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1 **Impact of a divergent selective breeding programme on individual feed**
2 **conversion ratio in Nile tilapia *Oreochromis niloticus* measured in groups by**
3 **video-recording**

4
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21

22 **Abstract**

23 Feed conversion ratio (FCR) is an important trait to target in breeding programs in order to
24 improve fish farming sustainability and increase environmental efficiency. Due to the
25 complexity of accurately measuring the individual feed consumption of fish, developing a
26 selective breeding programme to improve FCR is a challenge. Using video-recordings of
27 several consecutive meals in tilapia groups, we selected two divergent lines of Nile tilapia for
28 high (FCR+) and low (FCR-) FCR at juvenile stage (12.2 g) combining BLUP and within
29 family selection. After two generations, we observed a 12 % realised difference in FCR
30 between both divergent lines, indicating that the inclusion of FCR in a selective breeding
31 programme can be efficient in practice. This divergence was in line with a realized heritability
32 of 0.19 for FCR. The divergence in estimated breeding values of FCR between the two lines
33 was reduced (3%) but still present. Another important result was that the realized genetic
34 correlation between FCR and Daily Weight Gain (DWG) was highly negative ($r_g = -0.69 \pm$
35 0.16), meaning that improving growth by selective breeding would also indirectly improve
36 FCR in juvenile Nile tilapia, although direct selection for FCR would be more efficient than
37 indirect selection through growth to improve FCR.

38

39 **Keywords:** feed efficiency, aquaculture, genetic parameters, selection response

40

41 **1. Introduction**

42 Feed conversion ratio (FCR), the ratio of feed intake (FI) to body weight gain (BWG) is one
43 of the main traits to be improved in order to develop sustainable aquaculture (Aubin et al.,
44 2009; Besson et al., 2017; de Verdal et al., 2018a). However, there are currently no
45 commercial breeding programs that report introduction of FCR in their selection index
46 because this trait is difficult to select for. To estimate FCR, FI must be accurately measured at
47 the individual level, which is particularly challenging in fish reared in groups and in a three-
48 dimensional system and an aquatic environment. Furthermore, the FI of an individual fish
49 may vary from day to day (Jobling and Koskela, 1996; de Verdal et al., 2017). Therefore, an
50 optimal method for estimating individual FCR should enable the measurement of FI for each
51 meal over several consecutive days to be accurate and well represent the individual
52 performance of the fish. Under these constraints, two methods have recently been adapted and
53 upscaled to measure individual FI in several hundred fish, which is a necessary amount to
54 enable selective breeding. The first method involves rearing fish individually, with each fish
55 isolated in an aquarium. Growth and the amount of feed consumed are accurately measured
56 for each fish (Besson et al., 2019). This method gives a good estimate of individual FCR but
57 removes all social interactions between fish, which can have an impact on their own FCR,
58 depending on the fish species (Rodde et al., 2021). Moreover, the measure can only be done
59 on the individuals that accept this environmental condition (Besson et al., 2019). Others
60 methods have been developed in fish to accurately measure FI, like the “X-ray” method, but
61 cannot be applied in consecutive days (Kause et al., 2006; Grima et al., 2008), which limits
62 the repeatability of measurements. The last method (see review by Jobling et al., 2001) and
63 adapted for genetic studies by de Verdal et al. (2017) is to use small groups of fish reared in
64 aquariums. Using pellet-by-pellet feeding and video recording of several consecutive meals, it

65 is possible to count the number of pellets consumed by each fish and estimate individual FI
66 without removing social interactions between fish (de Verdal et al., 2017).

67 Phenotyping FCR is clearly a challenge in fish, but there are other important points to
68 consider before adding this trait to a breeding programme. It is essential to estimate the
69 genetic parameters of this trait, i.e. the heritability, and the genetic correlations with other
70 important traits, such as growth, in the population selected for the breeding programme. Few
71 studies have estimated the genetic parameters of FCR in fish. Using different methods for
72 measuring FI during several consecutive days (individual rearing or video analyses),
73 heritability has been estimated to range between 0.25 and 0.32 using pedigree-based models
74 (de Verdal et al., 2018b; Besson et al., 2019), with an interesting level of phenotypic variance
75 (22% coefficient of variation in both studies). It therefore seems possible to develop a
76 selective programme on this trait.

77 The main objective of the present study was to evaluate selection response in a small size
78 selective breeding programme, as a proof of concept to assess the real potential of such
79 selection to improve FCR in fish. Nile tilapia *Oreochromis niloticus* was naturally chosen to
80 develop such a programme because, besides the fact that it is one of the major aquaculture
81 species (Cai et al., 2019) with potentially major economic impact of FCR improvement,
82 several studies have already been conducted to accurately measure FI and evaluate the
83 potential of such genetic selection (de Verdal et al., 2017, 2018b; Rodde et al., 2020, 2021). In
84 addition, Nile tilapia has a relatively short generation interval, thus fish can be selected for
85 two generations in a relatively short period of time. As Nile tilapia is a sociable fish species
86 showing high between-individual interactions (de Verdal et al., 2019), the video-analysis
87 method was preferred to the rearing of isolated fish, as it had been previously shown that the
88 correlation of FCRs measured by these two methods was low in this species (Rodde et al.,
89 2021). A last aspect is that tilapias are mostly reared and selected in developing countries and

90 that affordable strategies of selection, such as within-family selection, have to be considered
91 as they are simpler and more robust than too complex programs based on family selection
92 (Doyle and Herbinger, 1994).

