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Genetic improvement of feed conversion ratio via indirect selection against lipid deposition in farmed rainbow trout (*Oncorhynchus mykiss* Walbaum)

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8 **Genetic improvement of feed conversion ratio via indirect selection**
9 **against lipid deposition in farmed rainbow trout (*Oncorhynchus mykiss***
10 **Walbaum)**

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21
22 **Running title:** Genetic improvement of FCR

23
24 **Keywords: Breeding programme: Feed intake: Index selection: Quantitative genetics**

25
26 **Abbreviations:** b , regression coefficient; BW, body weight; CV_G , coefficient of genetic variation; CV_R ,
27 coefficient of residual variation; DFI, daily feed intake; DG, daily gain; DHA, docosahexaenoic acid;
28 EPA, eicosapentaenoic acid; FCR, feed conversion ratio; h^2 , heritability; HP, high protein;
29 LifeFCR_{Indicator}, indicator of lifetime feed conversion ratio; LifeFI_{Indicator}, indicator of lifetime feed
30 intake; LifeRFI_{Indicator}, indicator of lifetime residual feed intake; LifeProtRetention_{Indicator}, indicator of
31 lifetime protein retention; LifeLipRetention_{Indicator}, indicator of lifetime lipid retention;
32 LifeERetention_{Indicator}, indicator of lifetime energy retention; NP, normal protein; RFI, residual feed
33 intake; r_G , genetic correlation; r_P , phenotypic correlation; V_G , genetic variance; V_R , residual variance;
34 ΔG , rate of genetic gain.

35 Abstract

36 In farmed fish, selective breeding for feed conversion ratio (FCR) may be possible via indirectly
37 selecting for easily-measured indicator traits correlated with FCR. We tested the hypothesis that
38 rainbow trout with low lipid% have genetically better FCR, and that lipid% may be genetically related
39 to retention efficiency of macronutrients, making lipid% a useful indicator trait. A quantitative genetic
40 analysis was used to quantify the benefit of replacing feed intake in a selection index with one of three
41 lipid traits: body lipid%, muscle lipid%, or percentage of viscera weight of total body weight
42 (reflecting visceral lipid). The index theory calculations showed that simultaneous selection for weight
43 gain and against feed intake (direct selection to improve FCR) increased the expected genetic response
44 in FCR by 1.50-fold compared to the sole selection for growth. Replacing feed intake in the selection
45 index with body lipid%, muscle lipid%, or viscera% increased genetic response in FCR by 1.29, 1.49,
46 and 1.02-fold, respectively, compared to the sole selection for growth. Consequently, indirect selection
47 for weight gain and against muscle lipid% was almost as effective as direct selection for FCR. The fish
48 with genetically low body and muscle lipid% were more efficient in turning ingested protein into
49 protein weight gain. Both physiological and genetic mechanisms promote that low-lipid% fish are more
50 efficient. The results highlight that in breeding programmes of rainbow trout, control of lipid deposition
51 improves not just FCR but also protein retention efficiency. This improves resource efficiency of
52 aquaculture and reduces nutrient load to the environment.

53

54 250 / 250 words.

55 Introduction

56 Feed is one of the largest costs of aquaculture production, making the improvement of feed conversion
57 ratio (FCR), the ratio of feed intake to weight gain, of great importance. Selective breeding
58 programmes aim for the genetic improvement of farmed animals. To directly select for FCR, feed
59 intake needs to be recorded, preferably from individual fish. However, fish are typically held in schools
60 and fed together making the recording of feed intake on individual fish a major challenge⁽¹⁻⁴⁾. A
61 potential alternative is to improve FCR by indirect selection for traits that are genetically correlated
62 with FCR. To be successful, such indicator traits need to have a firm biological and physiological
63 relationship with FCR.

64 Individually recorded feed intake or FCR is currently not selected in any fish breeding
65 programme, and indirect ways of improving FCR may be an effective alternative. Lipid deposition is
66 one potential indicator trait of FCR because in livestock, lean animals are typically more efficient in
67 converting feed to tissue growth compared to fat animals^(5,6). In farmed fish, there is some evidence that
68 the control of lipid deposition can be used to genetically improve FCR⁽⁷⁻⁹⁾. An additional benefit of
69 controlling lipid is that lipid deposition in different body parts influences fillet quality⁽¹⁰⁾ and slaughter
70 yield⁽¹¹⁾. In fish, lipid can be recorded non-destructively, making trait recording appealing^(12,13).

71 Studies on the genetic improvement of FCR in large rainbow trout *Oncorhynchus mykiss*
72 (*Walbaum*), marketed at body weight of 1.5-3 kg, will especially benefit from the assessment of FCR
73 when fish are reaching market size. This is the time when most of the feed is consumed, and hence the
74 time when most of the feeding costs are realized. Moreover, rainbow trout become less efficient as fish
75 grow. Simultaneously this is the time when lipid deposition is at high level, again reflecting the
76 potential link between lipid deposition and FCR⁽¹⁴⁻¹⁶⁾.

77 We quantified the benefit of using lipid deposition as a genetic indicator trait to indirectly select
78 for improved FCR in farmed rainbow trout. Feed intake of individual fish was recorded using the x-ray
79 method in which feed pellets are enriched with glass ballotini beads, the x-ray of a fish revealing the
80 amount of feed consumed⁽¹⁻⁴⁾. Specifically, the objectives were: 1) To estimate the genetic correlations
81 of FCR with whole body lipid%, muscle lipid%, and percentage of viscera weight of total body weight
82 (reflecting visceral lipid)⁽¹¹⁾; 2) To quantify the expected genetic response in FCR when lipid%
83 recording (indirect selection) is used as the substitute of feed intake recording (direct selection) in a
84 breeding programme. We tested the benefit of replacing feed intake by three alternative lipid traits:
85 body lipid%, muscle lipid%, and viscera%. Finally, 3) we tested whether lipid deposition is genetically

86 related to the indicators of retention efficiencies of energy, protein and lipid. The retention efficiencies
87 explicitly quantify the utilization of macronutrients and energy. A fish can produce protein growth only
88 from protein (amino acids) in feed, and high quality proteins are among the most expensive raw
89 materials in an aquafeed formulation, and often of a limited supply⁽¹⁷⁾. Hence, effective conversion of
90 protein in feed into tissue growth is preferred. Lipid in feed is intended to be used especially as an
91 energy source, and excessive levels of lipid deposition in tissues and viscera are not preferred.

92

93 **Material and methods**

94 *Experimental fish population*

95 The experimental fish originated from the Finnish national breeding programme and were housed at the
96 fresh water nucleus station, Tervo Fish Farm, in central Finland. All procedures involving animals were
97 approved by the animal care committee of the Natural Resources Institute Finland. To enhance animal
98 welfare and ameliorate suffering during all fish handling, the fish were always first anaesthetized using
99 tricaine methanesulfonate (MS-222).

100 The fish were from 210 families, produced from 89 sires and 109 dams. Each sire was mated to
101 an average of 2.3 dams (range: 1-5) and each dam to 1.9 sires (range: 1-3). Matings were completed
102 over three days in April 2001. For the first 8 months after hatching, the families were held separately in
103 150 L family tanks, each family in their own tank. The broodstock fish had been selected for high body
104 weight, late maturity age, silvery skin, spotless skin and body shape for three generations⁽¹⁸⁾.

