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1 **Measuring individual feed efficiency and its correlations with performance traits in Nile**
2 **tilapia, *Oreochromis niloticus***

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25 ABSTRACT

26 Estimating individual feed intake of fish held in groups has long been a challenge precluding
27 precise knowledge of the individual variation of feed efficiency (FE) in fish. In this study,
28 counts of the number of feed pellets (1.63 mg on average) eaten by individual tilapia
29 (*Oreochromis niloticus*) held in 8 mixed sex groups of 15 fish were measured from video
30 recordings made over a period of 10 days where fish were fed twice daily to achieve
31 compensatory growth after 10 days of fasting. The initial body weight of the fish was $9.77 \pm$
32 2.03 g. Accumulated measures of feed intake (FI) over 11 meals were found to achieve 95%
33 repeatability and a high accuracy of estimation of FI. During the FI measurement period, the
34 average fish growth was 12.0 ± 3.6 g, feed intake was $0.99 \text{ g}\cdot\text{day}^{-1}$, and feed conversion ratio
35 (FCR) was 0.86 ± 0.20 . FI differences accounted for 56 % of the observed individual growth
36 variations, and 44 % was related to individual variations of FE. On average males grew 24.2
37 % faster than females but consumed 12.1 % more feed. Males showed an 11.7 % better FCR
38 than females, whereas residual feed intake (RFI) differences were not significant between
39 sexes. FCR and RFI were moderately and significantly correlated (0.58 ± 0.06) but FCR and
40 FI, and body weight gain (BWG) and RFI, were not, highlighting the complex relationships
41 between feed efficiency traits. The approach described here demonstrates a means to
42 accurately investigate FE traits in fish and to assess the potential for their genetic
43 improvement.

44

45 *Keywords:* feed efficiency, sex, repeatability, Nile tilapia, feed conversion ratio, growth, feed
46 intake

47

48

49 **Highlights**

50

51 - This is the first study to estimate FE traits of individual fish reared in group for an extended
52 and continuous period of time.

53 - Provides the first accurate estimate of the phenotypic correlation between RFI and FCR in
54 fish

55 - Feed intake and feed efficiency traits between individual tilapias are highly variable

56 - Phenotypic differences of feed conversion ratio between males and females are significant.

57

58 1. Introduction

59 Aquaculture is playing an increasingly important role in fish supply with growth of farmed
60 fish production greater than 1.9 % per year since 1950 (Earth Policy Institute, 2013). Fish
61 farming will play a vital role in meeting future demand (FAO, 2016). Fish have a greater feed
62 efficiency (FE), the weight gain of animals per unit of feed consumed, compared with other
63 livestock species (Brown, 2006). However, the cost of feed, ranging from 50 to 70 % of the
64 total production cost, is still the largest single expenditure in intensive fish farming systems
65 (Bernier and Peter, 2001; Doupé and Limbery, 2004). Improving fish FE would thus reduce
66 production costs but also environmental impacts caused by uneaten feed and animal waste.
67 Consequently, it would contribute to both the economic and the environmental sustainability
68 of farmed fish production (Besson et al, 2016). Selective breeding could be an efficient way to
69 improve FE, but is not implemented in fish. As a prerequisite for its efficient development is
70 the capacity to measure or at least, estimate FE at the individual level.

71 Measuring individual FE requires accurate measurement of individual feed intake (FI) during
72 a given period of time during which body weight gain (BWG) is also measured. Most work on
73 FE has been done on individual fish kept separately to allow measurement of feed intake
74 (Martins et al, 2011). However, for realistic assessments of FE it is necessary to undertake
75 assessments of fish kept in groups since social interactions between fish can have large
76 influences on feeding behaviour (McComish, 1971; Hayward et al., 2000), and fish are
77 normally reared collectively in production systems. The most advanced approach currently
78 used to estimate individual FI of fish reared in a group is the use of X-radiography in which
79 X-ray dense markers (generally radio-opaque ballotini glass beads) are included in the feed
80 pellets (Talbot and Higgins, 1983; McCarthy et al., 1993; Silverstein et al., 2001; Jobling et
81 al., 2001; Boujard et al., 2006; Kause et al., 2006a; Quinton et al., 2007a, b; Grima et al.,
82 2008). Fish are X-rayed shortly after being fed this labelled feed, allowing the number of

83 pellets consumed by each fish to be counted. However, the number of times these
84 measurements can be made is limited by the need of anaesthetising and handling the fish each
85 time they are X-rayed, and in any case this method only permits to estimate feed intake on a
86 restricted number of meals over a period of growth where BWG is measured. As a result,
87 individual FI over the period can only be estimated using the average of the few meals
88 sampled. As there is low repeatability of measurements of X-ray method, (Kause et al, 2006a;
89 Grima et al., 2008) this raises questions about its accuracy and relevance.

90 This led some researchers to investigate potential indirect individual predictors of FE, such as
91 weight loss at fasting and compensatory growth, which were shown to be correlated to FE in
92 rainbow trout *Oncorhynchus mykiss* (Grima et al, 2008) and European sea bass *Dicentrarchus*
93 *labrax* (Grima et al, 2010).

94 Alternatively, FI can be measured for each fish by counting the number of pellets eaten during
95 a given time span. External individual identification of each fish is needed and care has to be
96 taken concerning the presence of observers as this can influence feeding behaviour. Video
97 recording the number of feed pellets eaten by each fish has been mentioned as an approach
98 that could address the issue of the presence of observers some time ago (Jobling et al. 2001).
99 However, this technique appears to have been rarely used for FI measurement in an
100 aquaculture context (Kadri et al., 1996) but has been used for analysing fish behaviour, for
101 example, on choice of feeds or effect of aggressive interactions on feed intake (Hart and
102 Salvanes, 2000; Goldan et al., 2003).