93

94 **2. Material and Methods**

95 2.1.Ethics statement

96 This study was carried out in accordance with the recommendations of Directive 2010-63-EU
97 on the protection of animals used for scientific purposes. The protocols were approved by
98 C2EA-36 (“Comité d'éthique en expérimentation animale Languedoc-Roussillon”) under
99 authorizations APAFiS n° 2018082008567792 #16582 v2 and n°2019101512138909 #22423
100 v4.

101 2.2.Origin and rearing of the base generation

102 The Nile tilapia used in this study were produced from a cross between Cirad-IRD dams,
103 initially originating from Egypt, kept in the Cirad-IRD facility (Montpellier, France) for
104 several generations, and sires from FishGen commercial strain introduced in 2018 in Cirad
105 facilities in Palavas-les-Flots (France). In the F0 founders, only FishGen males were
106 phenotyped at the juvenile stage, for practical reasons. Three hundred and fifty-one males
107 were reared in tanks until they reached an average of 10g body weight (BW). When they
108 reached this body weight, they were divided into two groups, with each group being measured
109 in sequence, due to space required to measure the fish. Indeed, for logistical reasons, it was
110 not possible to have more than 20 aquariums in the rearing room. The fish of each batch were
111 distributed in 38 L aquariums (maximum 10 fish per aquarium). After anaesthesia with clove
112 oil, each fish was tagged in the dorsal muscle with a unique combination of two coloured T-
113 bar tags (Avery Dennison tags, 25 mm), one tag on each side of the body, using an Avery

114 Dennison Mark III pistol Grip tool to identify them individually regardless of which side of
115 the body was shown and recorded in video. The fish were fed a commercial pelleted feed (Le
116 Gouessant, “Tilapia Starter Flot 1” and “Tilapia Starter Flot 2”) containing 38% crude
117 proteins, 8% crude fat, 3.9% crude fibre and 7% moisture throughout the experiment. The
118 water temperature was maintained at 28°C throughout the experiment.

119 2.3. Phenotyping for FCR

120 The experimental design was previously developed and reported in de Verdal et al. (2017,
121 2018b). Briefly, after seven days of adaptation to the group aquarium, all fish were
122 anaesthetized and weighed individually (BW_i). The fish were then fed twice a day with 100%
123 daily feed ration (DFR, in percentage of body weight), except on the day of weighing when
124 they were fed once in the afternoon for the first two generations (G₀ and G₁) and twice the
125 last generation (G₂). The DFR was calculated according to the formula published by Mélard
126 et al. (1997): $DFR = 14.23 \times BW_i^{-0.322}$. Although this formula is not perfect, using a formula
127 rather than an “*ad-libitum*” ration had some advantages. As different experimenters were
128 involved in the feeding process, a calculated ration was more reproducible from one
129 experimenter to another than an “*ad-libitum*” ration. This calculated ration was also useful to
130 ensure that the same maximal feed ration was given at each meal and in all aquariums. The
131 DFR was shared equally for each of the two daily meals. The feed was given through two
132 pipes to the aquarium, which reduced stress, as the fish did not see the experimenter when
133 they received the feed. The fish generally did not eat the whole ration and the choice was
134 made to stop the feeding when some pellets remained uneaten after about one minute on the
135 surface of the aquarium (which in fact corresponds to an *ad-libitum* ration). The uneaten
136 pellets were removed from the aquarium with a dip net. At the end of the measurement period
137 (after seven days, 12-13 meals), the fish were anesthetized a second time and weighed to
138 calculate their daily body weight gain (DWG). At that time, all fish were tagged with a

139 passive integrated transponder (PIT-tag, Biolog-ID®) for individual identification. The fish
140 were then placed in two 300L tanks until the phenotyping process was completed. All video-
141 recorded meals were analysed by counting the number of pellets consumed by each fish.
142 Assuming that all the pellets had the same weight (16.2 ± 1.8 mg), it was possible to estimate
143 the daily FI (DFI) of all fish individually during the measurement period. The FCR of all the
144 individual fish was estimated as the ratio of individual DWG to individual DFI.

145 2.4. Selective breeding scheme

146 With FCR phenotypes of all fish, estimated breeding values (EBV) were computed with a
147 classical pedigree-based model for all the fish using the BLUPF90 family of programs
148 (Misztal et al., 2014). The following model was used:

$$149 \quad y_{ijk} = \mu + Batch_i + Aquarium_j + Animal_k + e_{ijk}$$

150 where y_{ijk} is the FCR of animal k, μ is the overall mean, $Batch_i$ is a fixed effect of batch i (i
151 =1 to 3), $Aquarium_j$ is a random environmental effect corresponding to the common
152 environmental effect, $Animal_k$ is the random additive genetic effect of animal k and e_{ijk} the
153 random residual for animal k. At each generation, the pedigree file was updated to add the
154 new generation, and the model was fitted using all available information. The selective
155 breeding scheme is summarized in Figure 1. At the G0 generation, only males were
156 phenotyped and selected. Once selected, the selected fish were isolated individually in 40L
157 aquariums. The spawns from the non-phenotyped G0 females were divided in two to be
158 fertilized with one selected G0 male from those with the lowest EBV and one G0 male from
159 those with the highest EBV. Each G1 full-sib family was then reared separately. Fish were
160 sexed when they reached more than 30g of body weight and sex-ratio was almost balanced
161 with on average 51.5 % of males and 48.5 % of females. Two aquariums were used for each
162 family where ten full-sibs were reared and phenotyped per aquarium. The worst two (for the

163 non-efficient line) or best (for the efficient line) males and females were then selected within
164 each family (11-12 families per line, Figure 1) and the candidates were isolated individually
165 until they matured. Once mature, G1 males and females (one in each family) were crossed by
166 artificial fertilisation, taking care not to cross together fish from the same family. Only seven
167 G2 families could be produced in each of the lines (Figure 1) due to some difficulties in
168 maturing the fish and in performing artificial fertilisation.