105 In February 2002, each family was randomly split into two groups to be reared on different
106 experimental diets. The diets were a standard low protein and high lipid diet with protein levels of
107 44.9%, 44.6% and 39.5%, and with lipid levels of 30.5%, 30.3% and 33.4% for the pellet sizes of 3
108 mm, 6 mm and 7 mm, respectively (NP diet). The other diet was an experimental high protein and low
109 lipid diet with protein levels of 56.4%, 56.3% and 49.4%, and with lipid levels of 20.7%, 20.6% and
110 23.8% for the pellet sizes of 3 mm, 6 mm and 7 mm, respectively (HP diet). The impact of diets on fish
111 performance has been detailed previously^(19,20). The diets were originally used to test hypothesis that
112 high protein diet would reveal the individuals that are the most efficient in utilizing proteins.

113 The fish were individually tagged to link the individuals to the pedigree and to allow for repeated
114 measurements of individuals (Trovan Ltd., Köln, Germany). At tagging, fish weight at the two dietary
115 groups was very similar (mean±SD; NP=62.4±19.9 g, $n=1355$ fish, and HP=62.3±19.4 g, $n=1335$).
116 During their growth until 29 months of age, some of the fish were destructively recorded for body

117 composition for a purpose other than the current study⁽²⁰⁾. Hence, at the end of the experiment, there
118 were 1262 fish remaining.

119 Each diet treatment was replicated by four 20m³ indoor tanks with fish density of 20 kg/m³. The
120 families were equally distributed among the tanks. Feeding was automated using computer-controlled
121 pneumatic feeders (Arvo-Tec Inc., Finland), and fish were fed to satiation 4 h a day. Water temperature
122 during the experiment was natural and exposed to seasonal fluctuations.

123

124 *Feed utilization traits recorded*

125 Body weight, daily feed intake and daily weight gain were recorded three times during growth, in May
126 2002 (age 11 months, body weight 142.5g), October 2002 (age 16 months, body weight 747g), and
127 September 2003 (age 27 months, body weight 2113g).

128 At each time, a 3-week x-ray session with 3 repeated measurements of body weight and daily
129 feed intake was performed. Before x-raying, all fish from a given tank were fed to satiation 4h a day
130 the same way as any other day but the diet was labelled with radio-opaque ballotini glass beads
131 (Jencons Scientific Ltd., Leighton Buzzard, UK). The labelled pellets used at months 11, 16, and 27
132 consisted of 1, 0.5, and 0.3% beads, respectively, with a diameter of 400 to 600µm.

133 To record individual feed consumption with the ballotini enriched feed, fish were x-rayed using a
134 portable x-ray unit (Todd Research 80/20, Essex, UK)⁽¹⁾. Each of the 8 tanks was measured once
135 weekly (one NP and one HP tank per day). To avoid the potential effects of systematic feeding
136 rhythms, the recording order of NP and HP tanks was reversed on successive days. To initiate a
137 recording session, all fish (x-ray and non-x-ray) were weighed during the first week of each session,
138 and daily feed intake was measured from predetermined randomly selected individuals from each
139 family (average of 6.2 fish per family; range 5-7). In the second and the third weeks, the procedure was
140 repeated but only the fish x-rayed in the first week were reweighed and x-rayed again.

141

142 *Body composition traits recorded*

143 Three lipid traits were recorded at month 29, November 2003, at an average body weight of 2607g. All
144 fish ($n=1262$) from all 210 families were sampled for whole body lipid%, muscle lipid% and viscera
145 percentage (100 visceral weight / body weight). Body weight recorded from all fish at month 29 was
146 also used in the analysis and abbreviated as BW_{M29}. Muscle and chop lipid% and protein% of each fish
147 was determined using spectroscopy based on infrared transmission⁽²¹⁾, calibrated against analyses

148 according to^(22,23). Muscle was sampled above the lateral line as a 10 g portion of pure epaxial white
149 muscle. Chop was a 3-cm thick cutlet cut directly from behind the dorsal fin from each fish. Whole
150 body lipid% was predicted using predictive equation having chop lipid%, head%, viscera%, and body
151 weight as predictors. The R^2 of the predictive equation was 0.62 and the residual standard error
152 1.156⁽²⁰⁾. Body protein% was predicted in the same way, using chop lipid% and chop protein% as the
153 predictors ($R^2 = 0.58$; residual standard error = 0.505)⁽²⁰⁾. To minimize the possibility that the relation
154 of feed utilization with body composition was due to correlative effects with body weight, the statistical
155 models of body lipid%, muscle lipid% and viscera% had body weight at the time of trait recording as a
156 fixed covariate.

157 The state of maturity (mature, immature) and gender (male, female) were visually recorded at all
158 trait recording times. Males matured at 2, 3, or 3+ years, females at 3 or 3+ years, and there were also
159 fish with unknown gender and maturity state.

160

161 *Definition of feed utilization traits analysed*

162 Feed utilization traits were calculated for two different time periods that are of great importance for
163 producers of large rainbow trout. First, at month 27 (2+ years), four traits were calculated based on the
164 3-week x-ray trial: Average daily weight gain (DG) and average daily feed intake (DFI) based on the
165 records measured across the 3 week period, and FCR = DFI / DG. In all statistical models, body weight
166 at the beginning of the 3-week trial was used as a fixed covariate, to correct for the impact of body
167 weight on DG, DFI and FCR. Residual feed intake (RFI), defined as the difference between the
168 observed feed intake and the feed intake predicted from the maintenance costs (metabolic body weight)
169 and growth, was used as a complementary measure of efficiency⁽²⁴⁾. RFI is phenotypically independent
170 of body size, and is typically considered superior over FCR when animals with different sizes are
171 compared for feed utilization. For this reason, RFI has been included in the selection indices of many
172 terrestrial livestock species⁽²⁵⁾. RFI was calculated as the residuals from a regression in which
173 metabolic body weight and DG were used as predictors of DFI⁽²⁴⁾. Metabolic body weight at the
174 beginning of the 3-week trial was calculated as $BW^{0.824}$. A low RFI value indicates an efficient fish that
175 feeds less than expected based on its observed growth and maintenance requirements.

