collection of faeces was then resumed, and uneaten pellets were counted and actual feed intake calculated as previously described.

Faeces were collected from each tank every day at 9.30 a.m. and frozen (−20°C) immediately for later chemical analysis. Collections from each of the three periods were kept separately. The faeces sampled in period two and three were analysed for their content of protein, lipid, NFE and dry matter, while faeces collected in the first period only served as a back-up in case the other two samples deviated significantly form each other. This, however, was not the case in our studies. Chemical analyses were carried out as described

by McKenzie et al. (2007). The apparent digestibility coefficient (ADC) was calculated according the equation ADC(compound) = [(g ingested compound − g compound in faeces) × (g ingested compound^{-1})] × 100%.

Statistical analyses

Due to variations in growth, feed chemical composition, fish sizes and temperatures, data for each of the two experiments were treated separately. Each set of data for protein, lipid, NFE (carbohydrates) and dry matter digestibility as well as SGR, FCR and PRE were analysed by application of MANOVA, with family as the independent factor. Whenever an overall statistically significant difference was found (i.e. $P < 0.05$), further post hoc analysis was carried out by application of Tukey HSD tests in order to analyse for any specific differences between families. In one case (PRE analysis, first experiment) the data failed the equal variance test, so the Kruskal–Wallis analysis of variance on ranks was carried out on these data instead of MANOVA.

Pearson Product Moment correlation was used to analyse for possible correlations among the individual variables. SIGMA PLOT ver. 9.0 software (Systat Software, San Jose, CA) was applied to identify the equations generating optimal curve fits (Figs. 1–3).

Results

As shown in Table 2, we did not find any differences in the digestibility of any of the compounds among the four families studied in the first experiment. There were differences in growth measured as averages during whole periods in that family Dc showed a significantly higher SGR than the other three families. However, this difference in growth was not related to feed efficiency: for example, family Ba was significantly better in converting feed into body growth than family Ab, although these two families showed similar growth rates.

In the second experiment, significant differences were observed in digestibility as families Y and Z showed significant higher protein digestibility than family X, and family Y showed significant higher lipid digestibility than family V (Table 2). Families Y and Z performed better in terms of growth than families V and X, while families Y and Z showed significant lower FCR than family X.

Specific growth rates obtained during the growth experiments generally reflected those observed in the digestibility studies (see Table 2 for comparison).

Significant correlations were found following application of the Pearson product moment correlation between each parameter studied in each experiment. However, none of these were observed in both experiments, i.e. correlations obtained in the first experiment could not be confirmed in the second experiment. A positive correlation between protein digestibility and SGR was particularly apparent. In the second experiment, this correlation was highly significant ($R^2 = 0.77$, $P < 0.01$) (Fig. 1), whereas the correlation was not significant in the first experiment ($P = 0.13$). This result reflected the relationship between FCR and protein digestibility. In the first experiment, there was no correlation between these two parameters ($P >> 0.05$), but in the second experiment there was a significant correlation ($R^2 = 0.83$, $P < 0.01$) (Fig. 2). Accordingly, a strong linear correlation between SGR and FCR was found in the second experiment

Table 2 Digestibility percentages, specific growth rate, feed conversion ratio, relative feed intake and protein retention efficiency in each of the two experiments