169 2.5. Statistical analyses

170 2.5.1. Descriptive statistics

171 Descriptive statistics, including the number of observations, means and their standard
172 deviations and coefficient of variation (CV) were used to summarise all traits. All statistical
173 analyses were performed using the R software (R Development Core Team, 2018). Outliers
174 were highlighted using the `boxplot.stats` function of the R package “stats” (R Development
175 Core Team, 2018) and were not included in the analyses. Outliers were due to incorrect
176 entered or measured data (negative DWG, DFI or FCR estimates). Analysis of variance was
177 computed using the `lm` function of the R package “stats” (R Development Core Team, 2018).
178 Analysis of variance was performed at each generation to test for the fixed effect of line
179 (FCR+ or FCR-).

180 2.5.2. Retrospective analysis of genetic parameters and breeding values

181 Using the whole G0, G1 and G2 dataset, genetic parameters and phenotypic correlations for
182 all traits (BW_i, BW_f, DWG, DFI and FCR) were estimated by the REML (Restricted
183 Maximum Likelihood) method using VCE6 (Neumaier and Groeneveld, 1998; Kovac et al.,
184 2008). The following model was used for all the traits:

$$185 y_{ijk} = \mu + \text{Generation}_i + \text{Aquarium}_j + \text{Animal}_k + e_{ijk}$$

186 where y_{ijk} is the phenotype of the animal k, μ is the overall mean, $Generation_i$ is a fixed
 187 effect of the generation i (i = 0 to 2), $Aquarium_j$ is a random environmental effect of the
 188 aquarium j corresponding to the common environmental effect, $Animal_k$ is the random
 189 additive genetic effect of the animal k and e_{ijk} the random residual for animal k. The pedigree
 190 file included all individuals from the F0 base generation to the second generation of selection.
 191 The solutions for the animal effect were used as a posteriori estimates of breeding values, and
 192 averaged for each generation x line combination to estimate genetic trends for the traits of
 193 interest. As we have the complete matrix of additive relationships back to the base population,
 194 this approach is expected to yield more unbiased estimates of both breeding values and
 195 genetic parameters in the base population (Sorensen and Kennedy, 1986). In this a posteriori
 196 analysis, transformations were applied to the data to improve the normality of distributions. A
 197 logarithm transformation was applied to BWi, BWf and FCR, while a square root
 198 transformation was applied to DWG and DFI.

199 The following equation was used to estimate the realized heritability under a within-family
 200 selection scheme (Falconer and MacKay, 1996):

201
$$h_r^2 = \frac{R_w}{i\sigma_p(1-r)\sqrt{\left[\frac{n-1}{n(1-t)}\right]}}$$

202 where h_r^2 is the heritability of individual values, R_w is the observed response to selection
 203 (corresponding to the slope of the regression line of the selection differential between FCR+
 204 and FCR- lines), i is the intensity of selection ($i = 1.81$ on average, representing 9.55 % of
 205 selection pressure on average), σ_p is the standard deviation of phenotypic values, r is the
 206 genetic relationship ($r=1/2$ with full-sib families), n is the mean number of individuals in each
 207 family and t is the intra-class correlation of phenotypic values of members of the families,
 208 estimated as $t = 1 - (\sigma_w^2/\sigma_t^2)$ with σ_w^2 and σ_t^2 being the within-family and total variances.

209

210 **3. Results**

211 3.1. Basic statistics

212 Fish were phenotyped for FCR at the juvenile stage (Tables 1 and 2) with an average initial
213 weight (BW_i) and final weight (BW_f) of 12.2 ± 4.20 and 14.8 ± 5.02 g. This represents an
214 average individual daily growth of 0.38 ± 0.19 g and an average daily FI of 0.33 ± 0.13 g.
215 Combining all generations and lines (N = 993), the FCR averaged 0.97 ± 0.35 , with a CV of
216 36.3%, comparable to that of the weight measurements.

217

218 3.2. Response to selection and genetic parameters

219 The selection response was first estimated by comparing the LSmeans of the two selection
220 lines (FCR+, FCR-) across generations (Figure 2). There was a large year effect on FCR,
221 which affected both lines: the overall FCR decreased in generation 1, and increased in
222 generation 2. However, after two generations of selection (actually, one and a half
223 generations, as the females were not phenotyped and selected at the G₀ generation), FCR
224 differed significantly (P = 0.01) between line FCR+ (1.08) and line FCR- (0.96) lines,
225 corresponding to a 12 % difference of FCR between both lines. Thus, the divergence between
226 the two lines occurred as expected. When we looked at the genetic trends (the average EBVs
227 of each line in each generation for each trait - Table 2), the divergence was smaller, as
228 $\log(\text{FCR})$ was increased by 0.012 in line FCR+ in G₂ while it decreased by 0.017 in line
229 FCR-, which corresponds to a ≈ 3 % difference.