176 Second, five indicators of feed utilization were calculated across the whole lifetime. An indicator
177 of lifetime FCR was calculated as: $LifeFCR_{Indicator} = \text{Cumulative feed intake} / \text{Final body weight at}$
178 month 29 , where cumulative feed intake ($LifeFI_{Indicator}$) is the sum of all 9 daily feed intake records

179 measured at months 11, 16, and 27. An indicator of lifetime residual feed intake (LifeRFI_{Indicator}) was
 180 calculated, separately for each diet, as the residuals from a regression in which cumulative feed intake
 181 was regressed against metabolic body weight at month 16 (measure of average maintenance costs
 182 during the feed intake recording) and body weight at month 29 (measure of weight gain). For LifeRFI,
 183 the partial regression coefficients for BW_{M29} were 0.0064 and 0.0056 ($P < 0.0001$) and for metabolic
 184 body weight 0.0035 ($P = 0.32$) and -0.0052 ($P = 0.05$) with the R^2 s of 33.3% and 14.1% for the
 185 regression models on NP and HP diets, respectively. At the three separate ages, the partial regression
 186 coefficients for DG ranged between 0.2035-0.3391 ($P < 0.0001$) and for metabolic body weight
 187 0.0017-0.0234 (all but one significant) with the average R^2 of 32.0% for the regression models (range
 188 in $R^2 = 7.2\% - 57.8\%$). Indicators of lifetime retention efficiencies were calculated for three
 189 components, protein (LifeProtRetention_{Indicator}), lipid (LifeLipRetention_{Indicator}) and energy
 190 (LifeERetention_{Indicator}) as: Final component weight in a fish (in g) / Cumulative component intake (in
 191 g). For instance, LifeProtRetention_{Indicator} = Final protein weight at month 29 / Cumulative protein
 192 intake. In this formula, the numerator trait is recorded from the egg stage onwards, whereas the
 193 denominator trait is recorded from average body weight of 142.5g onwards during 9 days. Hence, all
 194 these traits are called indicators and their mean value *per se* has no explicit interpretation. Energy
 195 content of a fish was calculated from its protein and lipid weights, assuming energy concentration of
 196 23.6 kJ/g for protein and 39.5 kJ/g for lipid^(25,26). Feed intake was transformed to intake of the
 197 components using the known crude proximate composition of the diets⁽¹⁹⁾.

198

199 *Statistical analysis*

200 Phenotypic and genetic variances and correlations were estimated using the DMUAI software. The
 201 software analyses multivariate mixed models using the restricted maximum likelihood method, and
 202 accounts for all relationships between all animals in the pedigree using a relationship matrix⁽²⁷⁾. The
 203 pedigree had 362 ancestors in four generations for the offspring generation used in the experiment. The
 204 statistical model for DG, DFI, FCR, body lipid%, muscle lipid% and viscera% to estimate (co)variance
 205 components was:

206

$$207 \quad y_{ijkl} = anim_i + ExpTank_j + DietSexMat_k + b_{BW}Diet_l + \varepsilon_{ijkl}, \quad (\text{model 1})$$

208

209 where *anim* is the random genetic effect of an animal ($i = 1 \dots$ number of observations), *ExpTank* is the
 210 fixed test tank effect ($j = 1-8$ tanks), and *DietSexMat* is the fixed interaction of gender, maturity stage
 211 and diet ($k = 1-12$ levels), b_{BW} is the fixed regression coefficient of body weight on y , fitted separately
 212 for the two diets, $Diet_l$ ($l = 1-2$ diets). These body weight corrected traits are indicated by [BW] symbol
 213 in the trait abbreviations.

214 For residual feed intake and all lifetime traits, no additional correction for body weight was
 215 needed, and hence the statistical model was:

216

$$217 \quad y_{ijk} = anim_i + ExpTank_j + DietSexMat_k + \varepsilon_{ijk}, \quad (\text{model 2}).$$

218

219 For all traits, models with the random full-sib family effect (without a link to a pedigree) were also
 220 run, to quantify the environmental effect common to full sibs. The full-sib family variance (V_{FS})
 221 includes common environment effects due to separate rearing of the full-sib families until tagging, but
 222 also potential non-additive genetic as well as parts of maternal additive genetic effects. Most of the
 223 traits had negligible V_{FS} (see Results), and when including the family effect into the multitrait models,
 224 the genetic and full-sib family covariances were severely confounded in our data. Hence, for all traits,
 225 the correlations were estimated using models excluding the full-family effect.

226 Heritability was calculated as the genetic variance explained by the animal effect divided by
 227 phenotypic variance (V_P), where V_P is the sum of genetic (V_G), full-sib family (V_{FS}), and residual
 228 variance (V_R). Full-sib family variance ratio was calculated as $c^2 = V_{FS} / V_P$. To assess whether a low
 229 heritability of a trait results from low genetic variation or from high residual variation, coefficients of
 230 genetic ($CV_G = 100 \sqrt{V_G} / \text{trait mean}$) and residual variation ($CV_R = 100 \sqrt{V_R} / \text{trait mean}$) were
 231 calculated for traits recorded in the units of grams. CV s are not sensible for percentages or ratios⁽²⁸⁾.

232 Heritability was considered significantly different from zero if the h^2 estimate - 0.98 SE did not
 233 include zero (one-tailed hypothesis). Genetic correlation was considered smaller or greater than zero if
 234 r_G estimate +/- 1.96 SE did not include zero (two-tailed hypothesis).

235

236 *Comparison of alternative selection scenarios*

237 A deterministic simulation was performed with SelAction computer software⁽²⁹⁾ to quantify the
 238 expected genetic response in FCR (ΔG_{FCR}) when using alternative selection indices. The expected
 239 genetic response in $FCR_{[BW]}$ was calculated, firstly, when simultaneously selecting for $DG_{[BW]}$ and

240 against $DFI_{[BW]}$ (direct selection for FCR), and then this scenario was compared to the genetic
241 responses obtained with the index in which feed intake was replaced either by body lipid% $_{[BW]}$, muscle
242 lipid% $_{[BW]}$ or viscera% $_{[BW]}$ (indirect selection). Selection was based on breeding values estimated using
243 individuals' own and its sibs' trait records⁽²⁹⁾. For each scenario, the relative index weighting of $DFI_{[BW]}$
244 or a lipid trait was increased from zero (selection for $DG_{[BW]}$ only) to unity (no selection for $DG_{[BW]}$).
245 $FCR_{[BW]}$ was not used in the simulation directly, rather the genetic response in $FCR_{[BW]}$ was calculated
246 from the responses of $DFI_{[BW]}$ and $DG_{[BW]}$.

247 The phenotypic and genetic parameters estimated using the model 1, without the full-sib family
248 effect, were used as input. The simulated population structure was the same for all selection scenarios,
249 to make sure the proportion of selected individuals remained the same across all scenarios. The
250 population size was held small, to obtain realistic genetic responses in growth (around 4-10% per
251 generation,¹⁸). The population was a full-sib design with 100 selected sires and 100 selected dams, full-
252 sib family size of 4 animals, and the proportion of selected animals was 0.50.

253

254 Results

255 *Feed utilization at age of 2+ years of age*

256 *Genetic variation for feed utilization and body composition*

257 For $DG_{[BW]}$, $DFI_{[BW]}$, $FCR_{[BW]}$ and the composition traits, full-sib family variance ratio ranged between
258 0.00-0.034, so for these traits it was safe to focus on the estimates from the model excluding the full-sib
259 family effect (Table 1). $DG_{[BW]}$, $DFI_{[BW]}$, $FCR_{[BW]}$ and the composition traits recorded at 2+ years of
260 age displayed significant heritabilities (Table 1). Heritabilities of feed intake and FCR ranged between
261 0.10-0.11. Heritabilities of lipid traits ($h^2 = 0.43-0.57$) were 4.3-5.7 times higher compared to the
262 heritability of feed intake. Growth and feed intake both showed high coefficients of genetic variation,
263 ranging between 17.2-17.4. Coefficient of residual variation was higher for feed intake than for growth,
264 explaining the low heritability observed for feed intake. Residual feed intake displayed limited
265 heritability, and when full-family effect was included in the model, the h^2 estimate was reduced to 0.04
266 with large SE (Table 1).

