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1 **How to genetically increase fillet yield in fish: relevant genetic parameters and methods**  
2 **to predict genetic gain.**

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15 **Running head** : Estimating selection gain for fillet yield

16 **Keywords:** aquaculture, genetics, heritability, selection, linear index, residual fillet weight,  
17 selection response, simulation, processing yields

18 **Abstract:**

19 Fillet yield (*i.e.* the proportion of edible muscle in a fish) is a key economic trait for species  
20 sold as fillets. Its genetic improvement is complicated by several of its characteristics 1) it is a  
21 ratio trait, 2) its numerator (fillet weight) and denominator (body weight) are strongly  
22 correlated (correlations in the range 0.89-0.99), 3) it offers little phenotypic variation and 4) it  
23 cannot be measured on alive breeding candidates. In a former study, we showed that it could  
24 be improved by selection, especially with three selection indices, fillet yield, residual fillet  
25 weight and a ratio-specific linear index. However, it is well known that the heritability of ratio  
26 traits does not permit a reliable prediction of genetic gains. As predictability of genetic gains  
27 is a key requirement to define breeding programs, we investigated how genetic gains in fillet  
28 yield could be predicted by the genetic parameters of fillet yield, of residual fillet weight and  
29 of the component traits of the linear index. To this end, we compared simulated genetic gains  
30 with those estimated by classical prediction methods. This was done using real sets of genetic  
31 parameters obtained in nine populations of rainbow trout, European sea bass, gilthead sea

32 bream and common carp. We show that the genetic parameters of fillet yield cannot be used  
33 to reliably predict genetic gains in fillet yield. Conversely, selection index theory using a  
34 linear index, combining either fillet weight and body weight or fillet weight and waste weight,  
35 provides almost perfect prediction of gains. Still, it is highly sensitive to the precision of the  
36 genetic and phenotypic correlations estimates, which should not be rounded to less than three  
37 decimals for fillet weight and body weight, while two decimals are appropriate for fillet  
38 weight and waste weight. A simple, reasonably precise alternative to the linear index is the  
39 use of residual fillet weight (the residual of the regression of fillet weight on body weight) as  
40 a surrogate for fillet yield.

41

## 42 **1. Introduction**

43 In fish selective breeding programs, the initial focus for selective breeding has always been  
44 growth rate (Chevassus et al., 2004; Gjedrem, 2012). However, the value of the round weight  
45 gain obtained is not the same in fish with high or low fillet yield (fillet weight/body weight  
46 ratio). This value can easily be turned into economic gains for species sold as fillets, where  
47 fillet yield can have a large impact on value added and net profit (Kankainen et al., 2016).  
48 Increasing the edible part of fish is also expected to decrease the environmental impact of the  
49 production of a given amount of edible fish flesh (Acosta Alba et al., 2015). The same  
50 reasoning applies for similar traits in other aquatic species, such as tail percentage in shrimp  
51 (Campos-Montes et al., 2017) or meat yield in shellfish (Nguyen et al., 2011).

52 Selective breeding on a ratio is seen as a problematic issue, which has been studied in many  
53 farmed animals. The main focus has been given to feed conversion ratio (FCR), the ratio of  
54 average daily feed intake to average daily gain, which has a major economic impact in all  
55 intensive farming systems. Most studies about selection methods for ratio traits have thus  
56 focused on FCR (Famula, 1990; Gunsett, 1984; Lin, 1980; Lin and Aggrey, 2013; Varkoohi et  
57 al., 2010). The general conclusion of these studies is that selection on a linear index  
58 combining the numerator and the denominator trait is generally more efficient than direct  
59 selection on the ratio or on one of its component traits. We recently demonstrated by  
60 simulation that although the numerator and denominator of fillet yield are very highly  
61 correlated (genetic correlations in the range 0.93-0.99), selection for fillet yield should be  
62 efficient, albeit with moderate gains in the range 0.30-0.95% fillet per generation (Fraslin et  
63 al., 2018). This may be achieved with different selection indices, among which fillet yield  
64 itself, residual fillet weight (the residual of the regression of fillet weight on body weight) or a  
65 linear index combining fillet weight and waste weight, the latter being defined as the  
66 difference between body weight and fillet weight. In this previous study, we did not test a  
67 linear index combining fillet weight and body weight, but although these traits are more  
68 strongly correlated than fillet weight and waste weight, it would be plausible that linear index  
69 selection also works with such an index.

