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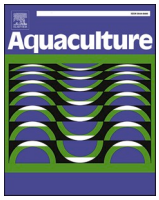

Differences in energy utilisation between a lean and fat strain of rainbow trout (*Oncorhynchus mykiss*)

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ABSTRACT

A good understanding of the utilisation of energy in fish diets is important for accurate feed formulation in aquaculture. One of the primary reasons for differences in the utilisation of digestible energy between fish species are differences that exist in the composition of growth (fat versus protein gain). However, it has also been observed that composition of growth can differ between genetic strains within a single fish species. The main focus of the current experiment was to investigate whether the genetic background of different strains of rainbow trout affects the relationship between digestible energy intake and retained energy. To test this, two different commercial trout strains were selected based on their differences in body fat content (a Lean-Strain and Fat-Strain) and therefore expected differences in composition of growth. Furthermore, this research investigated whether such a potential strain difference in the relationship between digestible energy and retained energy was dependent on the type of non-protein energy in the diet (a Carb-Diet versus a Fat-Diet). Three feeding levels were used in order to estimate the utilisation efficiency of digestible energy for retained energy, leading to a 2 by 2 by 3 factorial design. The results of this study showed that the relationship between digestible energy and retained energy was affected by both strain and diet, but not by an interaction effect between these two factors. Firstly, it was observed that the utilisation efficiency of digestible energy for growth (k_{gDE}) was higher in the Fat-Strain (72% in the Lean-Strain versus 87% in the Fat-Strain) which may be related to a higher potential for fat deposition. This higher k_{gDE} in the Fat-Strain was however balanced by a higher maintenance requirement (47 kJ/kg$^{0.8}$ per day versus 28 kJ/kg$^{0.8}$ per day) leading to a similar retained energy between strains in the current trial. Secondly, it was shown that the exchange of dietary carbohydrates for dietary fat on an isoenergetic basis also increased k_{gDE} (74% for the Carb-Diet versus 85% for the Fat-Diet). The lack of an interaction effect between strain and diet showed that k_{gDE} in both strains was affected by the exchange of carbohydrates for fat on an isoenergetic basis in a similar way. The results of the current trial demonstrated that both dietary macronutrient composition and the composition of growth of specific trout strains should be accounted for in calculating the true net available energy for fish in feed formulation.

1. Introduction

Accurate feed evaluation is important for feed formulation in aquaculture. This requires a good understanding of both the digestibility and utilisation of energy and protein in fish diets. In fish, there is large variability among species in the energetic utilisation efficiency of digestible energy for growth (k_{gDE}). This k_{gDE} partially correlates with the composition of growth (fat to protein gain) (Schrama et al., 2012) as fat gain is energetically more efficient than protein accretion (Rodehutscord and Pfeffer, 1999; Lupatsch et al., 2003). The higher energy

Abbreviations: DE, Digestible energy; ME, Metabolizable energy; RE, Retained energy; N, Nitrogen; DN, Digestible nitrogen; k_{gDE}, Utilisation efficiency of digestible energy for growth; DE_m, Requirement of digestible energy for maintenance; k_{gDN}, Utilisation efficiency of digestible nitrogen for growth; DN_m, Requirement of digestible nitrogen for maintenance; BW, Body weight; MBWm, Metabolic body weight; FCR, Feed conversion ratio; CP, Crude protein; Carb, Carbohydrates; NFE, Nitrogen fat free extract; NSP, Non-starch polysaccharides; HSI, Hepatosomatic index; VSI, Visceral somatic index; BUE, Branchial urinary energy; BUN, Branchial urinary nitrogen; ADC, Apparent digestibility coefficients; SEM, Standard error of the mean.

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costs for protein deposition are related to the fact that protein deposition includes the sum of protein synthesis and catabolism as well as other energy-consuming processes such as amino acid transport, formation and excretion of ammonia (Lupatsch et al., 2003).

In addition to variability among species, the composition of growth can also differ within fish species. In rainbow trout, several studies showed that body fat content can differ between strains (Quillet et al., 2005; Quillet et al., 2007; Kolditz et al., 2008; Skiba-Cassy et al., 2009; Kamalam et al., 2012; Kamalam et al., 2013; Song et al., 2018). In general, in these studies, the leaner strains have a higher growth potential, which is related to a better protein utilisation when compared to fatter strains. This coincides with the observation that in leaner strains dietary energy is preferentially used for protein deposition rather than for fat deposition. Furthermore, differences in growth composition in rainbow trout may also have an impact on the relationship between digestible energy (DE) intake and retained energy (RE) like differences in the DE requirements for maintenance (DE_m) and k_{gDE}. Differences in DE_m and k_{gDE} could also translate into differences in the optimal diet formulation for different strains within a single species.

One reason for the differences in growth composition between trout strains has been attributed to differences in carbohydrate utilisation. More specifically, this may be linked to a higher lipogenic potential which is also considered as one of the key factors that leads to high muscle fat content in more fat strains of rainbow trout (Kolditz et al., 2008; Skiba-Cassy et al., 2009; Jin et al., 2014; Song et al., 2018). This could imply that a higher rate of fat deposition in some strains is also dependent upon the dietary carbohydrate content. This raises the question whether the relationship between DE and RE is not only dependent on the specific strain of rainbow trout, but moreover if this is also influenced by the inclusion of carbohydrates in the diet.