267

268 *Relationship of feed utilization and growth*

269 Daily weight gain, corrected for body weight, was phenotypically and genetically favourably correlated
270 with $FCR_{[BW]}$ (Table 2). The faster growing fish were more efficient. The correlations between $DG_{[BW]}$
271 and RFI were close to zero, which results from the method to calculate RFI. The correlations of $DG_{[BW]}$
272 with $DFI_{[BW]}$ were moderately positive. High RFI was related to high $DFI_{[BW]}$, i.e. the fish with overly
273 high feed intake were inefficient. Similar but a weaker pattern was observed between $FCR_{[BW]}$ and
274 $DFI_{[BW]}$. Residual feed intake and $FCR_{[BW]}$ were highly positively correlated, implying they describe
275 partly the same phenomenon (Table 2).

276

277 *Relationships of feed utilization and lipid traits*

278 The low body lipid% $_{[BW]}$ and muscle lipid% $_{[BW]}$ were both genetically related to low $FCR_{[BW]}$ and RFI,
279 confirming the hypothesis that low-lipid% fish were genetically more efficient (Table 3). This results
280 because $DFI_{[BW]}$ was positively, yet non-significantly, genetically related with body lipid% $_{[BW]}$ and
281 muscle lipid% $_{[BW]}$, whereas $DG_{[BW]}$ was weakly or even negatively genetically related to these lipid
282 traits.

283 The genetic correlations of viscera% $_{[BW]}$ with growth and feed utilization were of the opposite
284 sign compared to those of body lipid% $_{[BW]}$ and muscle lipid% $_{[BW]}$, and none reached significance
285 (Table 3).

286

287 *Expected genetic responses*

288 The selection index calculations showed that selection solely for $DG_{[BW]}$ is expected to lead to +7.2%
289 genetic increase in $DG_{[BW]}$, +2.53% increase in $DFI_{[BW]}$, and consequently to -4.36% change in
290 $FCR_{[BW]}$, i.e. improvement in FCR (Table 4).

291 Figure 1 was used to identify the index weightings that maximize the expected genetic response
292 in FCR in alternative selection index scenarios. When having $DG_{[BW]}$ and one of the alternative traits in
293 the index, the index weighting that produced the greatest genetic response in FCR was -0.52 for
294 $DFI_{[BW]}$, -0.68 for BodyLipid% $_{[BW]}$, -0.70 for MuscleLipid% $_{[BW]}$, and -0.10 for Viscera% $_{[BW]}$ (Table 4).
295 Simultaneous selection for $DG_{[BW]}$ and against $DFI_{[BW]}$ (direct selection to improve FCR) increased
296 genetic response in $FCR_{[BW]}$ by 1.50 fold to -6.54% compared to the sole selection for $DG_{[BW]}$ (Table
297 4). Yet, this occurred at the expense of genetic response in $DG_{[BW]}$ reducing from 7.2% to 4.83%.

298 Replacing $DFI_{[BW]}$ in the selection index by body lipid% $_{[BW]}$, muscle lipid% $_{[BW]}$ or viscera% $_{[BW]}$,
299 increased genetic response in $FCR_{[BW]}$ by 1.29, 1.49, and 1.02 fold, respectively, compared to the sole

300 selection for $DG_{[BW]}$ (Table 4). Hence, using muscle lipid%_[BW] to indirectly select for FCR was
301 effective and simultaneously $DG_{[BW]}$ improved by 5.93%. These results are in line with the positive
302 genetic correlations of muscle lipid%_[BW] with $FCR_{[BW]}$ (and RFI) (Table 3).

303

304 ***Lifetime feed utilization***

305 *Genetic variation for the indicators of lifetime feed utilization*

306 For the lifetime traits, c^2 estimates ranged between 0.037-0.065, and in 3 out of 7 traits, the SE was
307 smaller than the c^2 estimate (Table 5). For these traits, the real heritability is likely to be between the
308 estimates obtained using the two models, one with and one without the full-sib family effect. Similar to
309 +2 years of age, the indicators of lifetime feed intake, FCR, residual feed intake and retention
310 efficiencies (Table 5) displayed lower heritability than growth and lipid traits (Table 1). Similar to the
311 traits in +2 age, the coefficient of genetic variation was of similar magnitude for BW_{M29} ($CV_G = 11.6\%$;
312 $CV_R = 15.5\%$) and $LifeFI_{Indicator}$ ($CV_G = 12.7\%$; $CV_R = 40.3\%$), but coefficient of residual variation was
313 higher for $LifeFI_{Indicator}$, explaining the low heritabilities of $LifeFI_{Indicator}$ (Table 5).

314

315 *Relationship of lifetime feed utilization and lipid traits*

316 Body weight at month 29 was phenotypically and genetically favourably correlated with
317 $LifeFCR_{Indicator}$ (Table 6). The correlations of BW_{M29} with lifetime energy, lipid and protein retention
318 efficiency indicators were also favourably positive but with large standard errors.

319 The correlations of body lipid%_[BW], muscle lipid%_[BW] and viscera%_[BW] with $LifeFCR_{Indicator}$ and
320 $LifeRFI_{Indicator}$ had the same pattern as at +2 age, muscle lipid%_[BW] and body lipid%_[BW] having the
321 strongest correlations and viscera%_[BW] the weakest (Table 6). Decreasing muscle lipid%_[BW] was
322 genetically related to increased efficiency to use feed (both $lifeFCR_{Indicator}$ and $lifeRFI_{Indicator}$).

323 Decreasing muscle lipid%_[BW] was genetically related to improving lifetime protein retention
324 efficiency, and the phenotypic correlation of body lipid%_[BW] with $LifeProtRetention_{Indicator}$ showed the
325 same trend (Table 6). The relationship between body lipid%_[BW] and muscle lipid%_[BW] with lifetime
326 lipid and energy retention indicators was weaker than with lifetime protein retention efficiency.

327

328

329 Discussion

330 *Improving FCR via control of lipid deposition*

331 Body composition was genetically related to the efficiency in which fish used feed. At +2 age, the
332 lower body lipid% and muscle lipid% were genetically related to improved FCR and residual feed
333 intake, confirming the hypothesis that fish with low lipid% are genetically more efficient. For the feed
334 utilization indicators recorded across the whole lifetime until age of 29 months, the pattern was similar.

335 The results highlight the benefit of controlling especially muscle lipid on the genetic
336 improvement of FCR in rainbow trout. The index theory calculations showed that direct selection to
337 improve FCR, via simultaneous selection for weight gain and against feed intake, is expected to
338 decrease FCR by 1.50-fold ($\Delta G_{FCR} = -6.54\%$) compared to the sole selection for weight gain. There is
339 hence room to improve FCR via methods other than growth selection. When feed intake is replaced in
340 the selection index with muscle lipid%, such indirect selection results in maximum genetic response of
341 -6.50% in FCR. These results are similar to the ones observed for the use of body lipid% to indirectly
342 improve FCR in European whitefish *Coregonus lavaretus* L.⁽⁸⁾. Also in terrestrial livestock leaner
343 animals are typically more efficient, and fat traits have positive genetic correlations with FCR^(5,6).