230 The present selection experiment also had impacts in terms of DWG and DFI, with a
231 reduction in DFI in both lines, with a stable DWG for the FCR- line and a decreased DWG in

232 the FCR+ line (Figure 2). Considering the genetic trends, the tendency was clearly divergent,
233 with a decrease of both DWG and DFI in the FCR+ line, and an increase of both traits in the
234 FCR- line (Table 2).

235 Genetic parameters and phenotypic correlations for growth, DFI and FCR are presented in
236 Table 3. With the exception of FCR for which heritability was limited (0.10 ± 0.05),
237 heritability estimates were different to 0 and moderate to high, ranging from 0.27 ± 0.07 for
238 DWG to 0.53 ± 0.07 for BWi.

239 For all traits, the genetic correlations were consistent with the phenotypic correlations, except
240 between DFI and FCR, where the genetic correlation was much more negative than the
241 phenotypic correlation, albeit with a high standard error ($r_g = -0.43 \pm 0.25$ vs. $r_p = -0.05$).

242 Body weight (initial and final), DWG and DFI were significantly and highly correlated. Feed
243 conversion ratio was negatively genetically correlated with DWG ($r_g = -0.69 \pm 0.16$). The
244 estimate for the realized heritability of FCR ($h^2_R = 0.19$) was higher than the mixed model
245 estimate for the same trait (0.10 ± 0.05).

246

247 **4. Discussion**

248 The overall objective of the present study was to evaluate the response to direct selection for
249 improved FCR in Nile tilapia, following previous research that showed 1) the ability to
250 accurately measure individual FCR in this species in using video-assisted technology (de
251 Verdal et al 2017), and 2) the existence of significant genetic variation for this trait (de Verdal
252 et al., 2018). To our knowledge, this is the first study to evaluate the realised response to
253 direct selection for FCR on FCR, growth and feed consumption in fish. For this purpose, two
254 divergent lines were selected for high or low FCR during two generations. The genetic
255 parameters of the traits were estimated in the two generations pedigree, and the response to

256 selection was evaluated, both as the phenotypic difference between lines and as the
257 divergence in breeding values, estimated with a mixed model. Due to logistical limitations,
258 the selective breeding programme conducted in this study was only a proof of concept, with a
259 small number of families, and focused only on the juvenile stage.

260 The average individual FCR measured in the different generations of the present study ($0.97 \pm$
261 0.35) on about 1,000 fish was close to previous FCR estimates made on the GIFT (Genetically
262 Improved Farmed Tilapia, Ponzoni et al., 2011) strain of Nile tilapia. With the latter strain,
263 selected for more than 15 generations for improved growth, de Verdal et al. (2018b) estimated
264 that the average individual FCR measured at a juvenile stage was 0.94 ± 0.21 . Although we
265 used a cross between two populations (as it was not possible to import extra-European tilapia
266 germplasm in the facility), the average FCR in our experiment was thus close to that of the
267 most common commercial line, and thus is industry relevant.

268 After an equivalent of 1.5 generation of divergent selection for FCR (as only F0 males were
269 selected in the base population), a difference of 12% was shown for FCR between FCR- and
270 FCR+ lines. If we consider that the response was symmetrical to the initial FCR of the G0
271 generation, the realised gain per generation when compared to the mean G0 FCR of the line
272 can then be estimated to be 6% for 1.5 generation and thus 4 % per generation. Selection
273 response in divergent selection is expected to be symmetrical, although this is not always the
274 case in practice (see e.g Aggrey et al., 2003), especially in short term selection experiments
275 where stochasticity of response can be high (Nicholas, 1980; Pélabon et al., 2021). Ideally, as
276 the practical aim of selection for FCR is to decrease FCR relative to its present value, we
277 should have compared the FCR- line to an unselected control line. However, as we expected a
278 low to moderate difference between lines, this would have increased the risk of not being able
279 to identify significant differences between the lines. Thus, we chose the divergent selection
280 approach, which yields higher differences, at the cost of the uncertainty regarding the

281 symmetry of response. When we evaluated selection response as the average EBV for logFCR
282 of each group, the divergence was +0.012 in G2 for line FCR+, and -0.017 in for line FCR-,
283 thus a $\approx 3\%$ divergence, which was symmetrical as expected (and thus, the improvement in
284 that case can be estimated to be 1% per generation for directional selection). The lower
285 divergence observed on EBVs could be due to the lack of pedigree information on the animals
286 from the FishGen males and Cirad females base populations, which are considered a random
287 sample of unrelated individuals from the same base population in the animal model, while it is
288 quite clear that they are from a limited number of (unknown) families, and that males and
289 females from generation G0 are not from the same population. Another possible reason could
290 be that as there is only one family per aquarium in G1 and G2 (but two aquariums per family),
291 the animal model estimate may be biased by suboptimal separation of family and permanent
292 environmental effects.

293 Under the symmetrical response hypothesis, the 4% improvement of phenotypic FCR per
294 generation can be considered an important gain, with a potential major economic impact.
295 With 2.8-3.7 million metric tons of feed consumed each year by the Nile tilapia industry
296 worldwide (de Verdal et al., 2017), these 4% would represent 112.000-148.000 tons of feed
297 saved each year, and thus a major economic benefit. Even with the conservative 1%
298 improvement per generation estimated with the animal model, the impact at the global level
299 would still be major, especially considering this will be a cumulative impact when generations
300 of selection will increment on each other.

301 In the present study, the realized heritability of FCR ($h_r^2 = 0.19$), was higher than that
302 estimated with the animal model (0.10 ± 0.05), probably for the same reasons of limited
303 deepness of the pedigree and partial confusion of family and environment effects, as
304 discussed above, that limit the genetic gains estimated with the animal model. Genomic

305 information could have been useful here both to assess the real genetic relationship between
306 G0 individuals and to better use within-family variance data to improve heritability estimates.