70 The fact that selection gain on fillet yield can be obtained by those methods does not imply  
71 however, that such selection gains can easily be predicted from their genetic parameters.  
72 Indeed, it was previously shown that the heritability of a ratio trait, estimated from the  
73 analysis of covariance between relatives, was substantially different from the estimate  
74 obtained from simulated genetic gains (Gunsett, 1987), thus showing that the heritability of

75 the ratio cannot be used to predict genetic gain. The same study showed that a method using  
76 selection index theory to approximate the process of selection on a ratio was more efficient,  
77 but still did not provide an exact estimate of genetic gain in all situations. On the contrary,  
78 when selection is done not on the ratio but on a linear index combining the numerator and the  
79 denominator in an optimal way, as proposed by Lin (1980) the genetic gain is expected to be  
80 perfectly predictable using standard selection index theory as long as the heritability, genetic  
81 and phenotypic correlations, and the phenotypic variance of both component traits are known  
82 (Lin and Aggrey, 2013).

83 In general, prediction of gain on a single trait is very simple, as it can be done (in the case of  
84 mass selection) using the classical breeder's equation  $\Delta_G = ih^2\sigma_P$ , which just requires the  
85 knowledge of the heritability  $h^2$ , the selection intensity  $i$  and the phenotypic standard  
86 deviation of the trait  $\sigma_P$  to estimate the genetic gain  $\Delta_G$  (Falconer and Mackay, 1996). On the  
87 contrary, predicting gain from a two-trait linear index requires  $h^2$  and  $\sigma_P$  for the two  
88 component traits, as well as the phenotypic and genetic correlation between them. In addition,  
89 it requires a bit of matrix algebra, versus a simple multiplication of three terms.

90 If we want to predict genetic gain when using a linear index aimed at increasing the fillet to  
91 waste ratio, as suggested in Fraslin et al. (2018), the genetic parameters of fillet weight and  
92 waste weight are not available in the fish breeding literature today. If we want to predict  
93 genetic gain using a linear index aimed at increasing fillet yield, the genetic and phenotypic  
94 correlations of fillet weight and body weight are probably not known, or at least published,  
95 with sufficient precision (*e.g.* 0.99 can be anything from 0.9850 to 0.9949, which makes a big  
96 difference for such values which are very close to unity). In the published literature, most  
97 studies give genetic parameters of fillet yield, and quite a number also genetic parameters of  
98 residual fillet yield or log-residual fillet yield (*e.g.* Haffray et al., 2012; Prchal et al., 2018;  
99 Vandeputte et al., 2017, 2014). Thus, assessing which parameters to use in order to predict  
100 genetic gain in fillet yield is important 1) to assess which information from the existing  
101 literature is usable to predict genetic gains efficiently and 2) to eventually propose new sets of  
102 parameters to estimate in genetic studies of fillet yield in fish.

103 To this end, we estimated the genetic parameters of body weight, fillet weight and waste  
104 weight (defined as waste weight= body weight – fillet weight) in nine field datasets from four  
105 important aquaculture species (rainbow trout *Oncorhynchus mykiss*, European sea bass  
106 *Dicentrarchus labrax*, gilthead sea bream *Sparus aurata* and common carp *Cyprinus carpio*).  
107 In the same datasets, we also estimated the genetic parameters of fillet yield and of residual

108 fillet weight. Then, we performed stochastic simulation of selection using different selection  
109 indices to determine the expected genetic gain in the first generation, and compared this  
110 simulated gain with estimates derived from the genetic parameters of the traits using standard  
111 quantitative genetics theory for single traits (fillet yield and residual fillet weight) and linear  
112 indices.

