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1 **Flesh characteristics: estimation of genetic parameters and correlated responses to selection**
2 **for growth rate in the GIFT strain**

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22 Suggested running title: Genetic parameters of flesh characteristics in the GIFT strain.

23 *Keywords:* GIFT strain; flesh characteristic; heritability; correlation; correlated response

24 **Abstract**

25 Flesh characteristics comprising chemical composition (protein, fat and moisture percentages and
26 pH) as well as a sensory attribute (colour) were measured in 1,951 fillet samples from two
27 generations of two populations (a selection line, selected for increased harvest weight, and a
28 control line, selected for average breeding values for harvest weight) of the GIFT (Genetically
29 Improved Farmed Tilapia) strain of Nile tilapia. These data were jointly analyzed with 5,331
30 harvest weight records from three generations to estimate genetic parameters and correlated
31 selection responses. Multiple trait animal models were used in the analyses. The potential for
32 correlated responses was evaluated by estimating heritabilities and genetic correlations between
33 body traits (weight, length, depth and width) and fillet traits (weight and yield) with the above
34 mentioned flesh characteristics. The heritabilities for protein %, fat % and colour were low (0.06
35 to 0.11), whereas for moisture % and pH they were moderate (0.15 to 0.20). Genetic correlations
36 among some flesh characteristics (moisture % with protein %, fat % and pH and with fat %) as
37 well as between body and fillet traits with flesh characteristics, were significantly different from
38 zero but low (-0.34 to 0.31). Correlated responses were evaluated by comparing the least squares
39 means between the Selection and Control lines. Our results indicate that selection for high growth
40 increased harvest weight in the Selection line relative to the Control line but it did not change the
41 flesh characteristics of the GIFT strain.

42 *Keywords:* GIFT strain; flesh characteristics; heritability; correlation; correlated response

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46 **1. Introduction**

47 The primary objective of breeding programs in aquaculture has been to improve growth rate,
48 measured as live weight at harvest. However, flesh characteristics are receiving increasing
49 attention as a consequence of greater awareness about consumer preferences, often linked with
50 their possible impact on human health and nutrition (Verbeke, Sioen, Pieniak, Camp & De
51 Henaauw, 2004; Bourre, 2005; Grunert, 2005). Understanding factors that influence flesh
52 characteristics is essential in our endeavor to satisfy consumer demand for high quality products.
53 In the future, the price paid for the fish may depend to some extent on flesh characteristics and
54 their consistency. Sensory and consumer-perceived flesh quality comprise a variety of
55 characteristics such as taste, flavour, freshness, juiciness, smell, texture and appearance, where
56 each may be influenced by genetics and a range of environmental factors including pre- and post-
57 mortem handling of the fish. These characteristics may be related to other flesh characteristics,
58 such as chemical composition (protein, fat, moisture% and pH) and colour, which are relatively
59 easy to measure compared to their sensory counterparts (Olafsdottir, Nesvadba, Di Natale,
60 Careche, Oehlenschläger, Tryggvadóttir, Schubring, Kroeger, Heia, Esaiassen, Macagnano &
61 Jørgensen, 2004).

62 Selection for harvest weight could have unfavourable, favourable or no effect on other traits,
63 including those related to flesh characteristics. Genetic parameters for flesh characteristics related
64 to quality have been reported for salmon (Iwamoto, Myers & Hershberger, 1990; Rye & Gjerde,
65 1996; Norris & Cunningham, 2004; Neira, Lhorente, Araneda, Diaz, Bustos & Alert, 2004;
66 Quinton, McMillan & Glebe, 2005; Vieira, Norris & Johnston, 2007; Powell, White, Guy &
67 Brotherstone, 2008) and rainbow trout (Gjerde & Gjedrem, 1984; Gjerde & Schaeffer, 1989;
68 Kause, Ritola, Paananen, Mäntysaari & Eskelinen, 2002; Tobin, Kause, Mäntysaari, Martin,

69 Houlihan, Dobby, Kiessling, Rungruangsak-Torrissen, Ritola & Ruohonen, 2007). Overall these
70 reports suggest that there is within population genetic variation for flesh characteristics, resulting
71 in heritability values that would enable achieving response to selection.