307 The realized heritability of FCR was in the lower range of previous heritability estimates
308 obtained in the GIFT strain of Nile tilapia using video recording and pedigree-based models
309 of 0.32 ± 0.11 and 0.21 ± 0.09 (de Verdal et al., 2018b; Barria et al., 2021) or in European sea
310 bass *Dicentrarchus labrax* using individual rearing (0.25, Besson et al., 2019). They are close
311 to estimates in the GIFT strain of Nile tilapia using video recording and genomic-based
312 models (0.12 ± 0.06 , Barria et al., 2021) and higher than estimates in salmonids obtained with
313 the X-ray method (0.04-0.07 in Quinton et al., 2007; 0.07-0.10 in Kause et al., 2016).

314 Furthermore, our heritability estimate for DWG (0.27 ± 0.07) was close to estimates on body
315 weight gain from previous study on the GIFT strain of Nile tilapia in the same type of
316 experimental settings (0.27 ± 0.08 in de Verdal et al., 2018b). The reason why realized
317 heritability, and even more animal model heritability across generations, was lower than the
318 single generation estimates obtained in Nile tilapia (0.21-0.32, see before) could be due to the
319 fact that selection was performed on the ratio (FCR), which is known not to be optimal, as
320 variation in a ratio can be obtained from different combined variations of its component traits
321 (DFI and DWG) as highlighted by several authors (Lin, 1980; Gunsett, 1984, 1987; Lin and
322 Aggrey, 2013). Indeed, it is not uncommon that selection on a ratio yields lower response than
323 expected from the genetic parameters of the ratio (see e.g. Webb and King, 1983, for FCR in
324 pigs, Campo and Rodríguez, 1990, for the egg mass to body weight ratio in *Tribolium*
325 *castaneum*, or Vandeputte et al., 2019, for fillet yield in rainbow trout *Oncorhynchus mykiss*).

326 Divergent selection also had a significant impact on DFI and DWG, which are the component
327 traits of FCR, as $FCR = DFI / DWG$. Phenotypic DWG was stable over generations in the
328 FCR- line and decreased in the FCR+ line, while DFI decreased in both lines. However, the
329 genetic trends for DWG and DFI showed a different picture, with an increase of both traits in

330 the FCR- (efficient) line, and a decrease of both in the FCR+ line (Table 2). This shows that
331 the phenotypic trends shown in Figure 2 are likely due to fixed effects of year on the
332 measurement, which are clearly visible for FCR, which goes down in the first generation then
333 increases in G2. For DFI or DWG, the year effects are not clearly visible on Figure 2, but do
334 exist, as phenotypic response is not symmetrical in the FCR- and FCR+ lines, as would be
335 expected. The divergent EBVs for DFI and DWG in the FCR+ and FCR- lines are also in
336 agreement with the negative genetic correlation of both traits with FCR. There was a negative
337 genetic correlation of DWG with FCR (-0.69 ± 0.16), similar to other results in obtained in
338 Nile tilapia by Barria et al. (2021) using genomic-based models ($r_g = -0.60 \pm 0.16$). However,
339 with the GIFT strain, de Verdal et al. (2018b) did not find significant genetic correlations
340 between growth and FCR using pedigree-based model. The decrease of DFI across
341 generations was substantial in both lines, which was not expected given the negative
342 (although non-significant) genetic correlation between DFI and FCR (-0.43 ± 0.25). When
343 looking at the genetic trends, there was a decrease in DFI in the FCR+ line, but an increase in
344 the FCR- line (Table 2), again highlighting the fact that the general decreasing trend in both
345 lines was probably caused by fixed effects of year on the measurements as the experimental
346 protocol which may have been marginally modified. Still, it has to be highlighted that an
347 opposite (positive) genetic correlation between DFI and FCR was found with the GIFT strain
348 ($r_g = 0.67 \pm 0.15$; de Verdal et al., 2018b) in a previous study, while in the recent study by
349 Barria et al. (2021) using genomic-based models, the genetic correlation between FCR and FI
350 is also positive ($r_g = 0.24 \pm 0.25$), although not significant.

351 All in all, our results show that selection for low FCR caused an increase in growth rate, and it
352 can thus be expected that selection for faster growth rate would also lead to improvements in
353 FCR in Nile Tilapia as also highlighted by the negative genetic correlation between DWG and
354 FCR. Improvement of FCR through selection for a better growth has also been reported in

355 different livestock species (Emmerson, 1997; Knap and Kause, 2018) and the response is
356 higher when considering at the same BW (and not the same age). However, in tilapia, the
357 abundant literature on response to selection for growth (Bolivar and Newkirk, 2002; Ponzoni
358 et al., 2005; Charo-Karisa et al., 2006; Thodesen et al., 2012; Thodesen (Da-Yong Ma) et al.,
359 2013; Thodesen et al., 2013; Bentsen et al., 2017) has never reported changes in FCR,
360 probably because it is difficult to precisely estimate in the production environment.