113

114

## 115 2. Materials and methods

### 116 2.1. Estimation of genetic parameters for fillet traits

117 In order to perform simulations of fillet weight, body weight and waste weight with realistic  
118 values, we first estimated their genetic and phenotypic parameters. The database used was  
119 composed of carcass traits recorded on nine commercial stocks from four species: European  
120 sea bass (*Dicentrarchus labrax*), gilthead sea bream (*Sparus aurata*), common carp (*Cyprinus*  
121 *carpio*) and rainbow trout (*Oncorhynchus mykiss*). All fish used to estimate parameters were  
122 from factorial or partly factorial designs, with the pedigree identified by genotyping of  
123 microsatellite markers. All families were mixed, in order to minimize the environmental  
124 effect common to full siblings or half siblings. Number of offspring, of parents and of families  
125 as well as the age of the fish are given in Table 1. In all cases, the pedigree used comprised  
126 only the parental and the offspring generation. The estimations of genetic parameters were  
127 performed using an animal model with VCE (version 6.0.2, Groeneveld *et al.*, 2010), using  
128 specific fixed effects for each population. For fillet yield, a single trait model was used. For  
129 residual fillet weight the same model was used with the addition of a linear regression term  
130 with body weight. Then we used two bivariate models 1) with fillet weight and waste weight  
131 and 2) with fillet weight and body weight in order to estimate the heritability, genetic and  
132 phenotypic correlations of the component traits. Genetic parameters for sea bass were  
133 estimated separately in two batches from the same population, the first one fed a standard diet  
134 with marine ingredients (Dla1\_M), and the second one (Dla1\_V) fed a plant-based diet  
135 (Bestin *et al.*, 2014), with sex (568 males and 289 females in Dla1\_M, 550 males and 307  
136 females in Dla1\_V) and dam batch (corresponding to 3 different subpopulations in the  
137 breeding nucleus, with N=301, 371 and 185 in Dla1\_M and N=281, 376 and 200 in Dla1\_V)  
138 as fixed effects. We chose to estimate genetic parameters separately in the two batches  
139 because we anticipated different heritability estimates in the two batches, as already seen  
140 before for growth on marine vs. plant-based diets in the same species (Le Boucher *et al.*,  
141 2013). In a third batch from a different breeding population (Dla2), only sex (893 males, 482  
142 females) was used as fixed effect. For sea bream, three datasets were available: two with fish  
143 reared in tanks and one with fish reared in sea cages. For the first batch of tank-farmed sea  
144 bream (Sau\_T1), tank (the group was reared in two different tanks, N=1249 and 751 ) and  
145 presence-absence of vertebral deformities were used as fixed effects (48 present, 1952  
146 absent), while only presence-absence of vertebral deformities (478 present, 1509 absent) was  
147 used for cage-farmed sea bream (Sau\_C). For the second batch of tank-farmed sea bream

148 (Sau\_T2), no fixed effects were included as the fish were all reared in a single tank, and the  
149 very few fish with vertebral deformities were discarded from the dataset. For the first batch of  
150 rainbow trout (Omy1), fixed effects were processing day (5 days, N= 379, 452, 457, 489, 240)  
151 and filleting operator (2 operators, N=414 and 1603). For the second batch (from a different  
152 population, Omy2) no fixed effects were included, as there was no effect of processing day  
153 and there was only one filleting operator. For common carp (Cca1), the only fixed effect  
154 included was sex (751 males, 754 females, 48 unknown). Maternal effects were tested in all  
155 populations and found non-significant, so they were not included in the models. Note that  
156 populations Dla1\_M, Dla1\_V, Sau\_T, Sau\_C and Omy1 were already used to obtain genetic  
157 parameters in our previous simulation work (Fraslin et al., 2018) with a different objective,  
158 identifying selection indices that can efficiently be used to improve for fillet yield. Population  
159 Cca1 is the same as the one used by (Prchal et al., 2018), and population Omy2 is the SIBS  
160 population in Vandeputte et al. (in press). As it was key for the present study to have the  
161 different genetic and phenotypic parameters shown in Table 1 estimated with the same  
162 models, on exactly the same fish and with the same fixed effects, we chose to re-estimate all  
163 of them starting from the base data, although some of those estimates have already been  
164 published before (but never the whole set of parameters that we use here, for any of those  
165 populations). The use of different software and of different rules to include/exclude animals  
166 may result in small changes compared to the initial publications.

167 Descriptive statistics (phenotypic means and standard deviation, adjusted for fixed effects)  
168 were computed and heritability ( $h^2$ ) was estimated for fillet weight, body weight, waste  
169 weight, fillet yield and residual fillet weight (Table 1). The additive genetic ( $r_A$ ) and  
170 phenotypic ( $r_P$ ) correlations were estimated for body weight, fillet weight and waste weight.

171

## 172 2.2. Stochastic simulations

### 173 2.2.1. Model used

174 The traits simulated were non-trimmed fillet weight FW and waste weight WW, which were  
175 correlated with additive genetic correlation  $r_A$  and phenotypic correlation  $r_P$ . The waste was  
176 composed of viscera, head and bones of the fish. The reason for this choice, rather than  
177 simulating fillet weight and body weight, was to have less correlated traits than the classically  
178 used fillet weight and body weight.