72 GIFT has undergone ten generations of selection for harvest body weight in Malaysia, but there
73 have been no reports on genetic parameters for flesh characteristics for this strain. In the present
74 study the effects of selection for increased harvest body weight on flesh chemical composition
75 (protein %, fat %, moisture % and pH) as well as in colour, were investigated in fillets from fish
76 of the GIFT strain. Heritabilities and genetic correlations of flesh characteristics with body
77 dimensions (weight, length, width and depth) and with fillet traits (weight and yield) were also
78 estimated. Body dimensions were of interest because if they were related to fillet weight and fillet
79 yield, they could be used as predictors of the latter traits in live fish instead of slaughtering the
80 animals.

81

82 **2. Materials and Methods**

83 *2.1 The GIFT strain in Malaysia*

84 The GIFT strain was introduced to the Aquaculture Extension Centre, Department of Fisheries,
85 Jitra, Malaysia in late 2001 and early 2002 from the GIFT Foundation International Inc. A total of
86 63 families from the 6th generation were received and quarantined in tanks for a month. Each
87 family consisted of 35 individuals (10g average weight). They were individually identified and
88 reared to an average size of 250g, when the fish were ready for spawning. Mating began late in
89 2002, producing the first generation of the selection program in Malaysia. Harvest weight was the
90 only selection criterion. Two lines were formed: i) the Selection line, selected for high estimated

91 breeding values for harvest weight, and ii) the Control line, selected for average estimated breeding
92 values for harvest weight (see Ponzoni, Nguyen, Khaw & Hamzah, 2011, for further details).

93

94 *2.2 Family production and rearing*

95 Mating of selected fish was performed in 1m³ nylon hapas of 2mm mesh size, installed in an
96 earthen pond. One male was mated to two females in the Selection line, whereas in the Control
97 line one male was mated to one female (single pair mating). The females were transferred to the
98 breeding hapas before the males. Only the most 'ready to spawn' (Longalong, Eknath & Bentsen,
99 1999) females were paired with a male in the hapa. After a week of mating, fertilized eggs were
100 collected from the mouth of the female and immediately transferred to the hatching jars for three
101 to five days until hatching. The date of spawning was recorded for each individual pair mated. The
102 male was then paired to the second female in another hapa. The male and female were mated again
103 if they produced less than 200 fry. In each generation the mating period lasted about 75 days. The
104 breeders were not fed when the females were expected to spawn in order to prevent them from
105 swallowing its eggs.

106 The hatched fry of each family were transferred from the incubators to the nursery hapas (1m³
107 with 2mm mesh size), stocked at a density of 200 fish per m³. At least three nursery hapa replicates
108 of each family were maintained in the same pond to reduce environmental differences between
109 families.

110 After three to six weeks of rearing (approx. 5g) the fry were tagged using Passive Integrated
111 Transponder (PIT) tags for individual identification. Seventy fry were tagged from each family for
112 performance testing. The tagged fish were released in earthen ponds for communal grow-out at a
113 stocking density of three fish per m². They were harvested in August and September at 200 to 450g

114 live weight, when they were eight months old (approx.) for the ongoing selection program (see
115 Ponzoni *et al.*, 2011 for details). In the fourth, fifth and sixth generations (spawning years 2006,
116 2007 and 2008) of selection, additional fry (30 fish per family) were randomly sampled, tagged
117 and reared in another 0.05ha pond for the filleting experiment. A total of 8,400 fish were reared
118 for this study. They were fed twice daily using a commercial pellet feed with 32% protein content
119 at a rate of 5% body weight. Culture management, water quality monitoring and feeding
120 management were closely monitored throughout the culture period. The family production and
121 rearing method are described in detail by Nguyen, Ponzoni, Abu-Bakar, Hamzah, Khaw and Yee,
122 (2010a) and Ponzoni *et al.* (2011). The number of sires, dams and the total number of fish measured
123 from different generations are presented in Table 1.