361 The interest of selecting for FCR directly or through indirect selection for growth can be
362 evaluated through the relative efficiency of selection (RES) with the growth predictor, defined
363 as $RES = h_1 |r_A|$ where h_1 is the square root of the heritability of the predictor, and $|r_A|$ is the
364 absolute value of the genetic correlation existing between the predictor and FCR (Vandeputte
365 et al., 2017). Using the genetic parameters from Table 3, the RES for BW_i is 0.11, while the
366 RES for DWG is 0.36. This means that for a same selection intensity, FCR improvement
367 through selection for BW will be only 11% of that obtained with direct selection for FCR, and
368 this will rise to 36% if selection is performed on DWG. Of course, it is much easier to
369 evaluate a large number of fish for BW or DWG than for individual FCR, thus selection can
370 be stronger. If the selection intensity differs between direct selection for FCR and indirect
371 selection, the relative response (RR) between direct and indirect selection will be
372 $RR = RES \cdot i_{IND} / i_{FCR}$, with i_{IND} the selection intensity with the indirect trait, and i_{FCR} the
373 selection intensity for direct selection with FCR. If we consider a reasonable selection
374 pressure of 0.20 for direct selection for FCR, the value of i_{FCR} would be 1.40. A very strong
375 selection for growth (1%) would correspond to $i_{IND} = 2.67$. With such values, the relative
376 response in FCR with BW_i would be 21% of that obtained with direct selection for FCR, and
377 would reach 69% with DWG. The interest of choosing one option or another will depend on
378 economic evaluation, but it is clear that direct selection for FCR has to be considered if FCR
379 is the breeding goal. In any case, selection for growth is applied in all fish breeding programs

380 (Chavanne et al., 2016) and should thus result at least in tilapia in indirect improvement of
381 FCR.

382 The method developed by de Verdal et al. (2017) and used in the present study was accurate
383 in measuring the FI of fish for several consecutive days. A positive aspect of this method is
384 that it allows fish to maintain social interactions with each other, which seems to be
385 important in Nile tilapia. With this species, it has been previously shown that FCR measured
386 at the individual level in isolation, method described in Besson et al.(2019), was not
387 significantly correlated with FCR measured using the video methodology (Rodde et al.,
388 2021). However, the negative aspect is that this method is particularly time-consuming as it is
389 necessary to feed the fish pellet by pellet, and then it is essential to analyse all the videos of
390 the meals. Improvements to add FCR to breeding programmes could be to simplify the video
391 analyses method using machine learning and convolutional neural networks. Such automation
392 of video analysis could greatly speed up the method and provide a real opportunity to improve
393 FCR in several aquaculture species.

394 Another constraint is related to the fish species chosen for this breeding programme. Nile
395 tilapia has the advantage of growing faster than most of the aquaculture fish species, but the
396 main disadvantage is that it is not possible, to our knowledge, to synchronize spawning date
397 efficiently. This reduces the possibility to develop factorial designs and contemporaneous
398 families, and therefore common-garden rearing practices are not recommended, as not all fish
399 are at the same stage of development, and cannibalism could occur if different families are
400 mixed at different body weight. This is a real problem as it is not possible in many cases to
401 distinguish the common environmental effects from the effects of variation between families.
402 An alternative is to index only males for which sperm is more easily available during several
403 weeks, but this compromise limits selection pressure to the male pathway by 50 %.

404 The present experiment was carried out on juvenile Nile tilapia rather than on adult fish even
405 though adults consume more feed and the financial cost of feed is higher for rearing adults
406 than juveniles. The genetic correlation between juvenile and commercial sizes need to be
407 estimated to transfer our results to bigger sizes. We first relied on the study by Rodde et al.
408 (2020) estimating that the FCR measured at juvenile stage (36 g) was correlated with the FCR
409 measured during the whole rearing period, from 36 to 260g body weight on average. But there
410 are several other logistical reasons for this choice: i) Nile tilapia mature early before
411 commercial BW and breed at a young age (Coward and Bromage, 2000) and females keep
412 their eggs and free-swimming fry in their mouths for about a week without eating (Coward
413 and Bromage, 2000). It is therefore important, in the case of mixed groups, to conduct
414 experiments before the maturation stage; ii) the volume of water (i.e. aquarium size) required
415 to rear Nile tilapia is smaller when studying juvenile fish rather than adults. With a limited
416 facility size, it was preferable to choose to phenotype a larger number of juvenile fish than a
417 smaller number of larger fish; and iii) as all meals were video-recorded and video were
418 analysed to count the number of pellets eaten by each fish, it was preferred to focus on
419 juvenile fish, eating less in quantity than adults, even though adults ate larger pellets.

420 It may now be interesting to compare the performance and feed efficiency related traits of
421 FCR+ and FCR- lines reared in large groups in tanks to better evaluate the potential of such
422 selection programme. Another future area of development would be to evaluate the impact of
423 such selection in other Nile tilapia rearing environment, i.e. in large groups in earthen ponds
424 or in recirculated systems. The selection environment, small groups reared in aquarium was
425 rather different from the classical rearing environment and it is thus questionable how
426 important the interactions between genetics and environment are.

427 This work provides favourable results for future experiment with more family to estimate
428 genetic parameters and accuracy estimated breeding values in keeping inbreeding to an
429 acceptable level.

430 **5. Conclusion**

431 Improving FCR in fish through genetics is feasible. After only 1.5 equivalent generations of
432 selection for this trait, a phenotypic divergence of 12 %, and a breeding value difference of
433 3% were observed between more efficient and less efficient lines, in a proof of concept
434 selective breeding programme with a reduced number of fish and families phenotyped in each
435 generation. If confirmed at a larger scale, selection for FCR could be greatly improved in Nile
436 tilapia, substantially and positively influencing the sustainable production of this fish species,
437 the second fish species consumed in the world. The transfer of video-assisted technology to
438 improve FCR will probably need adaptation to potential interspecific difference in feeding
439 behaviour, size or social interaction.