179 The phenotypes in the base population ( $G_0$ ) were generated according to an additive  
180 polygenic model:

$$181 \quad \begin{bmatrix} p_{FW0} \\ p_{WW0} \end{bmatrix} = \begin{bmatrix} \mu_{FW0} \\ \mu_{WW0} \end{bmatrix} + \begin{bmatrix} a_{FW0} \\ a_{WW0} \end{bmatrix} + \begin{bmatrix} e_{FW0} \\ e_{WW0} \end{bmatrix} \quad [1]$$

182 with  $p_{i0}$  the phenotypic value of an individual for the trait  $i$  ( $i=FW$  for fillet weight,  $WW$  for  
183 waste weight) in the base population,  $\mu_{i0}$  the phenotypic mean of the trait  $i$ ,  $a_{i0}$  the additive  
184 genetic value of the trait  $i$  and  $e_{i0}$  the environmental residual for trait  $i$ .

185 with  $\mathbf{p}$ ,  $\mathbf{a}$  and  $\mathbf{e}$  following bivariate normal distributions,  $\mathbf{p} = \begin{bmatrix} p_{FW0} \\ p_{WW0} \end{bmatrix} \sim N(\boldsymbol{\mu}_p; \mathbf{V}_p)$  with

$$186 \quad \boldsymbol{\mu}_p = \begin{bmatrix} \mu_{FW0} \\ \mu_{WW0} \end{bmatrix} \text{ and } \mathbf{V}_p = \begin{bmatrix} \sigma^2_{P_{FW}} & \sigma_{P_{FW}P_{WW}} \\ \sigma_{P_{FW}P_{WW}} & \sigma^2_{P_{WW}} \end{bmatrix}, \mathbf{a} = \begin{bmatrix} a_{FW0} \\ a_{WW0} \end{bmatrix} \sim N(\boldsymbol{\mu}_a; \mathbf{V}_a) \text{ with } \boldsymbol{\mu}_a = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$$

$$187 \quad \text{and } \mathbf{V}_a = \begin{bmatrix} \sigma^2_{A_{FW}} & \sigma_{A_{FW}A_{WW}} \\ \sigma_{A_{FW}A_{WW}} & \sigma^2_{A_{WW}} \end{bmatrix}, \text{ and } \mathbf{e} = \begin{bmatrix} e_{FW0} \\ e_{WW0} \end{bmatrix} \sim N(\boldsymbol{\mu}_e; \mathbf{V}_e) \text{ with } \boldsymbol{\mu}_e = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \text{ and } \mathbf{V}_e =$$

$$188 \quad \begin{bmatrix} \sigma^2_{E_{FW}} & \sigma_{E_{FW}E_{WW}} \\ \sigma_{E_{FW}E_{WW}} & \sigma^2_{E_{WW}} \end{bmatrix}$$

189 Note that under a strictly additive genetic model as considered,  $\sigma^2_{P_{FW}} = \sigma^2_{A_{FW}} + \sigma^2_{E_{FW}}$ ,  
190  $\sigma^2_{P_{WW}} = \sigma^2_{A_{WW}} + \sigma^2_{E_{WW}}$ , and that  $\sigma_{P_{FW}P_{WW}} = \sigma_{A_{FW}A_{WW}} + \sigma_{E_{FW}E_{WW}}$  under the reasonable  
191 hypothesis that  $\sigma_{A_{FW}E_{WW}} = \sigma_{E_{FW}A_{WW}} = 0$  (Lynch and Walsh, 1998). Thus, knowing  $\mathbf{V}_p$  and  
192  $\mathbf{V}_a$  is enough to determine  $\mathbf{V}_e$ , and all parameters are determined when the mean, phenotypic  
193 standard deviation, heritability of fillet weight and waste weight are known, together with the  
194 genetic and phenotypic correlations between them.

### 195 2.2.2. Selection indices

196 Three selection indices were tested, in order to compare their relative efficiency in terms of  
197 gain in fillet yield after one generation of selection. In the simulation program, these selection  
198 indices were used to calculate the estimated breeding values (EBVs) of the candidates in the  
199 base population. The indices tested were the following:

$$200 \quad 1) \text{ Selection on fillet yield: } I_Y = FY = p_{FW}/(p_{FW} + p_{WW}) \quad [2]$$

201 2) Linear selection index :  $I_{LFWR} = b_{FW} \cdot p_{FW} + b_{WW} \cdot p_{WW}$  as proposed by Lin (1980) with  
202 coefficients  $b_{FW}$  and  $b_{WW}$  derived from selection index theory to maximize the fillet to  
203 waste ratio  $FWR = p_{FW}/p_{WW}$ , after it was linearized using a first order Taylor series  
204 expansion. The resulting coefficients are:

205 
$$\mathbf{b} = \begin{bmatrix} b_{FW} \\ b_{WW} \end{bmatrix} = \mathbf{V}_p^{-1} \mathbf{V}_a \begin{bmatrix} 1/\mu_{FW0} \\ -\mu_{FW0}/\mu_{WW0}^2 \end{bmatrix} \quad [3]$$

206 3) Selection on residual fillet yield:  $I_{res} = rFW = p_{FW} - c(p_{FW} + p_{WW}) - d$  [4]  
 207 with  $c$  and  $d$  the slope and intercept of the linear regression of fillet weight FW on body  
 208 weight (BW=FW+WW) in the base (candidates) population.