The primary study aim was to investigate whether differences in both adiposity (i.e., growth composition) between different rainbow trout strains exert an influence on the relationship between DE and RE. To test this hypothesis, two different commercial trout strains were selected based on their differences in body fat content (initial body fat content on fresh weight basis was 91 g/kg for the Lean-Strain and 132 g/kg for the Fat-strain). The secondary aim was to examine whether such a strain difference in the DE and RE relationship is influenced by the dietary macronutrient composition. This was tested by exchanging dietary carbohydrates for fat on an isoenergetic basis.

2. Materials and methods

This experiment was part of project number AVD2330020197264 and was conducted in accordance with the Dutch law on the use of experimental animals (Act on Animal Experiments) approved by the Central Animal Experiments Committee (CCD) of The Netherlands. The experiment was performed in the experimental facilities of the Alltech Coppens Aqua Centre (Leende, The Netherlands), and fish were managed and handled in agreement with the current EU-legislation on maintaining experimental animals.

2.1. Aquaria system design

The experiment was performed in a system with twenty-four 200 L Guelph-style metabolic tanks. These Guelph style tanks were constructed according to the original Guelph type system (Cho et al., 1982) except for having one settling tank per fish tank. All fish tanks were connected into one recirculating system with a water purification unit and oxygenating reactor. In the system solids were removed by a drum filter and NH_4^+ by nitrification in a bio filter. Furthermore, a protein skimmer was present, and bacteria were controlled by ozonisation and UV disinfection. Fresh well water was added to the system daily (~ 29.1%/d). Total NO_2^- and NH_4^+ were measured twice a week in the outlet water of the tank using the MQuant® Ammonium test and MColortest™ Nitrite test (both from Supelco®). Over the experimental period, mean NO_2^- and NH_4^+ were respectively, 0.2 mg/L (SD 0.1) and 0.1 mg/L (SD 0.1). Water pH, redox potential, temperature and oxygen content were monitored continuously with a SCADA system (OxyGuard Pacific Monitoring Units). Average pH, redox potential and temperature values were respectively, 8.0 (SD 0.1), 283.8 mV (SD 21.0) and 16 °C (SD 0.1). The outlet water oxygen saturation remained between 95 and 105% during the whole experiment.

2.2. Experimental design and diets

The experiment lasted for 6 weeks and had a 2 by 2 by 3 factorial design. Two rainbow trout strains were studied which differed in body fat content: a Lean-Strain versus a Fat-Strain. Per strain, 12 groups of fish were formed, each stocked in a tank. Half of each strain was fed one of the two experimental diets which differed in the source of non-protein energy by exchanging carbohydrates for fat on an isoenergetic basis: a Carb-Diet versus a Fat-Diet. In order to estimate the relationship between DE and RE by linear regression, three feeding levels were applied for each diet within each strain.

The experimental diets were formulated using Bestmix Feed (Adifo, Industrielaan 11B 9990 Maldegem, Belgium). Diets were formulated to have a similar protein to energy ratio but utilize different sources of non-protein energy (fat versus carbohydrates). This was done by exchanging gelatinized corn starch in the Carb-Diet with rapeseed oil in the Fat-Diet on an isoenergetic basis. The measured protein to energy ratio was similar in both diets (Table 1). As fat possesses a higher energetic value per gram compared to carbohydrates, this resulted in a higher crude

Table 1
Formulation and analysed nutrient composition of experimental diets.

	Carb-Diet	Fat-Diet
Ingredient (g/kg on as is basis):		
Gelatinized corn starch	343	0
Fish meal [a]	167	209
Insect meal [b]	161	201
Rapeseed oil	0	177
Wheat	106	133
Wheat gluten [c]	66	82
Soya protein concentrate [d]	66	82
Fish oil	69	86
Monocalciumphosphate	8	10
Mineral and vitamin premix [e]	9	11
Choline chloride	5	6
Methionine	1	2
Yttrium	0.2	0.2
Nutrient composition (g/kg on as is basis):		
Dry matter	939	943
Crude protein	322	404
Crude fat	108	299
Crude ash	57	71
Carbohydrate [f]	453	169
NFE [g]	439	147
Starch	392	100
NSP [h]	62	70
Crude fiber	15	22
Gross energy (MJ/kg)	19.6	24.0
Protein/energy ratio	16.4	16.8

[a] Fish meal from Peruvian Anchovy, supplied by Köster Marine Products.
[b] Insect meal from black soldier fly, supplied by Protix.
[c] Wheat gluten supplied by Beneo.
[d] Soya protein concentrate supplied by Cefetra Feed Service.
[e] A commercial premix from Alltech Coppens to meet NRC 2011 requirements of rainbow trout.
[f] Carbohydrate content equals dry matter minus the sum of protein, fat and ash.
[g] NFE, nitrogen fat free extract, equals dry matter minus the sum of protein, fat, ash and crude fiber.
[h] NSP, non-starch polysaccharides, equals dry matter minus the sum of protein, fat, ash and starch.

protein and energy content for the Fat-Diet than for the Carb-Diet. In order to provide equal amounts of protein and energy within feeding levels, the applied the feeding levels were corrected for the differences in dietary protein and energy content. Both diets were formulated to meet the vitamin, mineral, essential fatty acid and amino acid requirements of rainbow trout (NRC, 2011). The diet formulae and the analysed macronutrient content are displayed in Table 1. Yttrium oxide was added to all diets as an indigestible marker to measure the apparent nutrient digestibility coefficients.