440

441 **Author contributions**

442 HDV designed the experiment; HDV and VD performed the experiment; HDV and MV
443 analysed the data; HDV, PH and MV wrote the manuscript. All authors read and approved the
444 final manuscript. All authors contributed to the article and approved the submitted version.

445

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449

450 **Conflict of interest**

451 The authors declare that they have no conflict of interest.

452

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456

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618 Table 1 – Basic statistics: Number measured (N), Mean± standard deviation (StdDev),
619 minimum (Min), maximum (Max) and raw coefficient of variation (CV) of all the traits
620 measured during the experiment.

Trait ¹	N	Mean ± StdDev	Min - Max	CV (%)
BWi	1,043	12.3 ± 4.29	4.15 - 28.2	34.9
BWf	1,030	14.9 ± 5.13	4.58 - 32.9	34.4
DWG	1,012	0.38 ± 0.19	0.003 – 1.03	48.3
DFI	1,010	0.34 ± 0.13	0.08 – 0.70	38.2
FCR	997	0.97 ± 0.35	0.30 - 2.49	36.3

621

622 ¹BWi : body weight in g at the beginning of the FCR measurement period; BWf: body weight
623 in g at the end of the FCR measurement period; DWG: daily body weight gain in g during the
624 FCR measurement period; DFI: daily feed intake in g during the FCR measurement period;
625 FCR: feed conversion ratio measured as the ratio between DFI and DWG.

626

627

628 Table 2 –Phenotypic mean (\pm standard deviation) and average estimated breeding values
 629 (EBV, in italics) of all the traits measured during the experiment for each generation and line.
 630 Phenotypic values (Pheno) are on untransformed data, estimated breeding values on
 631 transformed data (square root for DWG and DFI, natural logarithm for BWi, BWf and FCR)

Generation	Line		BWi ¹	BWf	DWG	DFI	FCR
0	Base pop	Pheno	14.2 \pm 4.54	17.1 \pm 5.27	0.41 \pm 0.15	0.41 \pm 0.12	1.06 \pm 0.31
		<i>EBV</i>	<i>0.001</i>	<i>0.001</i>	<i>0.001</i>	<i>0.001</i>	<i>0.000</i>
1	FCR+	Pheno	10.6 \pm 2.94	13.1 \pm 3.62	0.35 \pm 0.18	0.28 \pm 0.10	0.88 \pm 0.35
		<i>EBV</i>	<i>-0.002</i>	<i>-0.007</i>	<i>-0.017</i>	<i>-0.007</i>	<i>0.009</i>
2	FCR+	Pheno	10.4 \pm 3.49	12.0 \pm 4.04	0.27 \pm 0.16	0.26 \pm 0.10	1.08 \pm 0.43
		<i>EBV</i>	<i>-0.008</i>	<i>-0.013</i>	<i>-0.025</i>	<i>-0.010</i>	<i>0.012</i>
1	FCR-	Pheno	12.1 \pm 3.66	15.1 \pm 4.52	0.42 \pm 0.19	0.32 \pm 0.11	0.85 \pm 0.30
		<i>EBV</i>	<i>0.031</i>	<i>0.030</i>	<i>0.019</i>	<i>0.005</i>	<i>-0.008</i>
2	FCR-	Pheno	11.8 \pm 4.93	14.6 \pm 6.10	0.40 \pm 0.23	0.33 \pm 0.13	0.95 \pm 0.37
		<i>EBV</i>	<i>0.059</i>	<i>0.063</i>	<i>0.052</i>	<i>0.030</i>	<i>-0.017</i>

632 ¹BWi: body weight at the beginning of the FCR measurement period; BWf: body weight at
 633 the end of the FCR measurement period; DWG: daily body weight gain during the FCR
 634 measurement period; DFI: daily feed intake during the FCR measurement period; FCR: feed
 635 conversion ratio measured as the ratio between DFI and DWG.

636

637

638 Table 3 – Estimates (\pm standard error) of heritability (highlighted in grey, on the diagonal),
639 genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for
640 measured traits. DWG and DFI were square-root transformed, BWi, BWf, FCR were log-
641 transformed

Trait ¹	BWi	BWf	DWG	DFI	FCR
BWi	0.53 \pm 0.07	0.99 \pm 0.003	0.71 \pm 0.09	0.75 \pm 0.06	-0.15 \pm 0.21
BWf	0.98	0.48 \pm 0.07	0.79 \pm 0.06	0.81 \pm 0.05	-0.26 \pm 0.20
DWG	0.58	0.74	0.27 \pm 0.07	0.94 \pm 0.04	-0.69 \pm 0.16
DFI	0.56	0.66	0.75	0.41 \pm 0.07	-0.43 \pm 0.25
FCR	-0.25	-0.38	-0.68	-0.05	0.10 \pm 0.05

642 ¹BWi : body weight at the beginning of the FCR measurement period; BWf: body weight at
643 the end of the FCR measurement period; DWG: daily body weight gain during the FCR
644 measurement period; DFI: daily feed intake during the FCR measurement period; FCR: feed
645 conversion ratio measured as the ratio between DFI and DWG. Bold indicates that the
646 estimate significantly differs from zero.

Figures

Figure 1- Selective breeding scheme performed to develop divergent lines selected for their low (FCR- in orange) and high (FCR+ in blue) FCR.