209 The candidates were ranked using the candidate's own phenotypic performance for a given  
 210 index. This mass selection case is not possible in real life, but is easier to manage in terms of  
 211 results as the response depends only on selection intensity, genetic and phenotypic  
 212 parameters, and not on technical parameters such as the type (full and half-sibs) and the  
 213 number of sibs per family, which influence sib selection response. For each of the nine  
 214 populations tested, three selection intensities were tested (5%, 20% and 50% of the candidates  
 215 selected, corresponding to standardized selection intensities of 2.06, 1.40 and 0.80,  
 216 respectively). The number of selection candidates generated was 4000 for 5%, 1000 for 20%  
 217 and 400 for 50%. The best 100 males and the best 100 females were selected and their average  
 218 additive genetic values for fillet weight  $\overline{a_{FW}}$  and for waste weight  $\overline{a_{WW}}$  were used to estimate  
 219 the genetic gain for the index used (index=  $I_Y$ ,  $I_{LFWR}$ ,  $I_{res}$ ) in the first generation:

220 
$$\Delta FY_{sim}(index) = \frac{\mu_{FW0} + \overline{a_{FW}}}{\mu_{FW0} + \overline{a_{FW}} + \mu_{WW0} + \overline{a_{WW}}} - \frac{\mu_{FW0}}{\mu_{FW0} + \mu_{WW0}} \quad [5]$$

221 Fifty simulations were ran for each of the 27 combinations of parameters (9 populations \* 3  
 222 selection intensities), and the average simulated genetic gain used in further analyses was the  
 223 average of those 50 simulations. It has to be noted that the phenotypic and genetic parameters  
 224 of fillet weight and waste weight, as well as the selection intensity, were the only parameters  
 225 needed to simulate all selection scenarios.

226 **2.2.4. Comparison of indices**

227 We compared the simulated gains for the three indices  $I_Y$ ,  $I_{LFWR}$  and  $I_{res}$  (see 2.2.3) which were  
 228 previously shown to give similar results over 10 generations in five populations of fish with a  
 229 selection pressure of 20% by Fraslin et al. (2018). In the present paper, only the first  
 230 generation was simulated, with more (nine) populations and three selection intensities, thus  
 231 validating their efficiency was necessary.

232 **2.2.5. Prediction of gains with linear indices**

233 The next objective of the study was to evaluate the efficiency of the approach of Lin and  
 234 Aggrey (2013) to predict gains obtained with the linear index  $I_{LFWR}$ , aimed at improving the  
 235 fillet weight/waste weight ratio. The predicted fillet yield was computed as follows:

$$236 \quad \Delta FY_{pred}(I_{LFWR}) = \frac{\mu_{FW0} + \widehat{\alpha}_{FW}}{\mu_{FW0} + \widehat{\alpha}_{FW} + \mu_{WW0} + \widehat{\alpha}_{WW}} - \frac{\mu_{FW0}}{\mu_{FW0} + \mu_{WW0}} \quad [6]$$

$$237 \quad \text{With } \left[ \frac{\widehat{\alpha}_{FW}}{\widehat{\alpha}_{WW}} \right] = \mathbf{V}_a \mathbf{b} (i / \sqrt{\mathbf{b}' \mathbf{V}_p \mathbf{b}}) \quad [7]$$

238 where  $i$  is the standardized selection intensity. See 2.2.1 and 2.2.2 for the definitions of  $\mathbf{V}_a$ ,  $\mathbf{V}_p$   
 239 and  $\mathbf{b}$ .

240 A similar approach was tried with a linear index  $I_{LFY}$  aimed at improving fillet yield (the fillet  
 241 weight/body weight ratio):

$$242 \quad \Delta FY_{pred}(I_{LFY}) = \frac{\mu_{FW0} + \widehat{\alpha}_{FW}}{\mu_{BW0} + \widehat{\alpha}_{BW}} - \frac{\mu_{FW0}}{\mu_{BW0}} \quad [8]$$

243 Where  $\widehat{\alpha}_{FW}$  and  $\widehat{\alpha}_{BW}$  are estimated in the same way as with  $I_{LFWR}$ , using the genetic and  
 244 phenotypic parameters of fillet weight and body weight (instead of fillet weight and waste  
 245 weight) to establish  $\mathbf{V}_a$ ,  $\mathbf{V}_p$  and  $\mathbf{b}$ .