Diets were produced by SPAROS LDA (Olhão, Portugal). All powder ingredients (excluding both rape and fish oil) were mixed according to the target formulation in a double-helix mixer (model 500 L, TGC Extrusion, France) and ground (below 400 μm) in a micropulverizer hammer mill (model SH1, Hosokawa-Alpine, Germany). Diets with a pellet size of 3 mm were manufactured with a twin-screw extruder (model BC45, Clextral, France) with a screw diameter of 55.5 mm. The extruded pellets were dried in a vibrating fluid bed dryer (model DR100, TGC Extrusion, France) for approximately 12 min with a temperature gradient ranging from 120 °C in the first section and 70 °C at the exit. After cooling, the totality of oils were added by vacuum coating (700 mbar, for approximately 90 s) (model PG-10VCLAB, Dinnissen, The Netherlands). Immediately after coating, diets were packed in sealed plastic buckets and shipped to the research facilities of Alltech Coppens.

2.3. Animal management

The two strains of rainbow trout (*Oncorhynchus mykiss*) used in the experiment were selected based on having a contrast in body fat content and thus in composition of growth. The analysed initial body fat content on fresh weight basis was 91 g/kg for the Lean-Strain and 132 g/kg for the Fat-strain. Initial condition factors were 1.03 g/cm^3 (SD 0.09) for the Lean-Strain and 1.16 g/cm^3 (SD 0.07) for the Fat-strain. Each strain was obtained from a commercial farm, the Fat-Strain from a Danish fish farm and the Lean-Strain from a French fish farm. In the experiment 884 fish were used, which had a mean weight 93 g at the start of the experiment. All fish were fasted for 1 day prior to bulk weighing. Thirty-six fish were randomly assigned to each tank. The 24 tanks were randomly assigned to the treatments. An additional 10 fish per strain were euthanized with a lethal dose of phenoxyethanol (1 ml/L) and stored at −20 °C for the determination of initial whole-body nutrient composition. These 10 fish were randomly selected with the condition that they were ± 10% of the mean weight of each strain.

The fish were fed twice daily for 1 week before the start of the experiment in order to acclimate them to the test diets. Fish were fed equal amounts of protein and energy within each of the three feeding levels. Based on the differences in nutrient content between diets the applied absolute feeding levels were 13, 9.5 and 6.75 g/kg$^{0.8}$ per day for the Carb-Diet and 10.4, 7.8 and 5.2 g/kg$^{0.8}$ for the Fat-Diet. Two thirds of the daily ration was hand fed at 7:00 AM and the rest at 2:30 PM. Uneaten pellets were counted after each feeding period and multiplied by the average weight per pellet to calculate the amount of uneaten feed in grams. Faeces samples were collected in chilled bottles below each of the individual Guelph tanks during week 2, 4 and 6. Each faecal collection period lasted 7 days. Feacal material was recovered every day before each feeding period and stored at minus 20 degrees, samples were pooled per fish tank prior to freeze drying and analysis.

At the end of the experiment the fish were fasted for 1 day before the final sampling. The final sampling consisted of weighing all fish. Six fish per tank within ±10% of the mean final weight of the tank were randomly selected and euthanized with a lethal dose of phenoxyethanol and were stored at −20 °C prior to analysis of whole-body nutrient composition.

2.4. Sample analysis

All chemical analyses were performed in duplicate by Nutricontrol BV (Ncb Laan 52, 5462 GE Veghel). Upon completion of the trial, both faecal and fish samples were homogenized and then freeze-dried prior to analysis. The analysis of feed, faecal and fish samples consisted of the following determinations; dry matter (DM) content by drying at 103 °C until constant weight for 4 and 24 h respectively (ISO 6496, 1999); ash content after incineration at 550 °C for 4 h (ISO 5984, 2002); crude protein (CP) based on nitrogen × 6.25 using the Kjeldahl method (ISO 5983, 2005); fat after an initial acid-hydrolysis step followed by a petroleum-diethyl ether extraction (ISO 6492, 1999); phosphorus by an internal method using an optical spectroscopic technique based on NEN-EN 15510:2017; gross energy content with the adiabatic bomb calorimeter method (ISO 9831, 1998); starch after an enzymatic degradation using the hexokinase method (ISO 6493, 2000); crude fiber by an internal method and determined as the fat-free organic substance which is insoluble in acid and alkaline media (underlying method as in COMMISSION REGULATION (EC) No 152/2009). Carbohydrate content was calculated as DM – CP – Fat – Ash, nitrogen fat free extract (NFE) content was calculated as DM – CP – Fat – Ash – Crude fiber and non-starch polysaccharides (NSP) content as Carbohydrate – Starch.

Table 2
Calculations of the different parameters used in this study.