103 We used this approach to estimate individual FI and to calculate estimates of FE and
104 phenotypic correlations with performance traits in Nile tilapia *Oreochromis niloticus*,
105 comparing data for males and females, which shown strong differences in growth. The
106 development of accurate methods to estimate individual FE and knowledge of the relation
107 between growth and FE variables are necessary for assessing the feasibility of genetic

108 selection as a means of improving of FE. The specific objectives of the present study were 1)
109 to determine the minimum number of meals to be measured to have an accurate estimate of FI
110 and FE of individual fish over an extended period 2) to measure FI and FE and their
111 relationships, estimating the differences between males and females and 3) to estimate the
112 relationships between FE and other performance traits, especially weight loss at fasting and
113 compensatory growth which were previously shown to be indicator traits of individual FE.

114

115 2. Material and Methods

116 2.1. Rearing of fish

117 The study was carried out on the GIFT strain of Nile tilapia produced by natural spawning in
118 December 2014 by WorldFish at the Jitra Research station, Malaysia. After hatching, larvae
119 were kept in hapas in ponds until their transfer to the Penang WorldFish station where they
120 were reared until the fry reached approximately 10 g of body weight. After a one-week
121 quarantine in tanks, 120 fish weighing 9.77 ± 2.03 were dispatched to 8 aquaria in a
122 recirculating water system, with 15 fish per 100 L indoor tanks (120 cm length, 35 cm width
123 and 24 cm depth). The recirculating system included a biological and sand filters, with a
124 renewal water rate at 100 % per hour and constant aeration. The average temperature was 28
125 $\pm 1^\circ\text{C}$ and the photoperiod 12L:12D. Two coloured T-bar tags (Avery Dennison tags, 25mm)
126 were inserted in each fish (using an Avery Dennison Mark III pistol Grip tool) in the dorsal
127 muscle, close to the dorsal fin, after the fish had been anaesthetized with clove oil. A different
128 colour combination was used for every fish within an aquarium so that each fish could be
129 individually identified. The needles used to insert the tags were cleaned with alcohol between
130 each fish. Fish were fed a commercially available tilapia feed (34% crude proteins, 5% crude
131 fat, 5% crude fiber and 12% moisture) at a daily rate calculated according to M elard et al.
132 (1997) as follows:

133
$$DFR = 14.23 * BW^{-0.322} \quad [1]$$

134 where DFR is the daily food ration, expressed in % of body weight (BW) per day and BW is
135 the average body weight of the fish within each aquarium. Mortality was recorded daily and
136 feed ration changed accordingly. Fish were not fed until apparent satiation because this
137 method is widely variable from a person to another which reduce repeatability of the
138 experiment and increase the aquarium effect.

139

140 2.2. Feed intake measurements and analyses

141 After an adaptation period of two weeks in aquaria, fish were anaesthetized with clove oil and
142 weighed. A period of 10 days of fasting was followed by a period of 17 days where fish were
143 fed twice daily to achieve compensatory growth. Ten days of fasting was decided after pre-
144 experiment testing the mortality rate after several days of fasting, and was in accordance with
145 Wang et al. (2009). At the end of both fasting and compensatory growth periods, fish were
146 anaesthetized with clove oil and their BW measured. The loss of weight during the fasting
147 period was calculated as the difference in BW between the beginning and the end of this
148 period and from hereon is referred to as 'LOSS'. In the same way, the gain in BW during the
149 compensatory growth period was calculated as the difference of BW between the beginning
150 and the end of this period, which was also the beginning of the individual evaluation period
151 (BW_i) and from hereon is referred to as 'COMP'. After the compensatory growth period, FI
152 was recorded for each fish over a period of 10 days to estimate FE traits. During this
153 individual FI measurement period, feed was delivered to each aquarium pellet by pellet by
154 hand through two pipes in view to reduce the proximity between the experimenter and the
155 aquarium, twice daily at 7.00 am and 1.00pm (except for the first day where fish were
156 weighed the morning, and fed only once in the afternoon) until the calculated feed ration was

157 distributed. Each meal was video recorded and individual FI was then calculated by video
158 analyses counting the number of pellets eaten by each fish for each meal. After 10 days of FI
159 measurement (19 meals), fish were anaesthetised with clove oil and weighed (BWf). The
160 body weight gain (BWG) during the individual FI measurement period, was calculated as the
161 difference between BWf and BWi. The day after the end of the FI measurement period, fish
162 were anaesthetised and killed by decapitation, and sexed by visual observations of the gonads.
163 The video analyses were performed using Kinovea 0.8.15 software (Copyright © 2006-2011 –
164 Joan Charmant & Contrib.), which provided the capability to increase or reduce the speed and
165 to zoom in or out for more detailed observation of an event. For each aquarium, 19 meals
166 were recorded, each fish then having 19 FI values, one per meal. As pellet weight variability,
167 in terms of standard deviation (SD) and coefficient of variation (CV), was reasonably low
168 (Mean=16.4 ± SD=1.76 mg, CV = 10.7 %) it was assumed that each pellet had the same
169 weight, allowing the calculation of FI in grams for each meal. The total FI for an individual
170 was calculated as the sum of the FI of all meals consumed.