124

125 *2.3 Harvesting*

126 The fish were harvested after 180 days of culture using lift and seine nets. A lift net was used in
127 the first day of harvest to minimize stress to the fish. The net covered three quarters of the pond's
128 bottom and it was submerged in the water before harvesting. It was then hauled upward of the
129 water to catch the fish in the following day. Using the lift net, about three quarter of the total fish
130 in the pond could be harvested. The harvested fish were transferred to conditioning cages (3m x
131 3m x 1m) installed in another pond. Early in the morning of the next day, the seine net was applied
132 in the pond, seining in three drags. To harvest the remaining fish, the pond was dried. All the
133 harvested fish were conditioned in cages for two days before they were transferred in batches from
134 the grow-out farm in Jitra to the fish tank facility in WorldFish, Penang, 150 km away. During
135 transport the fish were kept in aerated tanks. Some fish died (<1%) due to the stress of the three

136 hour trip. Upon arrival, the fish were transferred to tanks at low density (5 fish per m³) where they
137 were conditioned for two days before slaughter. No food was provided during this period.

138

139 *2.4 Slaughter, filleting and measurements*

140 An hour before slaughter, the fish were collected from the tanks and were killed by cold shock
141 placing them in iced water. The fish were individually weighed using a digital scale (to the nearest
142 0.1g). Standard length (L) was measured from the tip of the snout to the rear end of the fleshy part
143 of the body. A calliper was used to measure body depth (D) and width (W) (to the nearest mm) at
144 the mid-side of the fish, where they are greatest. The tag number and sex (by visual assessment of
145 the genital papillae) were also recorded. After data recording and measurement, the fish were
146 filleted by two trained technicians. The fillets from both sides were manually skinned and weighed
147 using the same digital scale as for harvest weight. They were rinsed with tap water, dried with
148 absorbent paper and kept in separate plastic bags labeled with the PIT tag identification. All the
149 fillets were immediately stored in freezers at a temperature of -10°C before being sent to a
150 specialized laboratory (Union Laboratories Sdn. Bhd., Penang) for chemical analysis (protein, fat
151 and moisture percentages, pH) and colour measurement.

152

153 For the study of flesh characteristics a total of 1,951 fillets from two of the generations (spawning
154 seasons 2006 and 2007) were randomly sampled from all families, selection lines, sexes and
155 batches. A tissue sample from each fillet was analysed for chemical composition. Protein, fat and
156 moisture percentages were determined with the following standard methods: AOAC 991.20,
157 AOAC 920.39 and AOAC 984.25 respectively (AOAC, 2005). Crude protein was analyzed by the
158 Kjeldahl Nitrogen Method using Buchii Digestor B435 and Buchii Distillation Unit B323 to obtain

159 the nitrogen %. The latter figure was then multiplied by 6.25 to obtain an estimate of protein %.
160 Total fat was determined gravimetrically by the Soxhlet Method; the fat was extracted from the
161 sample by conventional Soxhlet Extractor for 6 hours, distilled to remove the solvent (hexane)
162 before it was dried in an oven and weighed to obtain the fat % of the sample. For moisture content,
163 samples were weighed to obtain fresh weight (w_0) before drying in an oven at $100 \pm 2^\circ\text{C}$, and then
164 cooled in desiccators. The procedure was repeated until a constant dry weight (w_1) was achieved.
165 The moisture percentage was obtained as $[(w_0 - w_1)/w_0] \times 100$. For pH, minced flesh samples from
166 the fillets were dissolved in distilled water in a 1:10 ratio of flesh to water and pH was measured
167 by a Corning, Model 320 machine. Fillet colour was visually assessed by scoring on a scale of 1
168 to 5, ranging from white, most preferred colour by the consumers, to red, least desirable colour (1
169 = white, 2 = grey, 3 = orange, 4 = pink and 5 = red). Fillet yield (FY) (dressing percentage) was
170 calculated as $(FW/BW) \times 100$ where FW is fillet weight of the fish and BW is its body weight.
171 At the time of conducting the analyses there were 5,331 fish with body and fillet measurements
172 (BW, L, D, W, FW and FY). Flesh characteristics were measured in a subset of 1,951 out the 5,331
173 fish. The information from all fish was combined for genetic analysis. Table 2 shows the number
174 of observations for each characteristic as well as raw data statistics.