Parameter	Calculation
MBWm (kg$^{0.8}$)	(Initial body weight (kg) + final body weight (kg))/2) $^{0.8}$
Growth (g/kg$^{0.8}$ per day)	(Final body weight (g) - initial body weight (g))/MBWm (kg$^{0.8}$)/days
Feed intake (g/kg$^{0.8}$ per day)	Feed consumed (g)/MBWm (kg$^{0.8}$)/days
FCR	Feed intake (g/kg$^{0.8}$ per day)/Growth (g/kg$^{0.8}$ per day)
ADC (%)	(1 - (yttrium feed (g)/yttrium faeces (g)) × (nutrient faeces (g)/nutrient feed (g))) x 100
Condition factor (g/cm^3)	100 × body weight (g)/body length (cm) ^{3}
HSI (%)	Liver weight (g)/body weight (g)
VSI (%)	Visceral weight (g)/body weight (g)
Corrected VSI for liver weight (%)	(Visceral weight (g) - liver weight (g))/body weight (g)
N intake (mg/kg$^{0.8}$ per day)	Feed intake (g/kg$^{0.8}$ per day) × dietary N content (mg/g)
Digestible N intake (mg/kg$^{0.8}$ per day)	N intake (mg/kg$^{0.8}$ per day) × N digestibility coefficient (%)
Retained N (mg/kg$^{0.8}$ per day)	Final - initial N body mass (mg)/MBWm (kg$^{0.8}$)/days
BUN losses (mg/kg$^{0.8}$ per day)	Digestible N intake (mg/kg$^{0.8}$ per day) - retained N (mg/kg$^{0.8}$ per day)
Gross energy intake (kJ/kg$^{0.8}$ per day)	Feed intake (g/kg$^{0.8}$ per day) × gross energy content of diet (kJ/g)
DE intake (kJ/kg$^{0.8}$ per day)	Gross energy intake (kJ/kg$^{0.8}$ per day) × energy digestibility coefficient (%)
BUE losses (kJ/kg$^{0.8}$ per day)	BUN losses (mg/kg$^{0.8}$ per day) × the energy concentration of NH_3-N (24.9 kJ N/g) (assuming that all N will be excreted as NH_3-N)
ME intake (kJ/kg$^{0.8}$ per day)	DE intake (kJ/kg$^{0.8}$ per day) - BUE losses (kJ/kg$^{0.8}$ per day)
RE (kJ/kg$^{0.8}$ per day)	Final - initial body energy quantities (kJ)/MBWm (kg$^{0.8}$)/days
Heat production (kJ/kg$^{0.8}$ per day)	ME intake (kJ/kg$^{0.8}$ per day) – RE (kJ/kg$^{0.8}$ per day)

MBWm, mean metabolic body weight; FCR, feed conversion ratio; ADC, Apparent digestibility coefficient; HSI, Hepatosomatic index; VSI, Visceral somatic index; N, Nitrogen; BUN, Branchial urinary nitrogen; BUE, Branchial urinary energy; DE, Digestible energy; ME, Metabolizable energy; RE, Retained energy.

2.5. Calculations

Calculations of the different parameters are displayed in Table 2. Furthermore, the utilisation efficiency of both digestible nitrogen (k_{gDN}) and energy (k_{gDE}) were estimated as the slope of the linear regression analysis on digestible nitrogen versus retained nitrogen (both as mg/$kg^{0.8}$ per day) and digestible energy versus retained energy (both as kJ/$kg^{0.8}$ per day). The requirement of both digestible nitrogen and energy for maintenance (DN_m and DE_m) was also estimated from these regressions as the point where the line crosses the x-axis at y = 0.

2.6. Statistics

Tank was used as experimental unit in all statistical analysis, which was performed using the program SPSS statistics 20, (IBM Statistics Inc., USA). The growth performance, digestibility coefficients, and nitrogen and energy balance parameters were analysed using a three-way ANOVA for the effect of strain, diet, feeding level and all interaction terms, followed by multiple comparison of means using Tukey's multiple range test. Analysis was performed with a confidence interval of 0.05. Univariate analysis on retained nitrogen and energy was performed with digestible nitrogen and digestible energy intake as covariates and strain and diet as fixed factors.

3. Results

In this study three feeding rations were applied to enable linear regression of DE intake against RE and DN intake against RN, but feeding level was not a goal to address in this study. An effect of feeding level was detected with most of the measured parameters and only a few interaction effects were observed with diet composition alone (6 parameters). Mean values of all 12 treatments and of the 3-way ANOVA are presented in the supplementary material. In this results section, only the main effect of diet (Fat-Diet versus Carb-Diet) and strain (Lean-Strain versus Fat-Strain) are presented because for all parameters (except for body protein content) the interaction effect between diet and strain was absent ($P > 0.05$; Supplementary Table 1–5). In other words, both strains of trout had an equal reaction to the Carb-Diet and the Fat-diet.

3.1. Performance

Performance data are shown in Table 3. On average across all feeding levels, the fish almost doubled their weight during the 6-wk experimental period. Growth and FCR were not different between the strains ($P > 0.05$). HSI tended to be higher in the Lean-strain than in the Fat-strain ($P < 0.10$). VSI including the liver was not different, but VSI excluding liver was lower in the Lean-strain than in the Fat-Strain (9.6 versus 10.3; $P < 0.05$). Feeding levels were set to provide similar amount of protein and energy at both dietary treatments. Consequently, diets gave similar growth rates ($P > 0.10$) but due to higher nutrient density of the Fat-Diet, FCR was low with the Fat-Diet compared to the Carb-diet ($P < 0.001$). Exchanging carbohydrates for fat on an isoenergetic basis decreased HSI and increased VSI (excluding the liver) ($P < 0.001$).

3.2. Body composition and apparent digestibility coefficients

Final body protein content was unaffected by the main effects of diet or strain. In contrast, body dry matter, fat and energy content at the end of the experiment were strongly affected by both diet and strain ($P < 0.001$; Table 4). The final body fat content in the Lean-Strain was 119 g/kg and 139 g/kg in the Fat-Strain. The final fat content was increased by 16% when dietary carbohydrates were exchanged for dietary fat on an isoenergetic basis (Table 4). Final body energy content paralleled the patterns in body fat content for both the effect of diet and strain.

The apparent digestibility coefficients (ADC) of most nutrients were different between trout strains and between experimental diets (Table 4). Exchanging dietary carbohydrates for fat on an isoenergetic basis increased the ADC of most nutrients except for phosphorous which was unaffected and for both crude ash and carbohydrates, which declined. Also, various nutrient ADC differed between both trout strains. Crude protein and energy ADC were lower ($P < 0.05$) and fat ADC tended to be lower ($P < 0.10$) in the Fat-Strain compared to the Lean-Strain. In contrast, crude ash and phosphorous ADC was higher in the Fat-Strain than in the Lean-Strain.