171 The feed conversion ratio (FCR=FI/ BWG) was used as an indicator of feed efficiency, which
172 is more commonly used than its inverse, the feed efficiency ratio FER=BWG/FI. The residual
173 feed intake (RFI) is defined as the difference between feed consumed by an animal and its
174 predicted consumption estimated by a regression model taking into account the feed
175 requirements for maintenance and growth as independent variables (Koch et al., 1963; Doupé
176 and Limbery, 2003; Martins et al., 2011). The equation used to estimate RFI was as follow:

$$177 \quad \text{RFI} = \text{FI} - \beta_0 - \beta_1 * \text{BW}^{0.8} - \beta_2 * \text{BWG} \quad [2]$$

178 with FI the feed intake, β_0 the regression intercept, β_1 the partial regression coefficient of
179 animal's FI on metabolic body weight, $\text{BW}^{0.8}$ the metabolic body weight using the metabolic
180 body coefficient developed by Lupatsch et al. (2003), β_2 the partial regression coefficient of

181 animal's FI on BWG, and RFI which corresponds to the residual of the model. Individuals
182 with positive RFI consume more than the average of fish with the same body weight and body
183 weight gain whereas animals with negative RFI consume less, suggesting the latter are more
184 efficient at converting feed to gain. The parameters of the regression equation were estimated
185 using the REG procedure of SAS (version 9.3, SAS Institute, Cary NC).

186

187 2.3. Statistical analyses

188 The normality of the data was tested using the Shapiro-Wilk test on R 2.15.3 software. All the
189 data were normally distributed except FCR and this trait was log transformed to match the
190 normal distribution.

191 The means, standard deviations and coefficients of variation (CV) were calculated using R
192 software (R Core Team, 2013).

193 To estimate the repeatability of the measurements, intra-class correlation coefficients (ICC),
194 indicating the part of the total phenotypic variance explained by permanent differences
195 between individuals were estimated. Package "ICC" (Wolak et al., 2012) under R software
196 was used for this analysis. This package allows an estimation of the ICC and the confidence
197 interval limit.

198 Using a Bayesian approach, the bivariate correlations between all studied traits were
199 estimated as well as all bivariate correlations between the FI of each individual fish for each
200 of the 19 meals. For the bivariate correlations, we assumed an inverse Wishart conjugate prior
201 distribution of the variance-covariance matrix. Package "rjags" (Plummer, 2011) under R
202 software was used for the analysis. The correlations between the total FI of all meals together
203 and FI for a specific number of meals ranging from 1 to 18 meals (randomly or consecutively

204 chosen) were also estimated. For all analyses, Gibbs sampling was used to estimate the
205 marginal posterior distributions of all parameters. A chain of 20,000 iterations was used, with
206 a burn-in of 2,000 iterations and lag of 10. A further 1,800 iterations were used for the
207 calculation of posterior means and posterior standard deviation of the correlations.

208 To assess the effect of sex on the studied traits, a model including the sex effect was used in a
209 Bayesian analysis. A bounded, flat prior was assumed for the sex effect, and a conjugate
210 inverse gamma distribution was assumed for the residual variance. The analyses were
211 performed using software written for the project. A chain of 60,000 iterations was used with a
212 burn-in of 10,000 iterations and lag of 10. A 50,000 iterations chain was used for the
213 calculation of the posterior means, posterior standard deviations and highest posterior density
214 at 95% (HPD_{95%}).

215 To test if the general model used to estimate RFI was applicable to both sexes, an
216 heterogeneity of slopes model was tested with the GLM (General Linear Model) procedure of
217 SAS (version 9.3, SAS Institute, Cary NC):

$$218 \quad FI_{ij} = \mu + S_i + \beta_1 * BW^{0.8} + \beta_2 * BWG + \beta_3 * (S_i)BW^{0.8} + \beta_4 * (S_i)BWG + e_{ij} \quad [3]$$

219 Where FI_{ij} is the FI of the fish j , μ is the general mean, S_i is the fixed effect of the sex i and
220 e_{ij} is the residual pertaining to fish j .

221

222 3. Results

223 3.1. Accuracy of the FI measurements

224 Given the average number of pellets eaten by an individual fish per meal was 31.8, the
225 average FI per fish and per meal was $31.8 * 16.4 = 522$ mg, and its standard error was
226 $1.76 * (31.8)^{0.5} = 9.92$ mg, or approximately 1.9 % of the estimated FI per meal. Furthermore,

227 the coefficient of variation of FI within a meal is estimated at 35.7% (Table 1). The posterior
228 means of the correlations between each meal taken separately were highly variable, ranging
229 from 0.09 to 0.70, with a mean of all the correlations of 0.45 ± 0.11 (Table SupplA).
230 To reach a correlation greater than 0.95 between the total FI in all 19 meals and an indicator
231 using the mean FI in only some of the meals, it was necessary to take into account 9
232 consecutive meals or 7 randomly chosen meals (Figure 1). The posterior standard deviation of
233 the correlation decreased with an increasing number of meals taken into account, from 0.06
234 for 1 meal to 0.01 for 9 meals, which shows an increase in the accuracy of the estimate when
235 more meals are measured.
236 The repeatability of this specific FI measurement was estimated with the ICC, which was
237 0.42. ICC was also calculated taking into account the meal of 2 to 19 meals, chosen randomly
238 or consecutively. Whether random or consecutive meals were taken into account, results were
239 similar. The repeatability is higher than 0.95 when 11 meals or more were averaged (Figure
240 2).

241

242 3.2. Impact of sex on feed efficiency traits

243 The differences between male and female were considered significant if the HPD_{95%} interval
244 of differences did not include 0, which is the case for LOSS, COMP, BWG, FCR, log FCR
245 and FI, but not for RFI (Table 2, Figure 3). Consequently, there is an important difference
246 observed between sexes for all variables except RFI. The impact of fasting is lower and gain
247 during compensatory growth is greater in males compared to females. On average, compared
248 to females, males gained 24.2 % more weight during the FI measurement period but
249 consumed only 12.1 % more feed. Males showed an 11.7 % better (lower) FCR compared to
250 females, whereas RFI differences were not significant between sexes.