344 In our selection index calculations, selection responses are determined by (co)variances of the
345 traits. The efficiency of muscle lipid% as an indirect indicator to improve FCR results, firstly, because
346 of the strong genetic correlation of muscle lipid% with feed intake, and a weaker correlation with
347 weight gain. Selection against muscle lipid% will hence suppress feed intake more than growth, leading
348 to improved FCR. High level of feed intake is likely related to high level of lipid deposition. Secondly,
349 muscle lipid% has higher heritability than feed intake. Lipid traits in general are highly heritable in
350 fish⁽²⁰⁾. Selection on a highly heritable trait is expected to result in higher genetic responses than
351 selection for a low heritability trait. Hence, indirect selection for a highly heritable trait, like lipid traits,
352 can be even more effective than direct selection⁽³⁰⁾. Feed intake and also FCR and retention efficiencies
353 displayed low heritabilities compared to weight gain and BW. Daily feed intake is an unusually
354 variable trait in fish⁽²⁻⁴⁾. Additionally, recording of the long-term feed intake is a major challenge in
355 fish. Using the x-ray method, only snapshots of fish behaviour can be recorded. In our data this is
356 indicated by the very high residual variation for feed utilisation traits ($CV_R > 40\%$). The high residual
357 variance reduces the heritability estimate, even though the genetic variation, measured as CV_G , in feed
358 intake is of similar magnitude compared to growth.

359 In the current study, all lipid traits were recorded destructively, but fillet and muscle lipid can be
360 recorded non-destructively in fish^(10,12,13). It is well established that the non-destructive methods can be
361 effectively used to obtain realised genetic response in lipid traits in rainbow trout^(7,9), but the non-
362 destructive methods are predictive tools that have measurement error and are not 100% accurate^(10,12,13).
363 Hence, the use of non-destructive methods to record lipid will reduce the efficiency of indirect
364 selection to improve FCR. Moreover, in line with a general finding⁽³¹⁾, in our study the genetic
365 correlations were higher than the phenotypic correlations. This may be a real phenomenon, but
366 additionally, genetic correlations may become biased when data set is small.

367 Naturally, lipid deposition should not be reduced to an extreme because lipid is essential for fish
368 reproduction, lipid is an important source of healthy fatty acids for humans⁽³²⁾, and lipid% of tissues
369 may have an intermediate optimum for product quality⁽³³⁾. Similar to pigs⁽³⁴⁾, to define the optimum
370 lipid level would require the combined analysis of economics, biology and novel information on the
371 genetics of the fatty acid profiles. Selection strategies should be further coupled with feeding practices
372 to obtain the desired lipid and fatty acid levels in farmed fish.

373 It is reliable to use lipid deposition as a genetic indicator trait of FCR in a breeding programme
374 because it has a physiological relationship with FCR. Assume two different fish, one with 17% and the
375 other with 25% body lipid%. For the time being, we can assume that body protein% is the same 16%
376 for both fish, because in general, protein% of tissues is both phenotypically and genetically very
377 invariable in fish^(20,35,36). Lipid% and water% are inversely correlated in rainbow trout above 50 g^(14,35),
378 and hence only lipid% and water% (with no energy value) differ between the two fish. Next, assume
379 the two fish grow 1 g of weight and their body composition remains unchanged. The energy content
380 needed for 1 g of growth for the low and high lipid% fish are 10.5 and 13.7 kJ (assuming the energy
381 concentration of 23.6 kJ/g for protein and 39.5 kJ/g for lipid). The cost of depositing different body
382 components does not need to be taken into account because only lipid differs between the fish.
383 Assuming energy concentration of 20 kJ/g for feed and 50% energy retention efficiency for both fish,
384 the low and high lipid% fish need 1.05 g and 1.37 g of feed to gain 1 g of weight. These are simply the
385 FCR values of 1.05 for the low lipid% fish and 1.37 for the high lipid% fish because we assumed 1 g of
386 weight gain, proving that decreasing body lipid%, adjusted for fixed growth, is related to improved
387 efficiency on wet weight basis. On the energy retention basis, the two fish were in fact equally
388 efficient.

389 Above we assumed that body protein% remained invariable among individuals. It is noteworthy
390 to consider the impact of protein deposition on the efficiency of low lipid% fish. In rainbow trout,
391 genetic variation in body and muscle protein% seem to increase significantly, yet remain low, when
392 fish obtain body weight of 2 kg⁽²⁰⁾, the size which is of greatest commercial interest for producers of
393 large rainbow trout. The increased genetic variation in protein% may be due to the extensive lipid
394 deposition and the large increase in differences for lipid% between families at this age, forcing
395 protein%, as a side effect, to vary⁽²⁰⁾. Moreover, in our data, both body lipid% ($r_P = -0.57$; $r_G = -0.95 \pm$
396 0.05) and muscle lipid% ($r_P = -0.33$; $r_G = -0.82 \pm 0.12$) are phenotypically and genetically negatively
397 correlated with the respective protein% trait. Hence, a low lipid% fish was in fact a high protein% fish.

398 One factor making lean animals more efficient is that deposition of protein induces more wet
399 weight gain compared to deposition of lipid^(25,37). In fish, deposition of 1 g of lipid is associated with
400 deposition of around 0.1 g of water. Deposition of 1 g of protein, in turn, is associated with deposition
401 of over 3 g of water. Consequently, the deposition of 1 g of lipid is expected to lead to wet weight
402 increase of 1.1 g (partial regression coefficient $b_{\text{lipid}} = 1.1$), whereas the deposition of 1 g of protein is
403 expected to lead to 4.5 g wet weight gain ($b_{\text{prot}} = 4.5$)^(25,37, but see 38). The partial regression coefficients
404 can be calculated from our data by regressing simultaneously both lipid and protein body weight (on x-
405 axis) against final wet weight (y-axis). In line with the literature, our data have $b_{\text{lipid}} = 1.45$ and $b_{\text{prot}} =$
406 4.24 for NP diet ($n = 416$ fish), and $b_{\text{lipid}} = 1.55$ and $b_{\text{prot}} = 4.12$ for HP diet ($n = 482$ fish). Consequently,
407 protein weight gain generally results in significantly more wet weight gain compared to lipid gain. This
408 phenomenon facilitates that lean fish, with high protein weight gain, are more efficient, when
409 efficiency is measured on wet weight basis.

410 However, depositing 1 g of protein (59.9 kJ / g of protein) is energetically more expensive than
411 depositing 1 g of lipid (55.3 kJ/g and 43.5 kJ/g from non-lipid and lipid origins). These approximate
412 values were calculated assuming energy concentration of protein and lipid of 23.6 kJ/g and 39.5 kJ/g,
413 and net energy costs of 2.54, 1.4 and 1.1 kJ per kJ for protein and lipid retention from non-lipid or lipid
414 origins, respectively⁽³⁹⁾. The values that Emmans⁽³⁹⁾ provides are calculated for terrestrial animals, but
415 costs of protein deposition appear to be similar across terrestrial and aquatic animals, whereas costs of
416 lipid deposition vary more⁽³⁹⁾. The higher cost of protein deposition does not overrule the efficiency of
417 protein deposition because the higher energy cost is small compared to the 4.5 fold effect on the
418 increased wet weight gain.