3.3. Nitrogen and energy balance

The differences in nitrogen and energy intake between strains as well as between diets were numerically small (Table 5), which was in line with the design of the experiment. However, due to differences in protein and energy digestibility (Table 4), some effects ($P < 0.05$) of strain and diet were noted for digestible nitrogen and digestible energy intake. Retained nitrogen was unaffected by strain or diet ($P > 0.05$). Heat production and retained energy were identical for both trout strains ($P > 0.05$). Despite a numerically similar metabolizable energy intake with both diets, heat production was lower with the Fat-Diet as compared to the Carb-Diet (50 versus 65 kJ/$kg^{0.8}$ per day; $P < 0.05$). This resulted in a 14% lower retained energy with the Carb-Diet than with the Fat-Diet

Table 3
Main effects from trout strain (fat versus lean) and diet (carbohydrates versus fat) on performance parameters and body indexes.

	Lean-Strain	Fat-Strain	SEM	*P*-value	Carb-Diet	Fat-Diet	SEM	*P*-value
Growth period (d)	42	42	–	–	42	42	–	–
No. of fish per tank	36	36	–	–	36	36	–	–
No. of tanks	2	2			2	2		
Survival (%)	98.6	99.3	0.86	0.422	98.1	99.8	0.86	0.076
Start biomass per fish (g)	93	93	0.5	0.438	93	93	0.5	0.917
Final biomass per fish (g)	174	176	1.5	0.532	174	176	1.5	0.202
Growth (g/$kg^{0.8}$ per day)	9.5	9.6	0.08	0.100	9.5	9.6	0.08	0.096
FCR	0.88	0.86	0.011	0.181	0.99	0.74	0.011	0.000
Condition factor (g/cm^3)	1.4	1.4	0.02	0.441	1.4	1.4	0.02	0.853
HSI (%)	2.5	2.2	0.15	0.078	3.5	1.3	0.15	0.000
VSI (%)	12.1	12.6	0.29	0.145	12.9	11.8	0.29	0.001
Corrected VSI for liver weight (%)	9.6	10.3	0.20	0.004	9.4	10.5	0.20	0.000

Carb, carbohydrates; FCR, feed conversion ratio; HSI, Hepatosomatic index; VSI, Visceral somatic index; SEM, standard error of the mean. Means are based on $n = 12$.

Table 4
Main effects of strain (fat versus lean) and diet (carb versus fat) on body composition and apparent digestibility coefficients of nutrients and energy.

	Lean-Strain	Fat-Strain	SEM	*P*-value	Carb-Diet	Fat-Diet	SEM	*P*-value
Body composition (on fresh basis) [a]								
Dry matter (g/kg)	308	326	1.4	0.000	311	323	1.4	0.000
Protein (g/kg)	164	163	1.2	0.423	164	162	1.2	0.190
Fat (g/kg)	119	139	1.9	0.000	120	139	1.9	0.000
Gross energy (MJ/kg)	8.4	9.1	0.08	0.000	8.4	9.0	0.08	0.000
Digestibility (%)								
Dry matter	83.2	82.8	0.43	0.341	81.3	84.6	0.43	0.000
Crude protein	90.6	90.0	0.15	0.001	90.1	90.6	0.15	0.013
Crude fat	96.4	95.8	0.31	0.090	94.3	97.9	0.31	0.000
Crude ash	46.3	51.0	0.93	0.000	51.5	45.8	0.93	0.000
Phosphorous	61.9	67.0	1.08	0.000	64.9	64.0	1.08	0.428
Crude fiber	−9.6	−5.4	4.51	0.368	−12.5	−2.4	4.51	0.046
Carbohydrates [b]	70.0	69.1	0.79	0.306	75.7	63.3	0.79	0.000
Starch	96.7	95.5	1.26	0.367	93.8	98.5	1.26	0.003
NSP[c]	−15.0	−14.8	4.34	0.960	−42.2	12.4	4.34	0.000
Energy	88.1	87.3	0.33	0.033	84.9	90.5	0.33	0.000

Carb, carbohydrates; SEM, standard error of the mean. Means are based on $n = 12$.
[a] Initial body composition on (on fresh weight basis) was as follows for the Lean-Strain: dry matter 275 g/kg; protein 161 g/kg; fat 91 g/kg; energy 7.2 MJ/kg; and for the Fat-Strain: dry matter 304 g/kg; protein 157 g/kg; fat 132 g/kg; energy 8.6 MJ/kg.
[b] Carbohydrates equals dry matter minus the sum of protein, fat and ash.
[c] NSP, non-starch polysaccharides, equals dry matter minus the sum of protein, fat, ash and starch.

Table 5
Main effects of strain (fat versus lean) and diet (carb versus fat) on nitrogen and energy balances.