251 The relation between observed and predicted FI (Figure 4) is similar between males and
252 females, with comparable slopes of the regression lines. This similarity is proven by the lack
253 of significance of all sex-linked effects in the heterogeneity of slopes test (model 3), with
254 $P > 0.60$ for the fixed effect of sex, $P > 0.91$ for the sex-specific regression coefficient on
255 metabolic body weight and $P > 0.44$ for the sex-specific regression coefficient on BWG.

256

257 3.3. Feed efficiency characteristics

258 During the fasting-refeeding challenge, fish lost on average 0.14 ± 0.03 g of BW per day
259 during the feed deprivation period and gained 0.94 ± 0.23 g of BW per day during the
260 compensatory growth period (Table 3).

261 During the full FI measurement period (10 days, 19 meals), fish growth was on average 12.0
262 ± 3.61 g (1.2 g.d⁻¹), with a CV of 30.2 %. The FCR was low, 0.86 ± 0.20 , which means that,
263 for each gram of feed consumed, the fish grew of 1.2 g but that there was wide variation
264 between fish in terms of individual FCR, as shown by the 23.4 % coefficient of variation, the
265 extremes being 0.56 and 1.78. The mean of RFI was zero as expected since the average is
266 considered as the base point to compare feed efficiency between fish. The metabolic body
267 weight $BW^{0.8}$ and BWG were both significant ($P < 0.0001$) in the regression equation for FI.

268 The general prediction equation of RFI was as follows:

$$269 \quad RFI = FI - 0.734 - 0.346 * BW^{0.8} - 0.325 * BWG$$

270 As expected, the correlation between BWG and FI was positive (0.74 ± 0.05 , Table3)
271 showing that there is significant variation in FCR. There was a significant negative correlation
272 between BWG and FCR (-0.62 ± 0.06), but not between BWG and RFI (-0.03 ± 0.10).
273 Neither the loss of weight during feed deprivation nor the gain of weight during the refeeding

274 period was correlated to any of the FE traits (Table 4). Gain of weight during the refeeding
275 period was correlated with BWG and FI. The correlations were not significant between FCR
276 (or logFCR) and FI, nor between BWG and RFI. The correlation between FCR and RFI was
277 positive but moderate (0.58 ± 0.06).

278

279 4. Discussion

280 4.1. Accuracy of the FI measurements

281 The first objective of the present study was to determine how many meals had to be measured
282 in order to accurately estimate FI over a given period of time, in order to accurately estimate
283 FE traits for individual fish held in groups. The most widely used method to date using X-ray
284 methods has a low repeatability (range 0.09-0.32) between two individual measurements in a
285 given experiment (Kause et al., 2006a; Grima et al., 2008). In the present study, the
286 repeatability of individual FI measurements was 0.42, better but still not accurate enough. The
287 repeatability and the overall accuracy of the estimation of FI were improved by taking several
288 meals into account. The repeatability between two meals and two other meals is 47.6 %
289 higher than between two single meals. In the present study, it was necessary to include
290 measurements of 58 % (11 out of 19 meals) of all meals given over the 10 day period to
291 achieve a repeatability of 95 %. This is regardless of whether consecutive or random meals
292 were considered. Further investigation is needed to understand how this may also vary for
293 different ages and species of fish, but is likely that preliminary experimentation will be
294 required to determine the optimum number of meals needed to be measured to ensure a given
295 level of accuracy in FI estimation for each particular circumstance.

296

297 4.2. Impact of sex on feed efficiency traits

298 Aquaculture of Nile tilapia is generally focused on all male production, for two main reasons.
299 The first one is the fact that a low proportion of females limits the unwanted increase of
300 population density into the ponds due to natural reproduction, which can occur quickly in
301 tilapia. The second reason is the existence of a sex dimorphism for body size in favour of
302 males (Lazard, 1980; Toguyeni et al., 1997, Lind et al., 2015), which is beneficial to
303 producers. The present results are in agreement with the general observation that males grow
304 faster than females and are in accordance with results of Toguyeni et al. (1997) who estimated
305 that the FCR of males was significantly better than that of females. It is interesting to
306 highlight that whereas males ate more than females, their FCR was significantly lower, due to
307 higher growth than females, confirming that from the perspective of FCR, it is more
308 beneficial to rear males than females with both an economic and an environmental benefit.

309 The links between sexual size dimorphism, FI and FE have not been studied until now, due to
310 the absence of reliable ways to estimate FI. Since FCR was only correlated to BWG and not
311 to FI, the differences of FCR between males and females are likely linked to the single growth
312 differences. This hypothesis is supported by the lack of significant differences between sexes
313 for RFI, which are not linked to the general prediction equation. This finding highlights the
314 fact that FCR and RFI are not the same trait and consequently, care needs to be taken in which
315 trait is targeted in attempting to genetically improve FE characteristics. According to several
316 studies, the differences in RFI can be essentially due to differences in maintenance
317 requirements (Luiting and Urff, 1991; Herd and Bishop, 2000; Martins et al., 2005). This
318 suggests that there is no difference of maintenance requirements between male and female
319 Nile tilapia in the present study, which is also reinforced by the non-significant difference of
320 the sex-specific partial regression coefficient for $BW^{0.8}$ in Model 3. In the same way, since
321 there are no significant differences for the sex-specific partial regression coefficient for BWG,
322 it can be hypothesized that the feed requirements for growth are not different in males and

323 females – and that the better FCR of males is just due to their faster growth, which
324 mechanically reduces the share of maintenance requirements in the use of the ingested feed. It
325 is also important to highlight that the variability of these feed efficiency traits is close between
326 males and females, which could be of interest for a genetic selection program on feed
327 efficiency traits since males and females would answer to the selection process. In future
328 studies, it would be of interest to measure these traits on older, mature fish to understand the
329 kinetics of FE traits in relation to age, sex and sexual maturity, and see if differential
330 maturation may, at some point, generate differences in FE between males and females.