Figure 2 – LSmeans (\pm standard error) of DWG, DFI and FCR according to the line (FCR+ in black, FCR- in grey) and the generation (0 to 2). Error bars represents the standard error of the LSmeans. Asterisks show the significant difference between lines at each generation.

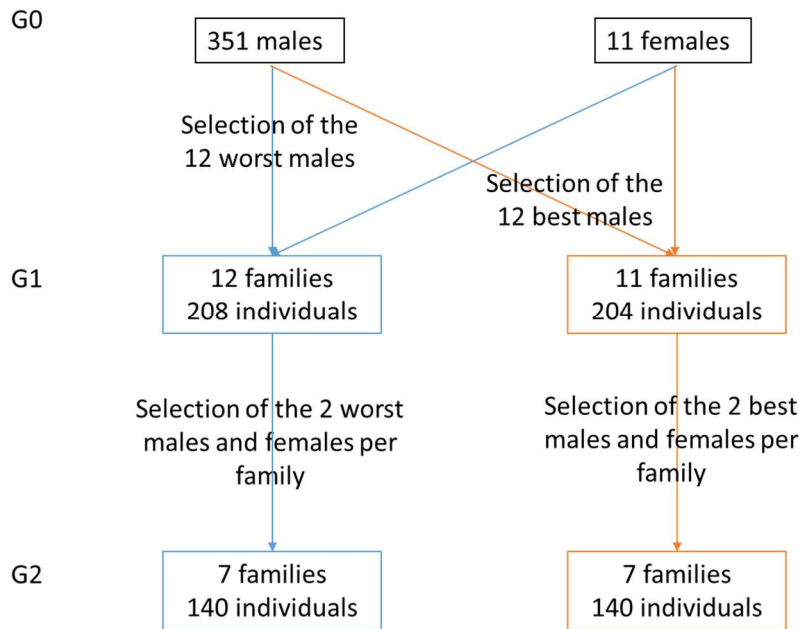


Figure 1

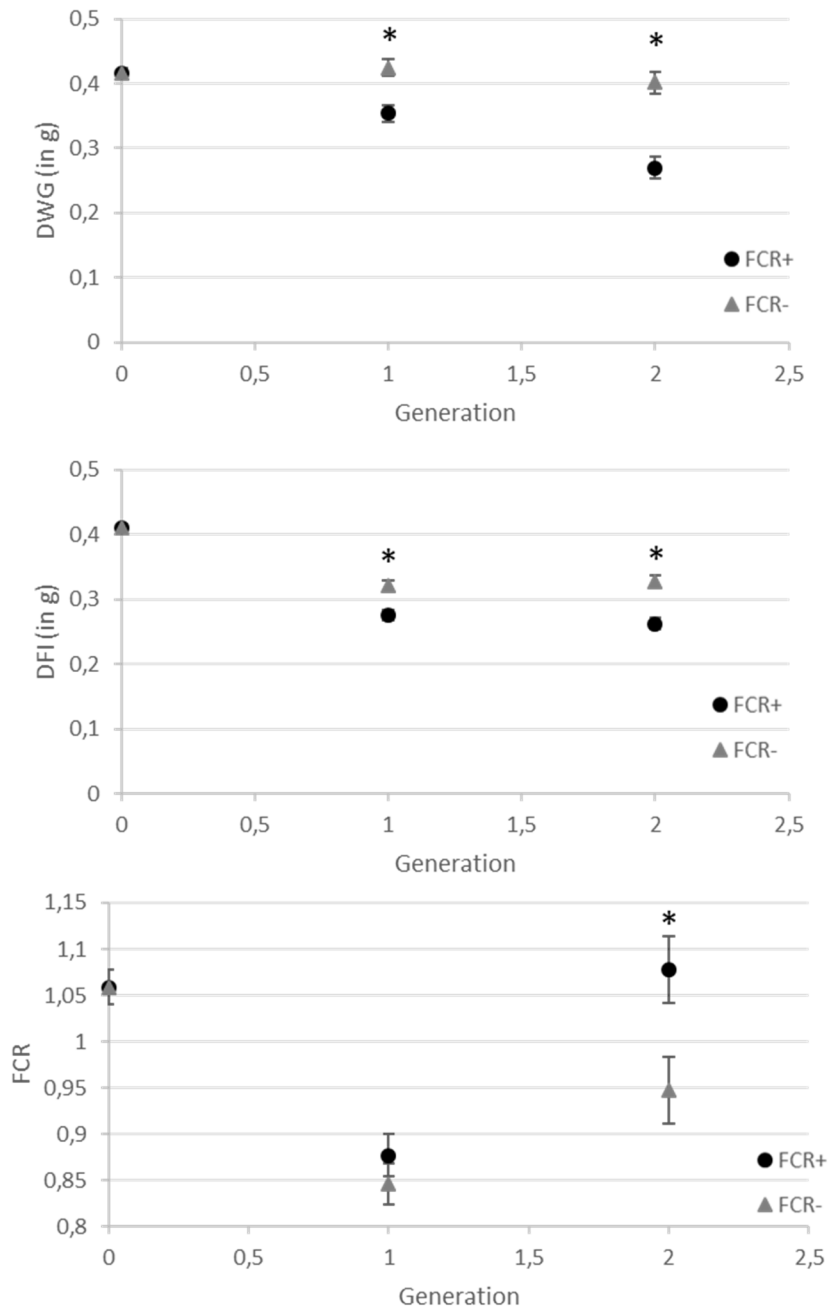


Figure 2