419 Maximising genetic improvement in FCR reduces considerably the genetic response in weight
420 gain, which may not be desirable (Fig. 1). Hence, the target of selection should be to obtain
421 economically optimized balance between genetic changes in weight gain, feed intake and FCR, to make
422 economically more efficient fish. This can be obtained by calculating economic values of the traits,
423 e.g., by using bio-economic models^(33,40).

424 Muscle lipid% but not viscera% was related to feed utilization. Visceral lipid is a major portion
425 of viscera weight, and viscera% can be regarded as a lipid trait⁽¹¹⁾. Lipid deposits at different body
426 locations are genetically different traits, and hence they are expected to have different correlations with
427 other traits^(20,41-43). Viscera% is easy to record in a breeding programme when sibs of breeding
428 candidates are slaughtered, and selection against viscera% can be used to genetically improve fillet%
429 and reduce slaughter waste, as is practiced in the Finnish breeding programme for rainbow trout⁽¹¹⁾.
430 Unfortunately our data indicate no additional impact on improved feed utilization.

431

432 *Getting around wet weight based traits: The retention efficiencies*

433 The wet weight based traits like FCR, weight gain and body weight are traits important to fish farmers.
434 Farmers that sell their fish to processors or directly to retailers are paid based on wet weight growth of
435 fish, typically gutted weight. However, pelleted feed has low water concentration (2-10%) and fish
436 ingest large amounts of water to obtain high body water concentration (70-80%). To directly assess the
437 efficiency in which macronutrients and energy of the feed are used, the analysis of indicators of
438 protein, lipid and energy retention efficiency was performed.

439 The results show that restricting excessive lipid deposition in a rainbow trout breeding
440 programme improves protein retention efficiency. This is favorable for aquaculture because even a
441 small improvement in protein retention efficiency has a large economic impact on the industry. High
442 quality protein raw materials are among the most expensive components in an aquafeed formulation,
443 and often of a limited supply⁽¹⁷⁾. Moreover, protein is the source of nitrogen, and the more nitrogen
444 from feed is deposited into a fish, the smaller the nutrient load to the environment will be per produced
445 kg of fish.

446 In contrast to protein retention efficiency, the effective genetic improvement of lipid retention
447 may be of less importance. In feed formulation, lipid is especially meant to be used as a major energy
448 source for a fish, sparing protein to be used for tissue growth⁽⁴⁴⁾. Hence, improving lipid retention
449 efficiency too much would make fish to allocate more of the ingested lipid to deposited lipid, which

450 may be unoptimal. Yet, the improvement of retention of EPA (eicosapentaenoic acid) and DHA
451 (docosahexaenoic acid) n-3 fatty acids would be of importance as these are the main healthy
452 components for humans. Moreover, fish need lipid deposits for basic life functions, and a suitable level
453 of lipid is required in farmed fish for fulfilling standards of eating quality. Accordingly, the ultimate
454 goal for both animal breeding and feed development would be a fish that optimally partitions different
455 macronutrients between tissue growth and energy requirements.

456 The observation that the fish with genetically low body lipid% and muscle lipid% were more
457 efficient in turning ingested protein into protein weight gain can be partly explained by the negative
458 relationship between lipid% and protein%. The 'low lipid%-high protein%' fish have high protein
459 retention efficiency. Indeed, in our data, body protein%_[BW] is phenotypically and genetically related to
460 improved indicator of lifetime protein retention efficiency ($r_P = 0.15$; $r_G = 0.81 \pm 0.32$). Our findings
461 are similar to the genetic responses observed when selecting for low and high muscle lipid%, corrected
462 for body weight, lines in rainbow trout. The line with low muscle lipid% has improved feed efficiency
463 and protein retention efficiency^(7,9,45,46).

464 Detailed studies on protein synthesis have revealed some of the mechanisms behind the highly
465 efficient fish. The protein synthesis is costly, about 11-42% of energy expenditure⁽⁴⁷⁾, and hence, fish
466 which grow more efficiently achieve this through adopting the low-protein turnover strategy⁽⁴⁸⁾. A
467 reduction in protein turnover, brought about by lower degradation of synthesised proteins, leads to
468 increased protein and wet weight growth efficiency. In this way, some individuals achieve faster and
469 more efficient protein accretion when consuming the same amount of food as individuals with slower
470 and less efficient growth⁽⁴⁹⁾.

471 It is worth noting that our and the previous observations^(7,9,45,46) on among-individual variation
472 differ from the results of diet comparisons. In contrast to our results, it is commonly found in diet
473 comparisons that high lipid diet enhancing lipid deposition improves protein retention efficiency. This
474 protein sparing effect occurs because the excess lipid in the diet fulfils the energy requirements of a
475 fish, allowing the fish to allocate ingested protein for growth, and less to maintenance⁽⁴⁴⁾. Naturally,
476 effects of diets on a pair of fish traits do not need to be of the same direction as the phenotypic, and
477 especially the genetic correlations between the same traits. For instance, the use of plant-based
478 ingredients in feed can increase feed intake and decrease body lipid% compared to a fully fish-based
479 diet, but simultaneously, within each diet, a fish with high feed intake can have high lipid%⁽⁸⁾.

480

481 *Implications*

482 In many fish species, lipid deposition is controlled in fish breeding programmes because of its impact
483 on reduced slaughter waste, increased fillet% and quality⁽¹¹⁾. The present and other studies^(7-9, 45,46)
484 contribute to the growing evidence that the control of excess lipid deposition by selective breeding
485 programmes would bring an additional benefit of improving not just feed conversion ratio but also
486 protein retention efficiency in fish.