331

332 4.3. Feed efficiency characteristics

333 The average daily gain was 1.2 g.day^{-1} , which is slightly greater than previously reported,
334 ranged from 0.7 to 1.06 (Siddiqui et al., 1991). This may be explained by the strain used in the
335 present study, the GIFT strain, which has been genetically selected for growth for more than
336 20 generations (Eknath et al., 2007; Ponzoni et al., 2011). Regarding FE traits, FCR ($0.86 \pm$
337 0.20) was in the lower range of previously published estimates on groups of tilapia, generally
338 ranging from 1.1 to 1.85 (El-Sayed and Kawanna, 2004; Koumi et al., 2011). It is not possible
339 to conclude that the differences between the estimates are explained by the protocol used to
340 measure FI (in group rather than in individual fish) as there were many differences between
341 these experiments (e.g. strain used, the age of fish used, the specific conditions of the
342 experiments).

343 Given that FE is the ratio between BWG and FI, it is important to consider the relationship
344 between these two traits. The determination coefficient r^2 of the linear regression between FI
345 and BWG is 0.56. This implies that FI differences accounted for 56 % of the observed
346 variance of individual growth, which means that the remaining 44 % were related to the

347 individual variation of FE. This relation between FI and BWG is lower than that previously
348 reported by Martins et al. (2011), who estimated $r^2 = 0.81$, but with individual FI
349 measurements on isolated fish, which omits the effects of social interactions. Such individual
350 rearing has been shown to improve FI and FE of the fish compared to group rearing
351 (McComish, 1971; Hayward et al., 2000). However, the correlation between FI and BWG in
352 our experiment is comparable to previous estimates in fish, which range from 0.51 to 0.98
353 (Kolstad et al., 2004; Doupé and Limbery, 2004; Kause et al., 2006b; Quinton et al., 2007a;
354 Martins et al., 2011) with the caveat that the previous measurements were made with less
355 accurate methods using X-ray or direct measurement of feed intake of the family group rather
356 than on the individual.

357 In the present study, the phenotypic correlations between LOSS, COMP and FE traits were
358 low and not different from 0. Grima et al. (2010) observed that European seabass
359 phenotypically selected for low weight loss during fasting showed an improved RFI, with
360 little even no effect of compensatory growth. The same authors, in rainbow trout, showed that
361 RFI was improved by the combination of low weight loss at fasting and high compensatory
362 growth (Grima et al., 2008). It appears that in tilapia, the relationship between those traits
363 seems to differ, and that neither the weight loss at fasting nor the compensatory growth are
364 predictive of RFI or FCR, at least in our conditions.

365 In addition to setting up an accurate methodology to estimate an individual FE, understanding
366 the relationships between FE and other performance traits is of importance to estimate the
367 potential impact of a genetic selection for FE in fish. In our study, FCR and RFI did not have
368 the same pattern of phenotypic correlations with FI and BWG: whereas FCR was correlated
369 with growth, RFI was not. The latter result was expected since RFI is recognized as
370 phenotypically independent of growth. In contrast, whereas RFI was correlated with FI, FCR
371 was not. The lack of any correlation between FCR and FI was not expected, as FCR is the

372 ratio between FI and BWG, and FCR expected to be linked with both variables. These results
373 can have a high impact if a selection scheme is developed using FCR or RFI as criteria, since
374 such selections may impact different metabolic processes, and the selection response would
375 be different. This is supported in the present study by the moderate correlation between FCR
376 and RFI.

377 Estimations of RFI and FCR are scarce in fish. To our knowledge, the present study is the first
378 to accurately estimate the phenotypic correlation between these two FE traits in fish. This
379 correlation (0.58 ± 0.06) is at the lower limit of the correlations generally found in livestock
380 species, ranging between 0.6 and 0.8 (Herd and Bishop, 2000; Arthur et al., 2001; Rauw et al.,
381 2006; Saintillan et al., 2013). Energy intake from the feed is used as growth, maintenance
382 requirement and physical activities. Since fish are poikilotherms, the energy used for
383 maintenance is lower than for livestock species, which could potentially explain the lower
384 correlation between RFI and FCR in fish.

385

386 5. Conclusion

387 The present paper is the first to measure individual feed efficiency in fish held in groups over
388 a continuous period of time rather than interspersed time points separated by several days or
389 weeks. We showed that estimating FI, FCR and RFI with a high repeatability and accuracy
390 can be achieved in the case of tilapia by integrating measurements over 11 meals. These traits
391 showed a high phenotypic variability, which is encouraging for future studies aimed at
392 understanding the underlying genetic variation for FE traits in fish and their potential
393 incorporation into fish selection schemes. We highlight the importance of treating FE traits
394 differently. Given RFI is phenotypically independent of the growth of the fish, selection for
395 growth may have an indirect response on FCR but not on RFI, and the effects of direct

396 selection on FE traits (FCR or RFI) will be different according to the FE trait selected.
397 However, it is important to note that all the correlations estimated in the present paper are
398 phenotypic correlations; it would be important to consider the genetic correlations of these
399 traits to conclude the impact of a selection process on feed efficiency. It also would be
400 interesting to analyse the relations between feed efficiency traits and behaviours. Hierarchy
401 could have a high impact on these traits, while from preliminary results using the same
402 methodology, hierarchy was not significantly correlated with feed efficiency (unpublished
403 data). Finally, compare the feed efficiency traits of groups of males alone, females alone and
404 mixed sexes could be interesting to understand the impact of the sex on these traits, with a
405 relation to the behaviours modifications due to the sex of the group.