175

176 *2.5 Statistical analyses*

177 To estimate the differences between the Selection and Control lines a fixed effects model was
178 fitted using the UNIANOVA procedure in SPSS (SPSS, 2011). The model included the effects of
179 generation (2006, 2007 and 2008), line (Selection and Control), sex (male and female) and the two
180 way interactions between these effects. Batch nested within pond and generation was fitted as a
181 fixed effect. Age at slaughter was included as a covariate. The fixed effect of technician (two

182 technicians) was included only for the fillet traits (fillet weight and fillet yield). Correlated changes
183 in fillet and flesh characteristics were estimated by comparing least squares means of the Selection
184 and Control lines. Note that the main focus of the present paper is in the latter comparison (i.e.
185 Selection vs. Control lines). Hence, some other effects were fitted because they are known to be
186 sources of variation but they are not discussed in detail.

187 Multiple trait animal model analyses were carried out to estimate genetic parameters. The model
188 included the same fixed effects and covariates as that described in the previous paragraph. The
189 random effects included in the model were the additive genetic effect of the fish (progeny of 173
190 sires and 280 dams), the common environmental effect (environmental effect common to full sibs)
191 and the residual environmental effect. The multiple trait animal model analyses were implemented
192 using the VCE 6.0 program (Groeneveld, Kovač & Mielenz, 2008).

193

194 **3. Results**

195 *3.1 Descriptive statistics and fixed effects*

196 Table 2 shows descriptive (uncorrected) statistics for body and flesh characteristics as well as for
197 age of the fish at slaughter. Moisture %, protein % and pH had very low coefficient of variation
198 (CV) ranging from 2.5% in moisture to 5.4% in protein. By contrast, colour and fat % had high
199 CVs (44 to 68%). Body and fillet traits exhibited low to moderate CV ranging from 7.6% to 29.8%.
200 The ANOVA results for flesh characteristics are shown in Table 3. The line effect was not
201 significant for any of the flesh characteristics. Sex and age at slaughter were significant for protein
202 %, moisture % and pH. Generation and batch (within pond and generation) were significant for fat
203 % and colour. For moisture %, all effects, except line, were significant.

204 *3.2 Heritabilities and correlations among flesh characteristics*

205 Variance components and heritability estimates for flesh characteristics are presented in Table 4.
206 The heritabilities for protein %, fat % and colour were low, whereas they were moderate for
207 moisture % and pH. Phenotypic and genetic correlations among flesh characteristics were low
208 (Table 5). Among these, the strongest were the negative genetic correlations of fat % with moisture
209 % and pH, and between protein % and moisture %. However, overall, flesh characteristics were
210 not strongly associated with each other.

211
212 *3.3 Correlations of flesh characteristics with body and fillet traits*

213 The majority of genetic correlations between flesh characteristics and body traits were low,
214 ranging from 0.01 between pH and body weight to 0.31 between fat % and body width (Table 6).
215 Phenotypic correlations between flesh characteristics and body and fillet traits were also low,
216 ranging from 0 to 0.19.

217
218 *3.4 Gender effect and correlated responses in flesh characteristics*

219 The least squares means and standard errors (se), obtained from the fixed effects model, for
220 Selection and Control lines and for male and female fish are shown in Table 7. The Selection line
221 had greater harvest weight than the Control line, indicating response to selection for that trait. This
222 is consistent with the responses to selection in the GIFT strain reported by Ponzoni et al. (2011).
223 By contrast, there were no statistical differences ($p>0.05$) between the Selection and Control lines
224 in any of the flesh characteristics studied, indicating the absence of correlated responses to
225 selection for harvest weight. Sex differences were statistically significant ($P<0.05$ to 0.001) for
226 harvest weight and for three out of the five flesh characteristics. Females were lighter and
227 exhibited higher protein % than males whereas the opposite was observed for pH and moisture %.
228 Fat % and colour were not significantly different ($P>0.05$) between sexes.