487

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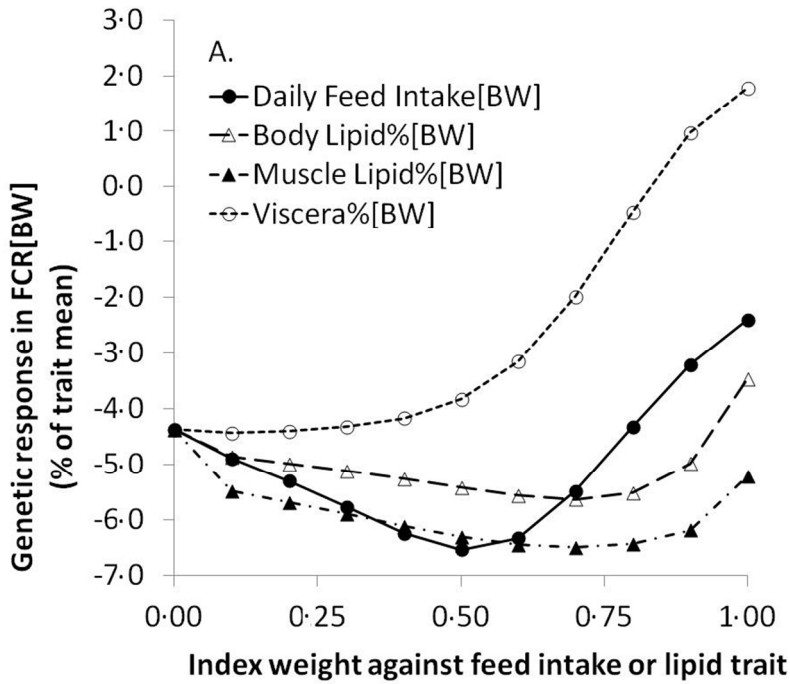
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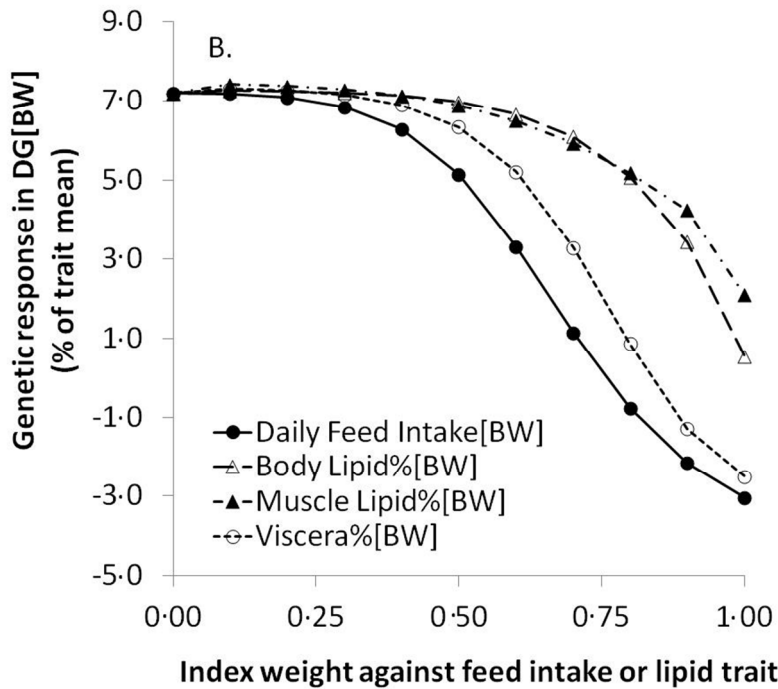
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Fig 1. Expected genetic response in A) feed conversion ratio ($FCR_{[BW]}$) and B) daily weight gain ($DG_{[BW]}$) when selecting simultaneously for $DG_{[BW]}$ and against one of the alternative traits: $DFI_{[BW]}$ or one of the lipid traits.

610 **Table 1.** Sample size (n), trait mean, phenotypic variance (V_p), heritability and its standard error ($h^2 \pm$
 611 SE), coefficients of genetic (CV_G) and residual variation (CV_R), and full-sib effect ratio ($c^2 \pm$ SE) for lipid
 612 traits and feed utilization traits recorded at +2 years of age estimated with an animal model either
 613 including or excluding the random full-sibs effect

Trait*	Full-sib effect excluded							Full-sib effect included			
	n	Mean	V_p^\dagger	h^2	SE	CV_G	CV_R	h^2	SE	c^2	SE
DG _[BW]	891	16.19	27.32	0.29	0.07	17.4	27.2	0.28	0.08	0.007	0.03
DFI _[BW]	815	16.11	69.58	0.11	0.06	17.2	48.8	0.07	0.06	0.023	0.03
FCR _[BW]	756	1.113	0.4394	0.10	0.05			0.07	0.06	0.034	0.04
RFI	756	0.000	64.15	0.11	0.06			0.04	0.05	0.057	0.05
BodyLipid% _[BW]	989	21.27	1.556	0.43	0.08			0.43	0.09	0.000	0.03
MuscleLipid% _[BW]	998	7.700	4.384	0.45	0.08			0.42	0.08	0.014	0.03
Viscera% _[BW]	1001	11.80	2.451	0.57	0.09			0.57	0.12	0.000	0.03

614 * Abbreviations: DG - daily weight gain; DFI - daily feed intake; FCR - feed conversion ratio; RFI -
 615 residual feed intake; BodyLipid% - body lipid percentage; MuscleLipid% - muscle lipid percentage;
 616 Viscera% - viscera percentage of body weight; [BW] - A trait corrected for a constant body weight.
 617 † Variance from the model 1 or 2 using which all the fixed effects have been removed.

618 **Table 2.** Phenotypic (above diagonal) and genetic correlations (below diagonal; \pm their standard error)
 619 for growth and feed utilization traits recorded at +2 years of age*

	DG _[BW]	DFI _[BW]	FCR _[BW]	RFI
DG _[BW]		0.29	-0.34	0.08
DFI _[BW]	0.36 (0.25)		0.65	0.97
FCR _[BW]	-0.63 (0.30)	0.36 (0.36)		0.79
RFI	-0.05 (0.29)	0.93 (0.042)	0.91 (0.10)	

620 * Abbreviations are given in Table 1.

621

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623

624

625 **Table 3.** Phenotypic (r_p) and genetic correlations ($r_G \pm$ their standard error) **between lipid, growth and**
 626 **feed utilization traits** recorded at +2 years of age*

	BodyLipid% _[BW]			MuscleLipid% _[BW]			Viscera% _[BW]		
	r_p	r_G	SEM	r_p	r_G	SEM	r_p	r_G	SEM
DG _[BW]	0.14	-0.07	0.18	0.07	-0.26	0.17	0.13	0.29	0.16
DFI _[BW]	0.09	0.37	0.26	0.06	0.41	0.24	0.09	0.09	0.23
FCR _[BW]	0.01	0.58	0.28	0.04	0.68	0.24	-0.02	-0.39	0.23
RFI	0.07	0.48	0.27	0.05	0.57	0.24	0.06	-0.07	0.24

627 * Abbreviations are given in Table 1.

628 **Table 4.** Expected maximum genetic response (ΔG) in growth, feed utilization and lipid traits in
 629 response to alternative selection index scenarios*

Traits in a selection index*	ΔG (% of original trait mean)					
	DG _[BW]	DFI _[BW]	FCR _[BW]	Body Lipid% _[BW]	Muscle Lipid% _[BW]	Viscera% _[BW]
DG _[BW]	7.20	2.53	-4.36	-0.11	-1.95	1.19
DG _[BW] -DFI _[BW] (-0.52)	4.83	-2.02	-6.54	-0.45	-3.52	0.83
DG _[BW] -BodyLipid% _[BW] (-0.68)	6.09	0.12	-5.63	-1.25	0.25	0.41
DG _[BW] -MuscleLipid% _[BW] (-0.70)	5.93	-0.96	-6.50	-1.03	-7.74	0.58
DG _[BW] -Viscera% _[BW] (-0.10)	7.31	2.55	-4.43	-0.07	-1.87	1.70

630 * Abbreviations are given in Table 1.

631 † Relative index weighting given in parenthesis.