406

407 **Conflict of interest**

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

409

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556

Meal	N	Mean	Min	Max	CV (%)
1	107	0.53	0.08	0.90	33.60
2	107	0.52	0.15	0.95	32.69
3	107	0.45	0.05	0.98	40.28
4	106	0.51	0.11	1.08	36.49
5	106	0.49	0.07	1.01	34.78
6	105	0.53	0.16	0.96	31.99
7	105	0.47	0.03	1.03	39.36
8	105	0.56	0.00	1.31	37.53
9	105	0.41	0.00	0.93	49.85
10	105	0.53	0.03	1.11	35.27
11	105	0.47	0.00	1.29	42.18
12	105	0.58	0.08	1.18	32.26
13	105	0.52	0.03	1.05	36.19
14	105	0.56	0.07	1.03	34.83
15	105	0.52	0.10	1.06	35.11
16	105	0.57	0.08	0.98	32.02
17	105	0.54	0.08	1.01	30.04
18	105	0.56	0.05	1.14	31.51
19	104	0.56	0.11	1.16	31.97
Overall	104	0.52	0.00	1.31	36.25

560 Table 1 - Summary statistics of individual feed intake (in g) at each measured meal.

	Male (N=65)	Female (N=37)	HPD _{95%} interval of difference	
LOSS	-0.07 ± 0.03	0.07 ± 0.03	-0.26	-0.003
COMP	16.40 ± 0.46	14.79 ± 0.63	0.06	3.21
BWG	12.81 ± 0.39	10.31 ± 0.53	1.17	3.84
FI	10.28 ± 0.31	9.17 ± 0.41	0.06	2.16
FCR	0.83 ± 0.02	0.94 ± 0.03	-0.18	-0.04
RFI	-0.007 ± 0.18	0.057 ± 0.25	-0.69	0.56

562

563 Table 2- Posterior least square means ± posterior standard deviation and the HPD 95%

564 interval of difference between males and females for the measured performance traits.

565 LOSS, the loss of body weight (g) during fasting period; COMP, the gain of body weight (g)

566 during compensatory growth; BWG, body weight gain (g); FI, feed intake total (g); FCR, feed

567 conversion ration; and RFI, residual feed intake.

568

569

Trait	N	Mean ± StdDev	Min	Max	CV (%)
LOSS	112	1.40 ± 0.32	0.34	1.09	22.6
COMP	107	15.9 ± 3.87	6.92	25.25	24.4
BWG	104	12.0 ± 3.61	3.32	20.78	30.2
FI	104	9.89 ± 2.43	4.68	16.30	24.6
FCR	104	0.86 ± 0.20	0.56	1.78	23.4
RFI	104	0.00 ± 1.45	-2.99	4.41	Ne

570

571 Table 3 – Summary statistics of variation of measured performance traits.

572 LOSS, the loss of body weight (g) during fasting period; COMP, the gain of body weight (g)

573 during compensatory growth; BWG, body weight gain (g); FI, feed intake total (g); FCR, feed

574 conversion ration; and RFI, residual feed intake; Ne: non-estimable

575

Traits	COMP	BWG	FI	FCR	LogFCR	RFI
LOSS	0.35 ± 0.08	0.13 ± 0.10	0.24 ± 0.09	0.02 ± 0.10	0.06 ± 0.10	0.03 ± 0.10
COMP		0.62 ± 0.06	0.66 ± 0.06	-0.11 ± 0.10	-0.12 ± 0.10	-0.01 ± 0.10
BWG			0.74 ± 0.05	-0.62 ± 0.06	-0.63 ± 0.06	-0.03 ± 0.10
FI				-0.02 ± 0.10	0.00 ± 0.10	0.60 ± 0.06
FCR					0.99 ± 0.00	0.58 ± 0.06
LogFCR						0.63 ± 0.06

576

577 Table 4 – Posterior means of the correlations ± posterior standard deviation between

578 measured performance traits. The significant relationships are indicated in bold.

579 LOSS, the loss of body weight (g) during fasting period; COMP, the gain of body weight (g)

580 during compensatory growth; BWG, body weight gain (g); FI, feed intake total (g); FCR, feed

581 conversion ration; logFCR, log of feed conversion ration; and RFI, residual feed intake.

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585 **Figures**

586

587 Figure 1 - Estimation of the posterior means of the correlations between FI (19 meals) and x
588 consecutive (in black) and randomly chose (in grey) meals (from 1 to 19).

589

590 Figure 2 – Estimation of the intra-class correlation (ICC) between FI (19 meals) and x
591 consecutive (in black) and randomly chose (in grey) meals (from 1 to 19).

592

593 Figure 3 - Posterior distributions of the least squares means (density) of males and females for
594 different studied traits. BWG, body weight gain (g); FI_{total}, feed intake total (g); FCR, feed
595 conversion ration; and RFI, residual feed intake.