229
230
231

4. Discussion

4.1 Variability in flesh quality characteristics and the effect of gender

232 The CVs for colour and fat % were greater than for moisture %, protein % and pH (Table 2). The
233 lower CVs (compared to earlier studies, e.g. Ponzoni, Hamzah, Tan & Kamaruzzaman, 2005;
234 Ponzoni *et al.*, 2011)) for body and fillet traits may have been due to improvement in management
235 in more recent generations. The CV for protein % (5.4%) was lower than that reported by Kause
236 *et al.* (2002) in Rainbow trout (8.3%) but similar to that reported by Kause, Quinton, Airaksinen,
237 Ruohonen and Koskela (2011) in European whitefish. We observed a lower CV for moisture%
238 than Kause *et al.* (2002) in Rainbow trout (6.9%), but similar to Quinton *et al.* (2005) in Atlantic
239 salmon (2.9%), and Iwamoto *et al.* (1990) in Coho salmon (2.4%). In contrast, the CVs for fat %
240 (67.5%) and colour (44.0%) in GIFT were higher than those reported by Kause *et al.* (2002) in
241 rainbow trout (18.3 and 5.5 %, respectively), Neira *et al.* (2004) in Coho salmon (14% fat only),
242 Kocour, Mauger, Rodina, Gela, Linhart and Vandeputte (2007) in common carp (36% fat only),
243 Powell, White, Guy and Brotherstone (2008) in Atlantic salmon (31.5 and 5.6%, respectively) and
244 Kause, Quinton, Airaksinen, Ruohonen and Koskela (2011) in European whitefish (26.4 and 5.7%,
245 respectively).

247

248 The higher protein % in females is consistent with the results from other studies in Nile tilapia
249 (Winfree & Stickney, 1981; Hanley, 1990; Clement & Lovell, 1994; Olvera-Novoa, Pereira-
250 Pacheco, Olivera-Castillo, Pérez-Flores, Navarro & Sámano, 1997; Hafedh, 1999; Garduño-Lugo,
251 2007). Visually scored flesh colour was significantly different between sexes in the studies by Rye
252 & Gjerde (1996) and Gjerde & Schaeffer (1989) in Rainbow trout. However, in agreement with
253 Gjerde & Gjedrem (1984) in a study on flesh colour in Atlantic salmon, we did not detect any

254 significant difference between sexes. Our results for fillet fat % are in agreement with Kause *et al.*
255 (2002) who found no significant differences between sexes.

256

257

258 *4.2 Heritabilities of flesh characteristics*

259 Consistent with other studies (Quinton *et al.*, 2005; Tobin *et al.*, 2006; Kause *et al.*, 2007; Kause
260 *et al.*, 2011) we found that the heritability for fillet protein % in the GIFT strain was very low
261 (0.06) (Table 4), so that changing it by selection would be difficult. However, body weight and
262 fillet yield can be genetically improved (Nguyen *et al.*, 2010a), offering an opportunity to increase
263 total protein by producing larger fish in a shorter grow-out period compared to an unimproved
264 strain. Our heritability estimate of fillet fat % (0.11) was lower than those (0.16 to 0.58) reported
265 in other species (Gjerde & Gjedrem, 1984; Kause *et al.*, 2002, 2011; Quillet, Le Guillou, Aubin &
266 Fauconneau, 2005; Kocour *et al.*, 2007; Powell *et al.*, 2008). Low to high heritability estimates
267 (0.06 to 0.37) have been reported for moisture % in different species (Kause *et al.*, 2002; Quinton
268 *et al.*, 2005; Kause *et al.*, 2011). Our estimate was 0.20, middle of the range in this context.