#### 246 2.2.6. Prediction of gains with the genetic parameters of fillet yield

247 To predict genetic gains with the genetic parameters of fillet yield, we used the breeder's  
 248 equation from Falconer and Mackay (1996):

$$249 \quad \Delta FY_{pred}(I_Y) = i h_{FY}^2 \sigma_{P_{FY}} \quad [9]$$

250 Where  $i$  is the standardized selection intensity,  $h_{FY}^2$  is the heritability of fillet yield and  $\sigma_{P_{FY}}$  is  
 251 the phenotypic standard deviation of fillet yield.

#### 252 2.2.7. Prediction of gains with the genetic parameters of residual fillet weight

253 In this case, we predicted the gain in residual fillet yield with the breeder's equation:

$$254 \quad \Delta rFW = i h_{rFW}^2 \sigma_{P_{rFW}} \quad [10]$$

255 Where  $h_{rFW}^2$  and  $\sigma_{P_{rFW}}$  are the heritability and the phenotypic standard deviation of residual  
 256 fillet yield. Then, the gain in fillet yield was estimated by dividing  $\Delta rFW$  by the body weight  
 257 in G0:

$$258 \quad \Delta FY_{pred}(I_{res}) = \Delta rFW / (\mu_{FW0} + \mu_{WW0}) \quad [11]$$

#### 259 2.2.8. Effect of the precision of heritability and correlations on predicted gains

260 In all simulations and for estimating predicted gains, the we used a precision of three decimals  
261 for “true” values of heritability and genetic and phenotypic correlations, except for the genetic  
262 and phenotypic correlations of FW with BW for which we used a precision of four decimals.  
263 The impact of rounding the genetic parameters to two or three decimals for the prediction was  
264 studied for  $\Delta FY_{pred}(I_{res})$ ,  $\Delta FY_{pred}(I_{LFWR})$  and  $\Delta FY_{pred}(I_{LFY})$ .

265 In addition, the genetic parameters we considered as “true” are only estimates, with an  
266 associated standard error (see Table 1). We investigated the consequences on predicted  
267 genetic gains of sampling the parameters in a normal distribution centered on the estimate of  
268 each parameter, with a standard deviation equal to the standard error of the estimate. For each  
269 case, we simulated 1000 sets of parameters and looked at the predicted gain for a selection  
270 intensity of  $i=1.4$  ( $P=20\%$ ).

271 For  $\Delta FY_{pred}(I_{res})$ , the estimated parameter influencing selection response is  $h^2_{rFW}$ , and thus  
272 1000 values of  $h^2_{rFW}$  were sampled in  $N(\widehat{h^2_{rFW}}, \widehat{\sigma_{h^2_{rFW}}})$  and  $\Delta FY_{pred}(I_{res})$  was calculated with  
273 equations [10] and [11], for each of our 9 populations

274 For  $\Delta FY_{pred}(I_{LFY})$ , the estimated parameters influencing predicted response are first the  
275 correlations  $r_a(FW, BW)$  and  $r_p(FW, BW)$ , which for each sample were both modified in the  
276 same direction by adding to their estimate the quantity  $X_1 \widehat{\sigma_{r_a(FW, BW)}}$ , where  $X_1$  is a standard  
277 normal deviate, considering that  $r_a$  and  $r_p$  generally covary in the same direction and are rather  
278 similar to each other for morphological traits (Roff, 1995). Second,  $\Delta FY_{pred}(I_{LFY})$  is also  
279 influenced by  $h^2_{FW}$  and  $h^2_{BW}$ , which also both modified simultaneously by adding to their  
280 respective estimates the quantities  $X_2 \widehat{\sigma_{h^2_{rFW}}}$  and  $X_2 \widehat{\sigma_{h^2_{rBW}}}$ , with  $X_2$  another standard normal  
281 deviate. Then  $\Delta FY_{pred}(I_{LFY})$  was calculated with equation [9].

282 The same reasoning was applied to  $\Delta FY_{pred}(I_{LFWR})$ , which was then calculated with equation  
283 [6].

284 Note that for both  $\Delta FY_{pred}(I_{LFY})$  and  $\Delta FY_{pred}(I_{LFWR})$ , these are only approximations with the  
285 following important hypotheses: 1) the genetic parameters are normally distributed 2) genetic  
286 and phenotypic correlations between FW and BW or WW covary by the same amount relative  
287 to their estimate when they are sampled 3) the heritability of FW and of BW or WW covary  
288 by the same proportion when ay are sampled and 4) the estimates of correlations are  
289 independent of the estimates of heritability.