	Lean-Strain	Fat-Strain	SEM	*P*-value	Carb-Diet	Fat-Diet	SEM	*P*-value
N intake (mg/kg$^{0.8}$ per day)	474	471	1.7	0.095	486	460	1.7	0.000
Digestible N intake (mg/kg$^{0.8}$ per day)	430	424	1.7	0.003	437	416	1.7	0.000
BUN (mg/kg$^{0.8}$ per day)	178	162	5.4	0.017	180	160	5.4	0.004
Retained N (mg/kg$^{0.8}$ per day)	252	261	4.7	0.090	258	256	4.7	0.679
GE intake (kJ/kg$^{0.8}$ per day)	198	177	0.6	0.095	185	171	0.6	0.000
DE intake (kJ/kg$^{0.8}$ per day)	157	154	0.9	0.010	157	154	0.9	0.013
BUE (kJ/kg$^{0.8}$ per day)	4.4	4.0	0.14	0.017	4.5	4.0	0.14	0.004
ME intake (kJ/kg$^{0.8}$ per day)	152	150	0.9	0.020	152	150	0.9	0.033
Heat production (kJ/kg$^{0.8}$ per day)	60	56	2.4	0.209	66	50	2.4	0.000
Retained Energy (kJ/kg$^{0.8}$ per day)	93	94	2.1	0.645	86	100	2.1	0.000
Retained Energy as Fat (kJ/kg$^{0.8}$ per day)	58	57	1.6	0.538	49	65	1.6	0.000
Retained Energy as CP (kJ/kg$^{0.8}$ per day)	37	39	0.7	0.089	38	38	0.7	0.679

Carb, carbohydrates; N, Nitrogen; BUN, Branchial and urinary nitrogen losses; GE, Gross energy; DE, Digestible energy; BUE, Branchial and urinary energy losses; ME, Metabolizable energy; CP, Crude protein; SEM, standard error of the mean. $P < 0.05$ indicates effect is significant. Means are based on n = 12.

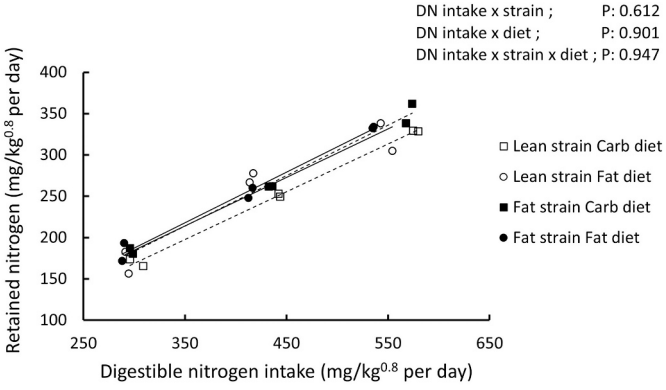

Fig. 1. The relationship between digestible nitrogen intake (mg/kg$^{0.8}$ per day) and retained nitrogen (mg/kg$^{0.8}$ per day) for two strains of rainbow trout (lean strain, dashed lines and open symbols; fat strain, solid lines and solid symbols) fed two different diets (carb and fat). The estimated regression lines are presented in Table 6.

($P < 0.05$).

For both strains the digestible nitrogen (DN) intake was linearly related to retained nitrogen (RN) irrespective of which diet was fed to the trout (Fig. 1). The estimated linear relationships between DN intake and RN for each strain and each diet are given in Table 6. The relationships between DN intake and RN were not different between trout strains and was also not different between diets ($P > 0.1$). Both the slopes and the intercepts of the lines were similar across treatments (Table 6). Average over all treatments, the slope was 0.60. This implies that for every unit of DN intake increase 60% is retained as N. In contrast

Table 6
The linear relationships between digestible nitrogen intake (DN intake, mg/kg$^{0.8}$ per day) and retained nitrogen (RN, mg/kg$^{0.8}$ per day) for two strains of rainbow trout (lean and fat) fed two different diets (carb and fat).

Strain	Diet	Regression line	R^2	DN_m (mg/kg$^{0.8}$ per day)
Lean	Carb	−4.765 (se 9.916) + 0.578 (se 0.022) × DN intake	0.994	8.244
Lean	Fat	8.119 (se 41.544) + 0.588 (se 0.096) × DN intake	0.903	−13.808
Fat	Carb	0.895 (se 13.420) + 0.609 (se 0.030) × DN intake	0.990	−1.470
Fat	Fat	3.894 (se 14.521) + 0.612 (se 0.034) × DN intake	0.988	−6.363

Carb, carbohydrates; se, standard error; DN, digestible nitrogen; DN_m, requirement of digestible nitrogen for maintenance.

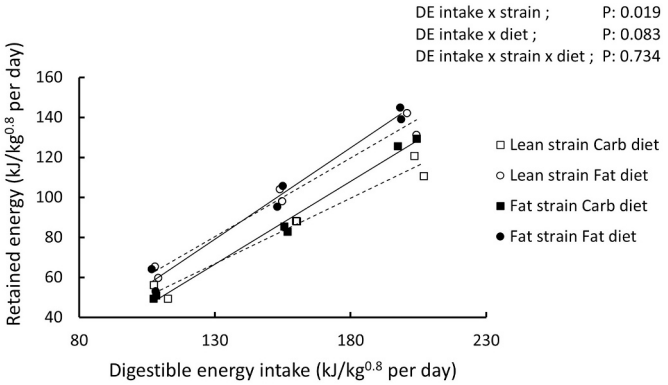

Fig. 2. The relationship between digestible energy intake (kJ/kg$^{0.8}$ per day) and retained energy (kJ/kg$^{0.8}$ per day) for two strains of rainbow trout (lean strain, dashed lines and open symbols; fat strain, solid lines and solid symbols) fed two different diets (carb and fat). The estimated regression lines are presented in Table 7.

Table 7
The linear relationships between digestible energy intake (DE intake, kJ/kg$^{0.8}$ per day) and retained energy (RE, kJ/kg$^{0.8}$ per day) for two strains of rainbow trout (lean and fat) fed two different diets (carb and fat).