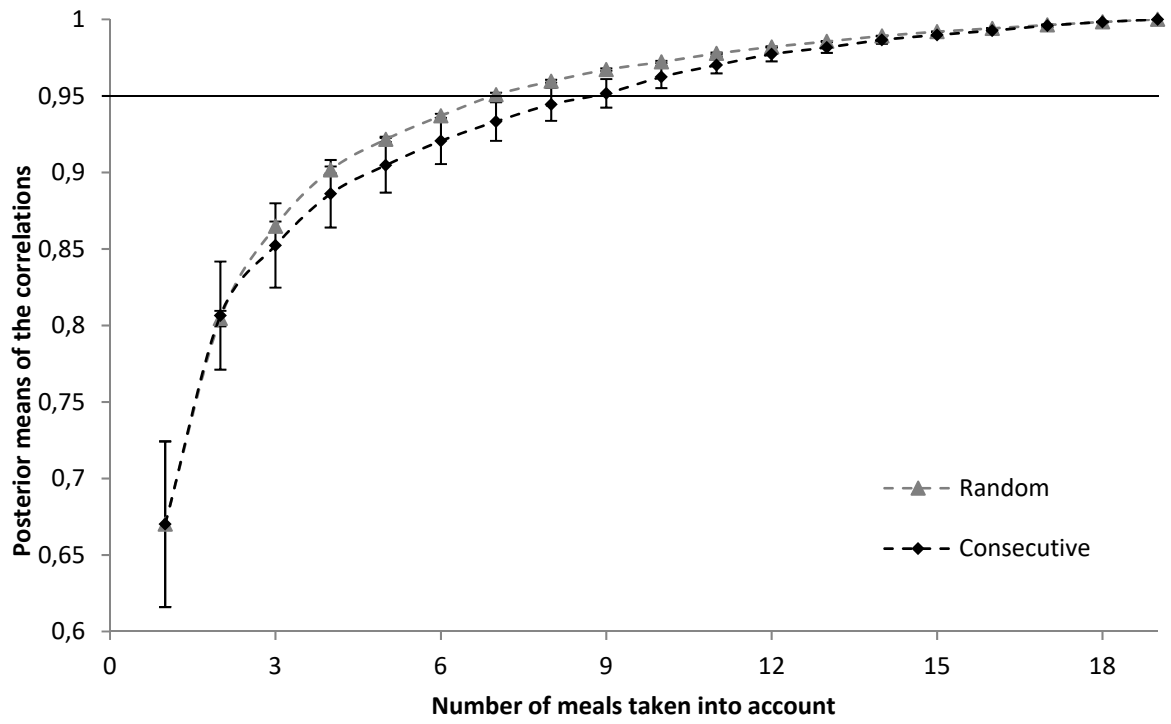
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597 Figure 4 – Regression between observed and predicted FI with model 3 for males (in black)
598 and females (in grey)

599

600

601 **Figure 1**



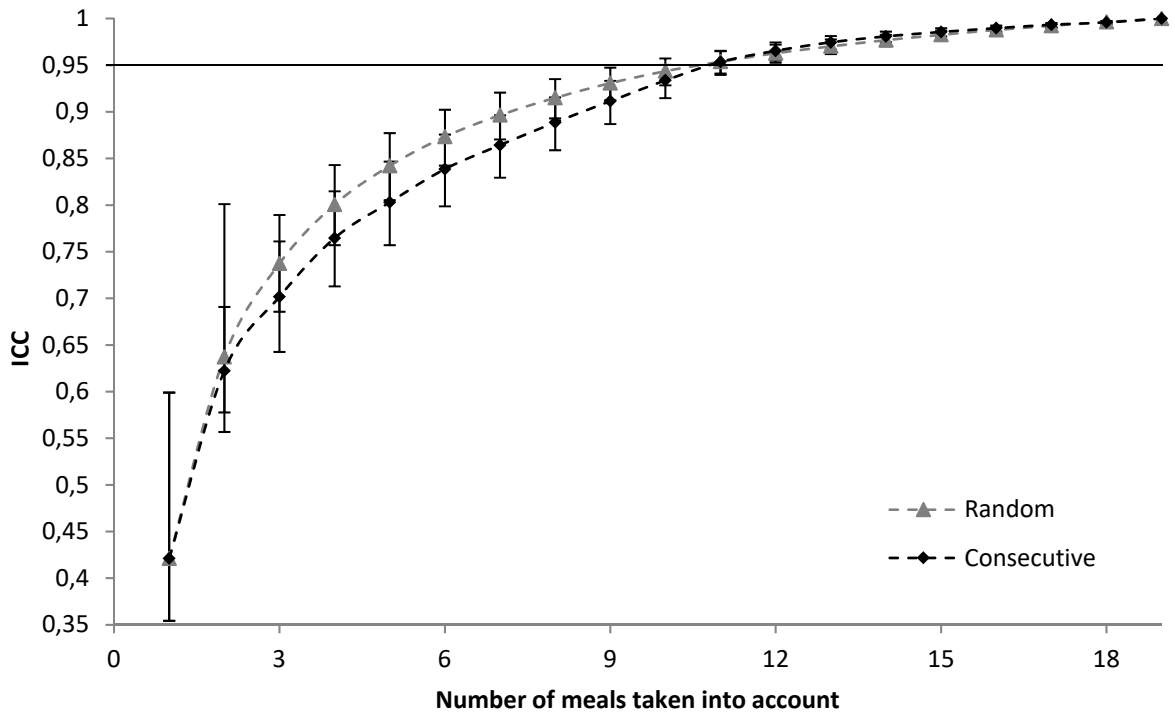
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605 **Figure 2**