290 2.2.9. Statistical analyses

291 The simulated values for the 27 combinations of parameters (9 populations \* 3 selection  
292 intensities, each value being the average of 50 simulations) were compared to the predicted  
293 ones using linear regression.

294

295

### 296 3. Results

#### 297 3.1. Estimation of genetic and phenotypic parameters

298 The detailed phenotypic and genetic parameters estimated for each population are reported in  
299 Table 1, and example distribution of the traits for population Omy2 are given in Suppl. Fig. 1.  
300 Fillet weight was highly correlated with waste weight in all species ( $r_A = 0.874-0.976$  and  $r_P =$   
301  $0.823-0.962$  on average). Fillet weight and body weight were even more correlated, with  
302 additive genetic correlation ranged from 0.9821 to 0.9952 and phenotypic correlation ranged  
303 from 0.9718 to 0.9937. The heritability of fillet yield was between 0.110 and 0.460, and that  
304 of residual fillet weight between 0.101 and 0.542. The heritability of fillet weight and body  
305 weight were in general very similar, in the range 0.184 to 0.632.

#### 306 3.2. Comparison of selection indices

307 The simulated gains in the first generation using  $I_Y$ ,  $I_{LFWR}$ ,  $I_{res}$  as selection indices are shown  
308 in Fig. 1. The higher gains were obtained with the linear index  $I_{LFWR}$ , but the gains obtained  
309 with selection on fillet yield and selection on residual fillet yield were only marginally lower  
310 (on average 95.2 % and 95.9% of the linear index gains, respectively). The correlation  
311 between the gains obtained with the three methods were very high (0.993 between  $I_{LFWR}$  and  
312  $I_{res}$ , 0.989 between  $I_{res}$  and  $I_Y$ , and 0.990 between  $I_{LFWR}$  and  $I_Y$ ).

#### 313 3.3. Prediction of gains with linear indices

314 We used standard selection index theory to predict the first generation gains in fillet yield in  
315 two ways: with a linear index aimed at improving the fillet weight to waste weight ratio,  
316 providing the  $\Delta FY_{pred}(I_{LFWR})$  predictor, and with a linear index aimed at improving fillet  
317 yield (the fillet weight to body weight ratio), which yielded the  $\Delta FY_{pred}(I_{LFY})$  predictor. As  
318 expected, both predictors resulted in a close to perfect prediction of the simulated gain  
319  $\Delta FY_{sim}(I_{LFWR})$ , as shown in Fig. 2.

#### 320 3.4. Prediction of gains with the genetic parameters of fillet yield

321 When the simulated gain  $\Delta FY_{sim}(I_Y)$  was predicted with  $\Delta FY_{pred}(I_Y)$ , using the breeder's  
322 equation with the genetic parameters of fillet yield, the prediction was by far less efficient.  
323 The coefficient of determination of the simulated gain by the predicted gain was 0.70, and the  
324 average simulated gain was only 84% of the predicted gain (Fig. 3a). However, this was very  
325 much dependent on the batch of fish: the average simulated gain was up to 142% of the  
326 predicted gain in the Dla2 stock of sea bass, while it could be as low as 65% of the predicted

327 gain in the D1a1\_V stock of sea bass (Fig. 3b). For each population, while the relation  
328 between the average simulated gain and the predicted gain could be very biased (as expressed  
329 by the slope of the regression), this bias did not depend strongly on the selection intensity, as  
330 the simulated response was highly linear with the predicted response (individual regressions  
331 within each population had a  $r^2$  between 0.936 and 0.998)

### 332 3.5. Prediction of gains with the genetic parameters of residual fillet weight

333 When the simulated gain  $\Delta FY_{sim}(I_{res})$  was predicted with  $\Delta FY_{pred}(I_{res})$ , the prediction was  
334 not perfect but reasonably accurate. The coefficient of determination of the simulated gain by  
335 the predicted gain was 0.952 on average, and the simulated gain was on average 92.7% of the  
336 predicted gain (Fig. 4a). This was also dependent on the batch of fish: the average simulated  
337 gain was up to 102% of the predicted gain in the D1a1\_V stock of sea bass, and down to 80%  
338 of the predicted gain in the CCa1 stock of common carp (Fig. 4b)