Experiment no.:	1				2			
Family:	Ab	Ba	Cd	Dc	V	X	Y	Z
Protein digestibility (%)	92.0 (0.3)	92.3 (0.4)	91.8 (0.9)	92.7 (0.5)	91.1 (0.7) c,d	90.2 (0.5) d	92.2 (0.6) c**	92.0 (1.1) c*
Lipid digestibility (%)	92.6 (0.8)	93.0 (1.1)	92.6 (1.4)	91.0 (0.8)	91.4 (0.8) d	91.9 (1.2) cd	93.7 (0.7) c*	92.5 (0.7) c,d
NFE digestibility (%)	68.5 (1.8)	71.4 (3.4)	70.1 (3.6)	75.3 (5.7)	78.0 (1.4)	77.0 (2.7)	78.8 (2.4)	77.8 (2.9)
DM digestibility (%)	84.5 (0.7)	85.4 (0.7)	85.1 (1.0)	85.6 (0.8)	85.1 (0.8) c,d	84.5 (0.8) d	86.6 (0.9) c*	85.8 (1.2) c,d
SGR (% × day^{-1})	1.66 (0.03) b	1.64 (0.02) b	1.64 (0.01) b	1.78 (0.07) a*	2.31 (0.02) d	2.16 (0.01) e***	2.41 (0.01) c**	2.39 (0.03) c**
SGRds[a] (% × day^{-1})	1.67	1.44	1.45	1.52	2.20	1.75	2.07	1.93
Feed intake (g × g BW^{-1} × day^{-1})	11.9 (0.4) a*	10.9 (0.1) b	11.5 (0.4) a,b	11.8 (0.2) a*	16.4 (0.1) d	17.1 (0.1) c**	16.3 (0.2) d	16.3 (0.0) d
FCR	0.97 (0.03) b	0.89 (0.01) a*	0.94 (0.03) a,b	0.93 (0.01) a,b	0.92 (0.00) d	1.00 (0.01) e***	0.89 (0.01) c*	0.90 (0.01) c,d
PRE (%)	41.9 (0.4)	42.3 (1.4)	41.7 (0.2)	41.4 (0.7)	39.1 (0.5) a	34.9 (0.8) b***	38.5 (0.5) a	39.9 (0.6) a

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Values (mean, with the standard deviation in parenthesis) followed by different letters are statistically significant at the levels indicated. Each experiment involving four rainbow trout families was treated separately with regards to statistics

DM, Dry matter; NFE, non-nitrogen extracts; SGR, specific growth rate; BW, body weight; FCR, feed conversion rate; PRE, protein retention efficiency

The formulae for determining SGR, FCR and PRE are given in the Materials and methods (Fish husbandry)

[a] Specific growth rates during the 9-day digestibility study (SGRds) are shown only for comparison with long-term growth of the fish

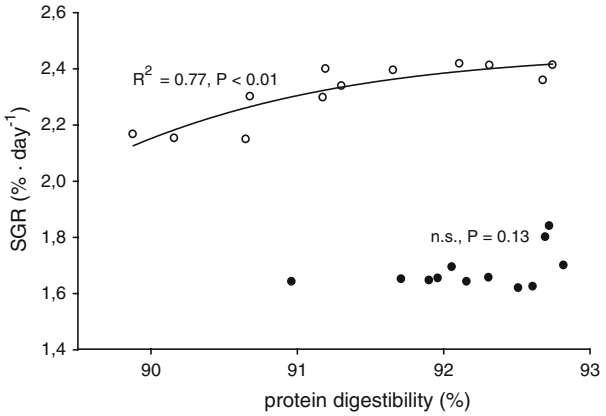

Fig. 1 Average specific growth rate (*SGR*) [SGR(%) = (ln W_2 − ln W_1) × 100% × $days^{-1}$] in each tank throughout the whole experiment in relation to protein digestibility (%). In the first experiment (*black dots*), no significant relationship was found between the two parameters ($P = 0.13$); in the second experiment (*white dots*), there was a significant correlation ($P < 0.01$). The *line* provides the best fit and is described by the equation: SGR (%) = $2.462 \times (1 + e^{-(\text{protein digestibility (\%)} - 87.411)/1.335})^{-1}$. $R^2 = 0.77$, $P < 0.01$