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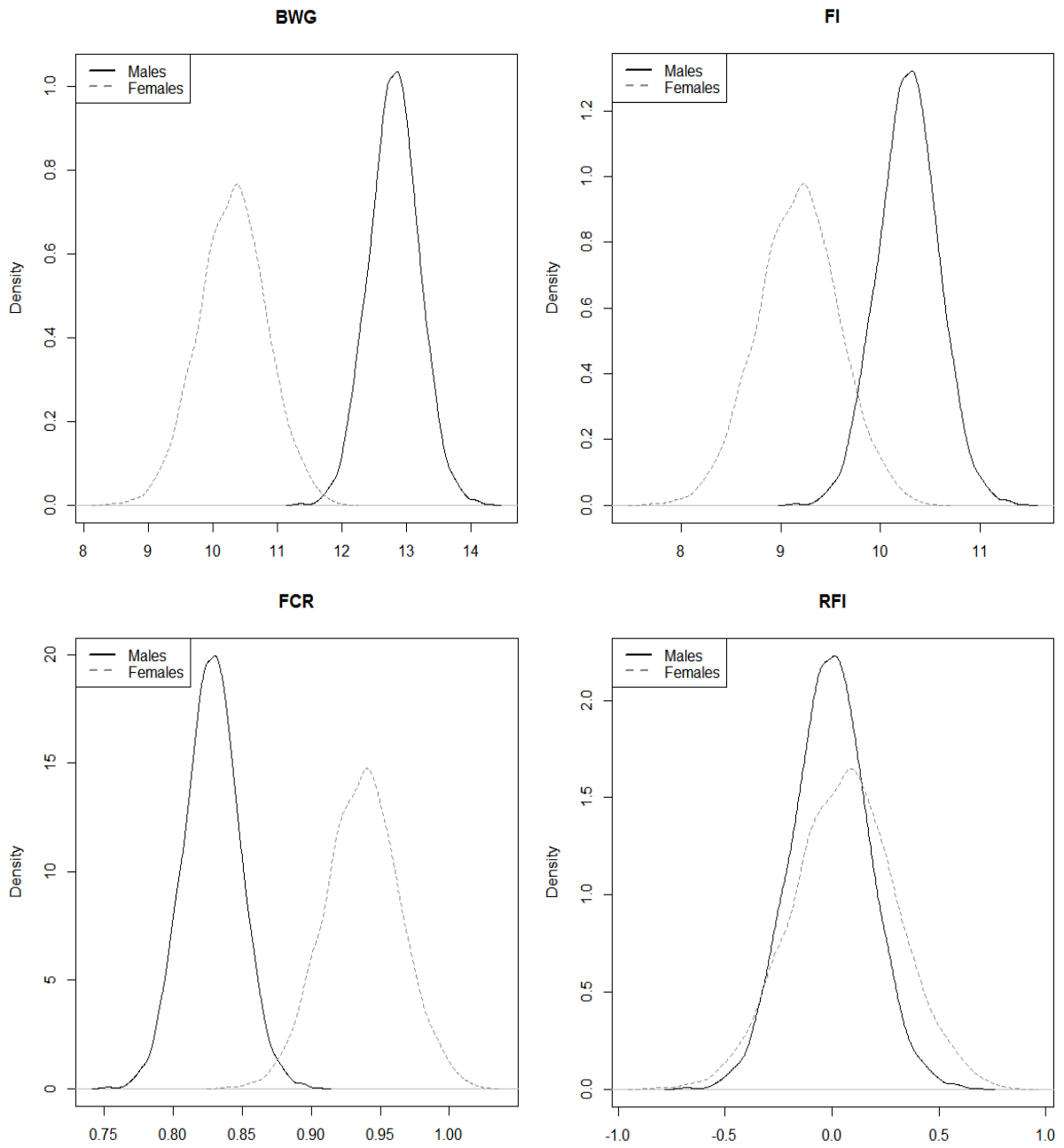


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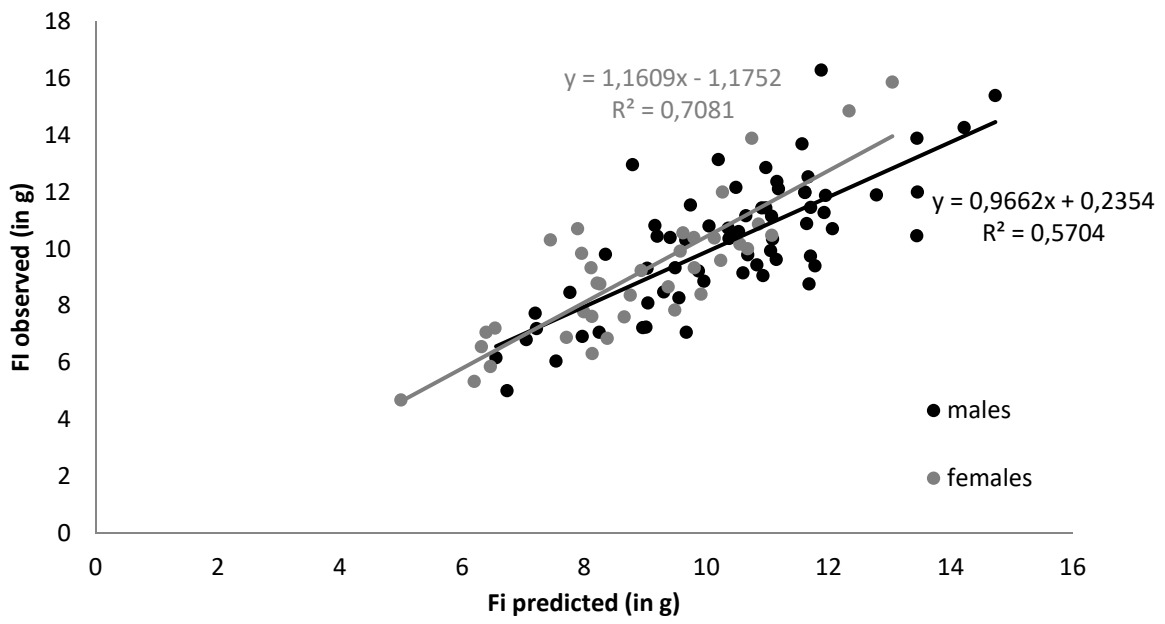
610 **Figure 3**



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613 **Figure 4**



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