269 Low to medium heritabilities (0.04 to 0.20) have been reported for visually scored flesh and fillet
270 colour in coho salmon, Atlantic salmon, rainbow trout, European whitefish and striped catfish
271 (Gjerde & Gjedrem, 1984; Withler & Beacham, 1994; Rye & Gjerde, 1996; Kause *et al.* 2002,
272 2010; Norris & Cunningham, 2004; Gjedrem, 2005; Tobin *et al.*, 2006; Powell *et al.*, 2008; Sang,
273 Klemetsdal, Ødegård & GjØen, 2012). Our estimate (0.09) was close to the lower end of this range
274 and in agreement with Gjerde & Gjedrem (1984) in rainbow trout, Tobin *et al.* (2006) in European
275 whitefish and Sang *et al.* (2012) in striped catfish. The subjective way in which colour was
276 assessed may be a contributing factor to our low heritability value. Overall, our work showed that

277 heritability estimates for flesh characteristics in the GIFT strain were low, indicating that response
278 to selection would be slower than for traits such harvest weight, of greater heritability.

279

280 *4.3 Phenotypic and genetic correlations*

281 Phenotypic and genetic correlations among flesh characteristics were either very low or low (Table
282 5). Similar results were observed in rainbow trout (Tobin *et al.*, 2006) and European whitefish
283 (Kause *et al.*, 2011). The genetic correlations (-0.26 to -0.31) between body traits (weight, depth
284 and width) and moisture % in the GIFT strain were comparable to those reported in salmon
285 (Quinton *et al.*, 2005; Vieira, Norris & Johnston, 2007), suggesting that selection for greater
286 growth rate could result in a drier flesh. Similar correlations were observed at the phenotypic level
287 (-0.13 to -0.19). A range of positive genetic correlations (0.11 to 0.80) between body weight and
288 fat % have been reported in salmon (Iwamoto *et al.*, 1990; Kause *et al.*, 2002; Neira *et al.*, 2004;
289 Quinton *et al.*, 2005; Vieira *et al.*, 2007; Powell *et al.*, 2008) and in common carp (Kocour *et al.*,
290 2007). Our estimate was within this range (0.26). The low correlation indicated that selection for
291 high growth rate is unlikely to be accompanied by large changes in fat %, but it may result in
292 gradual, small increases.

293 Gjerde & Schaeffer (1989) and Kause *et al.* (2002) suggest that a study of fat in fish should
294 consider its distribution in different body compartments. Tobin *et al.* (2006) propose that fat
295 deposits in different body locations should be measured as genetically different traits. In rainbow
296 trout Kause *et al.* (2007) measured muscle and body lipid as two different traits. Muscle samples
297 were dissected above the lateral line of the fish whereas for body composition, samples of un-
298 gutted fish were minced and homogenized before lipid analysis. Across studies, the genetic

299 correlations between fat % in fillet and in the whole fish were low. Therefore, fillet fat % should
300 be considered as a genetically different trait from the fat deposits in other body locations.

301 There are no estimates of genetic correlations between flesh colour and body weight in tilapia.
302 Most of the published reports on genetic correlations between flesh colour and body weight are on
303 salmon and rainbow trout. Since tilapia has white flesh, it is irrelevant to compare the correlations
304 with those obtained in salmon or trout where white is not the desired colour. The low genetic
305 correlations between colour and body traits observed in the present study suggest that selection for
306 high growth rate would not result in changes in flesh colour.

307

308 *4.4 Correlated responses*

309 It is unlikely that flesh quality traits will become part of the breeding objective of tilapia in the
310 near future (Nguyen, Ponzoni, Hamzah, Yee, Abu-Bakar & Khaw, 2010c). However, monitoring
311 of genetic improvement programs is necessary in order to detect, as early as possible, undesirable
312 correlated responses. For instance, in terrestrial animals, rapid growth is associated with high meat
313 fat content (Muller, Moser, Bartenschlager & Geldermann, 2000; Suzuki, Irie, Kadowaki, Shibata,
314 Kumagai & Nishida, 2005; Kvame & Vangen, 2007). The genetic correlation between body
315 weight and fat% reported in the present study cannot be considered conclusive, but it suggests that
316 that could be the case in tilapia as well. A similar trend was found in studies of other fish species
317 (Gjerde & Gjedrem, 1984; Rye & Gjerde, 1996; Neira *et al.*, 2004; Powell *et al.*, 2008).