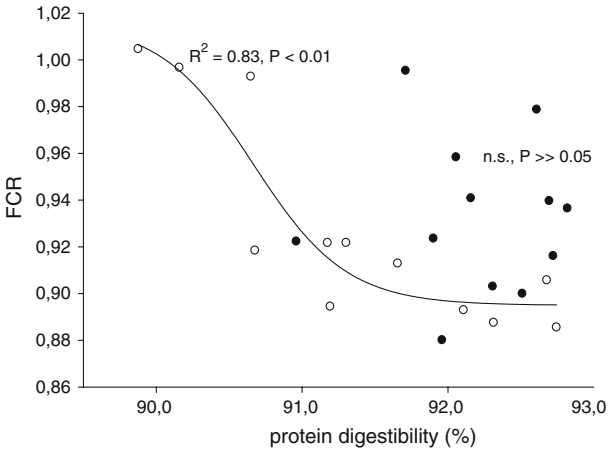

Fig. 2 Average feed conversion ratio (*FCR*) (g feed ingested × g body weight $gain^{-1}$) in each tank throughout the whole experiment in relation to protein digestibility (%). In the first experiment (*black dots*), no significant relationship was found between the two parameters ($P >> 0.05$); while in the second experiment (*white dots*), there was a significant correlation ($P < 0.01$). The *line* provides the best fit and is described by the equation: FCR = $0.895 + 0.121[1 + (\text{protein digestibility (\%)} \times 90.665^{-1})^{284.424}]^{-1}$. $R^2 = 0.83$, $P < 0.01$

($R^2 = 0.95$, $P < 0.001$), while no such relation was observed in the first experiment ($P >> 0.05$). Another outcome of our analyses was that PRE decreased ($R^2 = 0.87$, $P < 0.0001$) when protein was provided at a level exceeding approximately 6.1 mg digestible protein g BW^{-1} day^{-1} (Fig. 3).

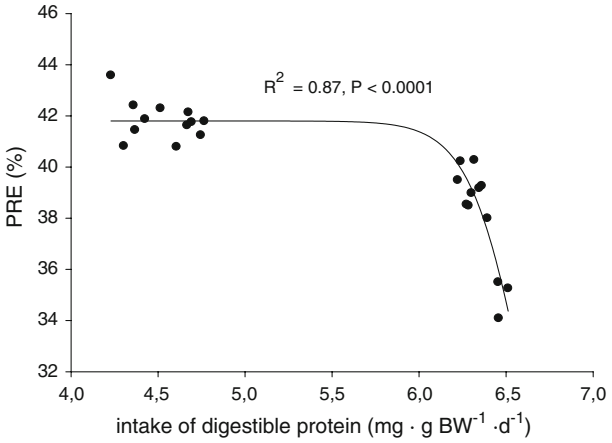

Fig. 3 Protein retention efficiency (*PRE*; %) correlated with relative intake of digestible protein. Results from both experiments are shown and analysed together. The relation between the two parameters is described by the equation: PRE (%) = 18.90 + 22.90 × [1 + (intake of digestible protein × 6.63^{-1})$^{39.68}$]$^{-1}$. $R^2 = 0.87$, $P < 0.0001$

Discussion

The digestibility values for protein and lipid obtained in our experiments were slightly lower than those obtained by Nielsen et al. (2005) in an comparable experiment on rainbow trout fed to satiation at 16°C (protein digestibility range 92.6–3.9%; lipid digestibility range 97.2–98.5%). This was despite the fact that Nielsen et al. (2005) used the stripping method for collecting faeces, which is generally considered to generate lower digestibility values than the faeces collection method, and yttrium oxide as a marker. One possible explanation for our lower values may be that leakage of nutrients from the faeces may occur before collection so that digestibility is overestimated by not integrating all compounds in the faeces. The two methods used in digestibility measurements are more thoroughly described by Vandenberg and De La Noüe (2001) and Glencross et al. (2005). Based on a comparison of our results with those of Nielsen et al. (2005), we consider the faeces collection method applied in our facilities as being suitably for digestibility measurements. However, since leaking from faeces in particular may be attributed to specific compounds in the feed, such as carbohydrates (Glencross et al. 2005), and may change over time due to the continuous development of fish feed, we believe that this topic deserves more focus in future studies. This point has also been emphasized by Storebakken et al. (1998) who reported that significant interactions exist between feed composition and collection methods.