632

633 **Table 5.** Sample size (n), trait mean, phenotypic variance (V_p), heritability and its standard error ($h^2 \pm$
 634 SE), and full-sib effect ratio ($c^2 \pm$ SE) for lifetime traits estimated with an animal model either including
 635 or excluding the random full-sibs effect

Trait*	n	Mean	Full-sib effect excluded			Full-sib effect included			
			V_p †	h^2	SE	h^2	SE	c^2	SE
BW _{M29}	1262	2591	252866	0.36	0.07	0.26	0.09	0.055	0.032
LifeFI _{Indicator}	736	21.79	84.83	0.09	0.05	0.06	0.06	0.037	0.039
LifeFCR _{Indicator}	692	0.845 E-02	1.46E-05	0.13	0.07	0.07	0.07	0.048	0.047
LifeRFI _{Indicator}	692	0.000 0	69.439	0.14	0.08	0.06	0.06	0.065	0.062
LifeERetention _{Indicator}	545	73.69	993.61	0.10	0.07	0.05	0.07	0.046	0.053
LifeLipidRetention _{Indicator}	545	124.2	3750.8	0.13	0.08	0.07	0.06	0.049	0.053
LifeProtRetention _{Indicator}	545	48.76	416.98	0.10	0.07	0.06	0.07	0.042	0.052

636 * Abbreviations: BW_{M29} -Body weight at month 29; LifeFI_{Indicator} - Lifetime feed intake; LifeFCR_{Indicator} -
 637 Lifetime feed conversion ratio; LifeRFI_{Indicator} - Lifetime residual feed intake; LifeERetention_{Indicator},
 638 LifeLipidRetention_{Indicator}, LifeProtRetention_{Indicator} - Lifetime retention efficiency for energy, lipid and
 639 protein.

640 † Variance from the model 1 or 2 using which all the fixed effects have been removed.

Table 6. Phenotypic (r_P) and genetic correlations ($r_G \pm$ SEM) for lifetime feed utilization and lipid traits*

	BW _{M29}			BodyLipid% _[BW]			MuscleLipid% _[BW]			Viscera% _[BW]		
	r_P	r_G	SEM	r_P	r_G	SEM	r_P	r_G	SEM	r_P	r_G	SEM
LifeFCR _{Indicator}	-0.15	-0.47	0.24	0.13	0.60	0.29	0.05	0.54	0.23	0.11	0.11	0.24
LifeRFI _{Indicator}	0.05	-0.04	0.27	0.09	0.29	0.28	0.05	0.64	0.25	0.08	-0.23	0.23
BW _{M29}	na†	na†	na†	0.08	-0.19	0.17	-0.02	-0.28	0.15	-0.01	-0.04	0.15
LifeFI _{Indicator}	0.30	0.31	0.25	0.15	0.59	0.22	0.04	0.50	0.26	0.10	0.16	0.25
LifeERetention _{Indicator}	0.02	0.24	0.28	-0.04	-0.08	0.29	0.02	-0.46	0.30	-0.06	0.20	0.26
LifeLipidRetention _{Indicator}	0.04	0.24	0.27	0.01	0.03	0.27	0.03	-0.39	0.29	-0.04	0.21	0.25
LifeProtRetention _{Indicator}	-0.04	0.20	0.29	-0.18	-0.38	0.30	-0.04	-0.60	0.29	-0.09	0.12	0.27

* Abbreviations are given in Table 1 and Table 5.

† Not estimable.

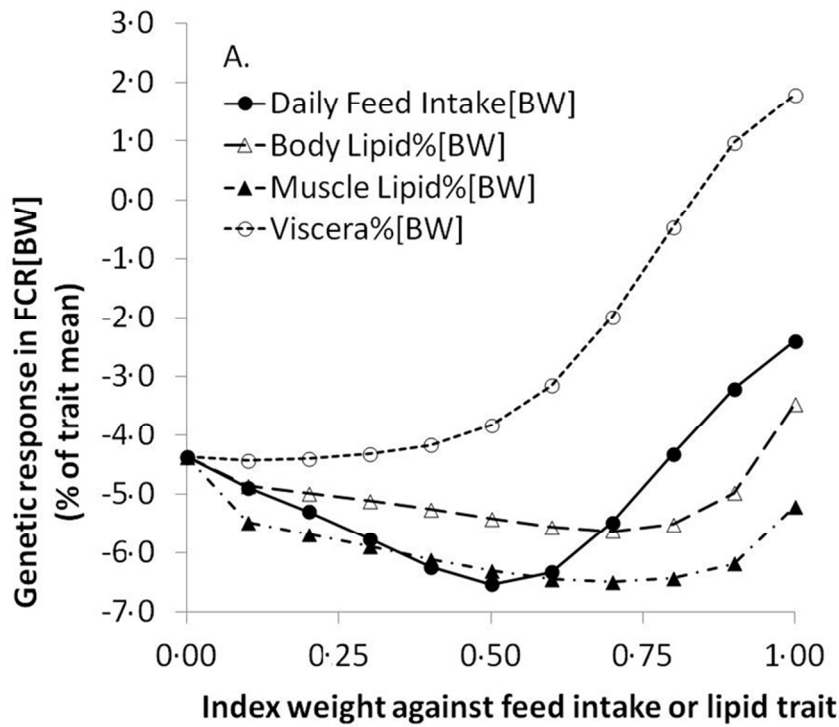


Fig 1. Expected genetic response in A) feed conversion ratio (FCR[BW]) and B) daily weight gain (DG[BW]) when selecting simultaneously for DG[BW] and against one of the alternative traits: DFI[BW or one of the lipid traits.

361x270mm (72 x 72 DPI)

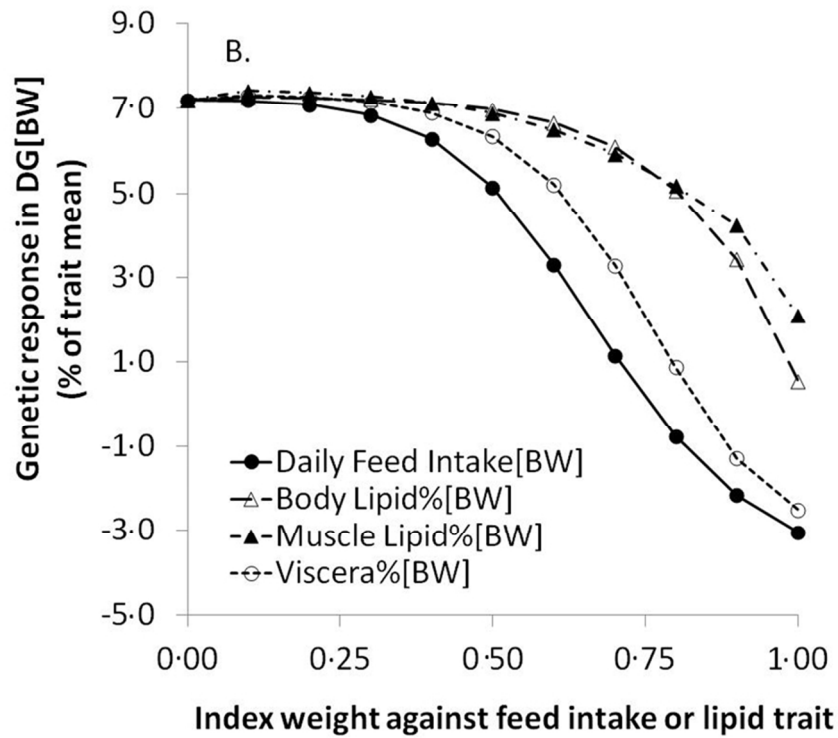


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