Strain	Diet	Regression line	R^2	DE_m (kJ/kg$^{0.8}$ per day)
Lean	Carb	−18.6 (se 9.91) + 0.657 (se 0.061) × DE intake	0.967	28.311
Lean	Fat	−21.6 (se 10.26) + 0.785 (se 0.064) × DE intake	0.974	27.516
Fat	Carb	−41.1 (se 6.62) + 0.828 (se 0.041) × DE intake	0.990	49.638
Fat	Fat	−40.0 (se 9.95) + 0.916 (se 0.063) × DE intake	0.981	43.668

Carb, carbohydrates; se, standard error; DE, digestible energy; De_m, requirement of digestible energy for maintenance.

to nitrogen (protein) retention, the linear relationship between DE intake and RE differed between trout strains ($P < 0.05$) and tended to be affected by diet ($P = 0.083$; Fig. 2). The slope of the lines, which reflects the partial efficiency of DE intake for growth (k_{gDE}), was not affected by an interaction effect between diet and strain. This implies that both trout strains reacted identically to both diets regarding energy utilisation. Averaged over both diets, k_{gDE} was 0.72 for the Lean-Strain and 0.87 for the Fat-Strain, indicating that the Fat-Strain converts energy more efficiently into energy gain (Table 7). Next to a different k_{gDE}, also the intercept, which reflects that the fasting heat production differed between the strains ($P = 0.043$). This fasting heat production was lower in the Lean-Strain than in the Fat-Strain. This difference was also reflected in a difference in the estimated maintenance requirement of digestible energy (DE_m), being 68% higher in the Fat-Strain compared to the Lean-Strain (47 versus 28 kJ/kg$^{0.8}$ per day; Table 7). Averaged over both strains, k_{gDE} was slightly lower at for trout fed the Carb-diet compared to those fed the Fat-diet (0.74 versus 0.85). DE_m was not different ($P > 0.05$) between diets, averaging 39 and 36 kJ/kg$^{0.8}$ per day, respectively with the Carb-Diet and the Fat-Diet.

4. Discussion

The present study investigated whether the genetic background of different rainbow trout strains exerts an influence on the relationship between DE and RE. Two commercial strains were selected based on their differences in body fat content and expected differences in composition of growth (protein versus fat gain). Secondly, this research assessed whether any difference in the relationship between DE and RE in the different strains was dependent upon diet composition (in this case fat versus carbohydrates) in the form of an interaction effect with strain.

Digestibilities of protein, energy, ash and phosphorous were all different between the two strains of rainbow trout. Whilst the absolute differences in protein and energy digestibility were only approximately 1%, this could nonetheless impact feed evaluation from an industrial and practical point of view. Conversely, the ash and phosphorus digestibility data presented more obvious differences, with an approximately 5% higher digestibility in the Fat-Strain in absolute terms. This higher digestibility may indicate a difference in the phosphorus requirement between strains as this will lead to more available phosphorus which they may require to support the body during growth. It is well known that morphological differences in the digestive physiology of different fish species can affect nutrient digestibility (Hua and Bureau, 2010; Gilannejad et al., 2019), however comparatively few studies have focused on the effect of different genetic strains. To the authors' knowledge, only one study in rainbow trout has previously reported differences in the digestibility of protein between different families (Rasmussen and Jokumsen, 2009). Here these authors hypothesized this to be caused by differences in the activity of digestive enzymes between families. Although not measured in the current trial, it has previously been reported that gut length and weight are somewhat heritable in Nile tilapia (Charo-Karisa et al., 2007) and Atlantic salmon (Powell et al., 2008). Genetically driven differences in gut morphology could therefore also potentially impact nutrient digestibility between strains of a single species. One example of such differences could be passage rate in the gut, whereby a faster passage rate is known to lead to a lower digestibility of nutrients as there is less time available to complete the digestion process (Dvergedal et al., 2019).

No differences were found in the relationship between DN intake and RN between treatments. The k_{gDN} was high in both strains and diets, reaching approximately 60%, which is comparable with other published studies on trout carried out at similar feeding levels (Bureau et al., 2006; Glencross et al., 2007; Glencross et al., 2008; Glencross, 2009). The lack of an effect of strain on digestible nitrogen (protein) utilisation runs counter to much of the published literature on fat versus lean strains. Many of these publications demonstrate that lean strains possess better growth potential compared to fat strains, which may be associated with an improved feed efficiency and protein utilisation (Quillet et al., 2007; Kolditz et al., 2008; Kamalam et al., 2012; Kamalam et al., 2013; Song et al., 2018). The high k_{gDN} in the current trial could partly be related to the low protein to energy ratio in both diets as this is known to increase protein utilisation in salmonids (Hillestad and Johnsen, 1994; Lanari et al., 1995; Einen and Roem, 1997). However, another reason could be the fact that the fish were fed restrictively in this experiment. A number of studies have reported that protein retention decreases at higher feeding levels than those applied in the current trial, which suggests that rainbow trout reach a maximum protein deposition at higher levels of protein intake (Bureau et al., 2006; Glencross et al., 2007; Glencross et al., 2008; Glencross, 2009). This might also suggest that the differences in protein utilisation between strains as described above might only occur at higher feeding levels compared to the levels used in the current trial or could further indicate a difference in the maximum protein deposition potential between strains.