The potential for improved protein digestibility in rainbow trout subjected to selective breeding has previously been reported (Austreng and Refstie 1979), although this observation has not been consistent (Refstie and Austreng 1981). Our studies, in which modern aquafeeds were used, confirm the conclusions drawn by Austreng and Refstie (1979) and indicate that variations in digestibility among families may only emerge if growth is considerable. Hence, protein digestibility seems to be a trait that can be improved by selective breeding of rainbow trout. Lipid digestibility was also significantly improved in

the fast-growing families in the second experiment, but overall lipid digestibility did not correlate with growth in a consistent manner.

It was only the results of the second experiment that suggested a direct relationship between improved growth of rainbow trout and the higher digestibility of feed ingredients. In contrast to the first experiment, the results from the second experiment showed a highly significant correlation between SGR and protein digestibility (Fig. 1) as well as between FCR and protein digestibility (Fig. 2). These differences between experiments emerged even though only minor variations in fish size, water temperature and feed composition occurred. Regardless of these similarities and the fact that fish were fed to satiation in both experiments, a noteworthy difference in feeding did take place (Table 2). It is likely that this difference explains the variations in protein digestibility. Sanchez et al. (2001) note that in fish culture where genetic gains have been achieved, it may be a fundamental requirement to induce high growth rates for phenotypic traits to be exposed. Zimmerman et al. (2005) also stressed the importance of a relationship between feeding and the digestive capacity of the fish, and Kolstad et al. (2004) reported that the effect of family on feed utilisation was more pronounced than in other studies on the same species by Thodesen et al. (2001), where fish growth was only half as fast.

A number of publications address the potential importance of nutrient digestibility on the growth of fish (Dutil et al. 1997; Takii et al. 1997; Valente et al. 1998). When protein digestibility is improved in fast-growing fish, as observed in our studies, the growth of these fish may to some extent be due to the enhanced absorption of nitrogen in the gut. However, the question arises to what degree this isolated increase in nitrogen uptake contributes to fish growth. As seen in Fig. 1, improved protein digestibility appears to support the growth of fast-growing trout. Figure 3, however, shows that in the same fish (the second experiment), a significant amount of nitrogen is lost to the water environment when protein intake and growth is substantial. The explanation for this is that feed protein is deaminated in the last metabolic step, leading to nitrogen excretion from the fish body. This nitrogen is consequently not used for other purposes, such as body growth (Forster and Goldstein 1969). Thus, studies on trout have shown that when high amounts of protein are supplied to the fish, the percentage of protein retained in the fish body decreases (Arzel et al. 1998; Rasmussen et al. 2000). Since Fig. 3 shows the retention of ingested crude protein, the advantage of increased protein digestibility on fish growth is clearly outdone by the overall reduced protein retention at high growth rates. The threshold indicated in Fig. 3 at which protein retention efficiency is reduced is just around 6.1 mg digestible protein g BW^{-1} day^{-1}. This corresponds to 6.6 mg crude protein g BW^{-1} day^{-1} if the protein digestibility is 92% (average value in the present studies). This threshold is close to the threshold identified at 6.5 mg crude protein g BW^{-1} day^{-1} in, however, smaller (on average) rainbow trout (Rasmussen et al. 2000).

Although the overall protein utilisation is reduced at high SGR, a significantly higher protein digestibility is evident when rainbow trout grow quickly (Fig. 1). The reason for this relationship is possibly an increased activity of trypsin: an increased activity of this protease has previously been associated with growth increase in Atlantic salmon (Rungruangsak-Torrissen et al. 2006) and Atlantic cod (*Gadus morhua* L.) (Lemieux et al. 1999).

Based on our results, we conclude that significant variations in growth, feed and digestibility do exist among rainbow trout families—even in families that have undergone selective breeding for many years. Our results indicate a close relationship between protein digestibility, growth and the FCR in rainbow trout provided that feed intake and growth is substantial. Differences in digestibility among families are important to bear in mind when

selecting fish strains for digestibility studies, in particular if these are to be compared to studies with other strains of the same species.

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