318 Consistent with what one may have predicted from the genetic correlations in the present study,
319 the Selection line did not differ from the Control line in flesh characteristics (Table 7), indicating
320 that selection for high growth rate has so far had no impact on them. This is consistent with the
321 earlier study on sensory attributes assessment of GIFT flesh characteristics by trained (Khaw,

322 Ponzoni, Abu-Bakar, Hamzah, Kamaruzzaman & Nguyen, 2006) and untrained panels (Ponzoni,
323 Khaw, Abu-Bakar, Hamzah, Kamaruzzaman & Nguyen, 2006). That study indicated that the
324 selection emphasis on growth had not changed flesh characteristics in GIFT. On the other hand,
325 selection for high growth significantly increased fillet weight by 4% per generation (Nguyen *et*
326 *al.*, 2010a) but there were no major changes in fatty acid composition of the flesh (Nguyen,
327 Ponzoni, Yee, Abu-Bakar, Hamzah & Khaw, 2010b). To date, there have been no comparable
328 studies on correlated responses of flesh characteristics in tilapia or other aquatic animal species.
329 However, similar trends have been reported in terrestrial farmed animals resulting from short term
330 selection programs. For instance, selection for higher body weight did not affect meat quality traits
331 in Pirenaica cattle (Altarriba, Varona, Moreno, Yagqe & Sañudo, 2005) and composition of muscle
332 in swine (Cameron & Curran, 1995). Hernandez, Aliaga, Pla and Blasco (2004) also did not detect
333 any effects on carcass and meat quality traits in rabbits selected for increased growth rate.

334

335 In summary, there was limited genetic variation in flesh characteristic in the GIFT strain.
336 Heritabilities were low, except for fat %, where it was moderate. In addition to the limited scope
337 for genetic improvement, selection for flesh characteristics would require a special effort for a
338 number of reasons: (i) high cost of chemical analysis; (ii) most flesh characteristics require the
339 slaughter of the fish; (iii) complex biological and physiological control of flesh characteristics, and
340 (iv) lack of pricing systems that reward producers. With regard to the first and second constraints,
341 alternative analytical methods for flesh characteristic assessments could be considered such as
342 infrared spectroscopy that could be used to analyze thousands of fish samples for colour, lipid and
343 protein content estimation (Kause *et al.*, 2007), Distell Fish Fat Meter for fat and lipid percentage

344 (Kause *et al.*, 2011; Quillet *et al.*, 2005), ultrasound scanner for muscle thickness measurement
345 (Quillet, Le Guillou, Aubin, Labbé, Fauconneau & Medalé, 2007).

346 The lack of pricing systems is partly due to the inconsistency in the definition of the optimal values
347 of the traits that describe 'quality'. Hence, pricing systems based on 'quantity' are generally
348 accepted world-wide. The definition of quality may differ from market to market within a country,
349 as well as between countries, resulting in different pricing systems for the cultured fish.

350 The comparison between the Control and the Selection lines shows that the GIFT genetic
351 improvement program, focusing mainly on harvest weight, had no impact on flesh characteristics.
352 These results are consistent with the low heritability estimates for these traits (exception made of
353 fat % for which it was moderate), and with the very low and low genetic correlations with body
354 weight. The highest genetic correlations of body and fillet weight were with fat and moisture %
355 and colour, but they were still low. As a long term strategy in the GIFT strain these traits should
356 be periodically monitored to avoid the risk of producing fatter, drier and more reddish flesh.

357 358 **Conclusion**

359 The results of this study showed that selection for increased growth rate has so far had no
360 detrimental effects on the flesh characteristics of the GIFT strain. The phenotypic and genetic
361 parameters for these traits suggest that this situation is likely to remain unchanged, but to ensure
362 the continued success of the GIFT strain periodic monitoring of flesh characteristics is
363 recommended.

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