K_{gDE} was different between the two strains with higher values for the Fat-Strain with both diets (72% in the Lean-Strain versus 87% in the Fat-Strain). The observed differences in k_{gDE} may be a consequence of higher fat deposition in the Fat-Strain which is energetically very efficient (Rodehutscord and Pfeffer, 1999; Lupatsch et al., 2003). This higher k_{gDE} in the Fat-Strain is not only higher compared to the Lean-Strain, but also notably higher when compared to values found in literature which are commonly reported between 55 and 75% (Schrama et al., 2012). The higher values in the Fat-Strain are therefore actually more comparable to values found for Atlantic salmon with a k_{gDE} of 80% (Helland et al., 2010). This might be at least partly explained through the use of higher

dietary fat levels in salmon diets but could also be linked to a comparatively higher body fat content when compared to trout. This could therefore be related to the composition of growth in salmon, with a higher retention of fat. A further influence may be an improved utilisation of glucose due to a higher lipogenic potential in the Fat-Strain which is also suggested as one of the key factors that can lead to higher muscle fat content in some strains (Kolditz et al., 2008; Skiba-Cassy et al., 2009; Jin et al., 2014; Song et al., 2018). In addition to the higher k_{gDE} measured in the Fat-Strain, the estimated DE_m in these fish was also 68% higher when compared to the lean fish (47 kJ/$kg^{0.8}$ per day versus 28 kJ/$kg^{0.8}$ per day). This higher DE_m may therefore have compensated for the higher k_{gDE} in this strain leading to a similar retained energy between strains in the current trial. The use of a higher feeding level would have been required to test this theory as the relative influence of maintenance would have then been reduced. Although different between strains, the DE_m was comparable with other studies where values have been found between 16 and 45 kJ/$kg^{0.8}$ per day (Schrama et al., 2012).

In terms of performance, the higher DE_m observed in the Fat-Strain could be viewed as a disadvantage as it would mean that less energy can be directed towards growth. In African Catfish it has for example been observed that an elevated stress response is coupled with a higher residual feed intake which is associated with higher maintenance requirements and a reduction in feed efficiency (Martins et al., 2006). Although a higher DE_m could thus lead to a lower feed efficiency it is also important in the context of the robustness of the animal and its potential to cope with suboptimal conditions (Kaushik and Schrama, 2022). However, the opposite trend has also often been reported, and a higher DE_m does not necessarily always lead to a more robust animal. This has been reported in pig nutrition (Hermesch et al., 2015), but has also been noted in trout, where challenging conditions such as hypoxia can downregulate DE_m (Glencross, 2009). Variations in DE_m within fish species have often been attributed to differences in environmental conditions among trials; differences in diet composition; methodology of the trial and the statistical methods applied (Kaushik and Schrama, 2022). However, the potential influence of genetic background within single fish species has received relatively little attention in the literature. In studies on pigs it has been observed that variation in the efficiencies of protein and lipid deposition influence maintenance requirements to a lesser extent and that for example variable protein turnover rates explain <5% of the total variance in this regard (Knap, 2016; Knap and Kause, 2018). Other studies on pigs have also shown that the viscera contribute more than three times as much as the muscle to the maintenance requirement (van Milgen et al., 1998; van Milgen and Noblet, 1999). In the present study it was also observed that the VSI when corrected for liver weights was higher for the Fat-Strain as compared to the Lean-Strain. It might therefore also have been the case that the metabolically active organs in the viscera had an increased level of activity. However, the HSI, which indicates the relative liver weight of the fish in an organ where many anabolic processes such as lipogenesis occurs, was not different between strains.

In both strains it was observed that the Carb-Diet did lead to a lower k_{gDE} as compared to the Fat-Diet (74% for the Carb-Diet versus 85% for the Fat-Diet) suggesting that carbohydrates were less efficiently utilised for retained energy in rainbow trout when compared to fat. The lower utilisation efficiency of the carbohydrate diet was also reflected in a higher heat production in fish fed this diet, which is indicative of an increase in energy loss when using carbohydrates as an energy source. This is in line with the lower utilisation of carbohydrates for RE found in both rainbow trout and a range of other fish species (Schrama et al., 2012; Schrama et al., 2018; Phan et al., 2019; Phan et al., 2021a; Phan et al., 2021b). However, there was no interaction effect between diet and strain, which indicates that k_{gDE} was affected by diet in both strains in a similar way. In terms of DE_m, no differences were found between the diets (39 kJ/$kg^{0.8}$ per day for the Carb-Diet and 36 kJ/$kg^{0.8}$ per day for the Fat-Diet).

5. Conclusion

The current study demonstrated that different fish strains can differ regarding energy metabolism. First of all, strain differences can occur in nutrient and energy digestibility. Secondly it was shown that the relationship between DE and RE in rainbow trout is determined by both the composition of growth of specific strains and the dietary macronutrient composition. However, the difference in the relationship between DE and RE for the different strains was not dependent upon the diet as shown by the lack of an interaction between strain and diet. These results therefore indicate that (1) fat is more efficiently used for retained energy as compared to carbohydrates and (2) strains of rainbow trout which possess a higher degree of fat deposition will have a higher energetic utilisation efficiency of both digestible carbohydrates and fat for retained energy. Both dietary macronutrient composition and the composition of growth of specific trout strains should therefore be accounted for in calculating the true available net energy for precise feed formulation in this fish species. Furthermore, this study shows that large differences exist in the energy requirement for maintenance between genetic strains of rainbow trout differing in body fat content. The implications of these findings could be translated to the formulation of specific feeds and/or different feeding strategies for different strains of rainbow trout. This could result in a departure from generalized feeds within one species towards a concept of feeding according to genetic potential of that species.

CRediT authorship contribution statement

Ruben Groot: Conceptualization, Methodology, Formal analysis, Investigation, Project administration, Writing – original draft, Visualization. **Philip Lyons:** Conceptualization, Resources, Writing – review & editing. **Johan W. Schrama:** Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors report no declarations of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2022.738681.

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