### 339 3.6. Impact of the precision of genetic parameters in prediction equations

340 Figure 5 shows the impact of rounding the genetic parameters to three or two decimals before  
341 using them in prediction equations to predict the simulated gain in fillet yield  $\Delta FY_{sim}(I_{LFWR})$ .  
342 For the linear index based on fillet weight and body weight, the precision of  $\Delta FY_{pred}(I_{LFY})$   
343 was little affected when rounding to three decimals (Fig. 5a, left panel) compared with four  
344 decimals (Fig. 2b), as the coefficient of determination of the simulated values by the predicted  
345 values changed from 0.9991 to 0.9955. However, it dropped dramatically, down to 0.45, when  
346 the genetic parameters were rounded to two decimals. This effect was smaller when the  
347 simulated gain was predicted with a linear index of fillet weight and waste weight, with  
348  $\Delta FY_{pred}(I_{LFWR})$ , as the coefficient of determination changed from 0.9992 with three decimals  
349 to 0.9824 with two decimals. The prediction metric which was least affected by rounded  
350 genetic parameters was  $\Delta FY_{pred}(I_{res})$ , for which the coefficient of determination was 0.952  
351 with two decimals and 0.953 with three decimals.

352 We also examined the uncertainty on genetic gain by predicting genetic gains with resampling  
353 of the genetic parameters according to the standard errors of their estimates (Fig. 6). It shows  
354 that with the precision of our estimates, the predicted genetic gains with the three methods are  
355 comparable, although the predicted response with residual fillet yield seems slightly more  
356 variable in several cases.

357

#### 359 4. Discussion

360 The simulations we performed, using estimated genetic parameters from real data from nine  
361 population of four fish species, clearly confirm that fillet yield, defined as the ratio of fillet  
362 weight to body weight, can be genetically improved by selection. We simulated selection with  
363 different indices, identified among the most efficient in a previous study (Fraslin et al., 2018),  
364 and their performance was confirmed over a wide range of populations and selection  
365 intensities. The linear index  $I_{LFWR}$  (Gunsett, 1984; Lin, 1980; Lin and Aggrey, 2013),  
366 developed to improve selection gains on ratio traits, was the most efficient, approximately 4%  
367 better than selection on residual fillet weight  $I_{res}$  and 5% better than direct selection on fillet  
368 yield  $I_Y$ . This is in line with theory, as Lin and Aggrey (2013) showed that the linear index  
369 should always give better results than direct selection on the ratio. These results hold for the  
370 first generation, but may not be repeatable on the longer term as Frasin et al. (2018) showed  
371 that after simulating 10 generations,  $I_{LFWR}$  was in general a little outperformed by  $I_{res}$  and  $I_Y$ .  
372 For longer term (genetic trend) studies, Bayesian methods may be more efficient, have they  
373 have shown to be for studying another ratio (FCR) in pigs (Shirali et al., 2018).

374 This possibility for genetic gain is real, despite the very high correlations between FW and  
375 BW, which in our nine study cases range from 0.982 to 0.996 for the additive genetic  
376 correlation, and from 0.983 to 0.993 for phenotypic correlation, somehow higher than  
377 published values from previous studies in various fish species, which typically range from  
378 0.93 to 0.99 for the additive genetic correlation and from 0.89 to 0.99 for the phenotypic  
379 correlation (Gjerde et al., 2012; Haffray et al., 2012; Kause et al., 2007, 2002; Navarro et al.,  
380 2009; Nguyen et al., 2010; Powell et al., 2008; Rutten et al., 2005a). We hypothesize that the  
381 higher values we obtain are linked to the very careful dissection of fillet that was done in all  
382 our experiments, with the aim to minimize environmental noise.

383 In order to plan selection for fillet yield, it is essential to be able to project potential gains  
384 from genetic parameters. Many studies have been conducted to estimate the genetic  
385 parameters of fillet traits in fish (Gjerde et al., 2012; Haffray et al., 2012; Kause et al., 2007,  
386 2002; Kocour et al., 2007; Navarro et al., 2009; Nguyen et al., 2010; Powell et al., 2008;  
387 Prchal et al., 2018; Rutten et al., 2005b; Saillant et al., 2009; Sang et al., 2012; Schlicht et al.,  
388 2019; Thodesen et al., 2012; Tsai et al., 2015; Turra et al., 2018; Vandeputte et al., 2017,  
389 2014). All of them estimated genetic parameters of fillet yield, and only a few estimated



390 genetic parameters for (log-transformed) residual fillet yield (Haffray et al., 2012; Prchal et  
391 al., 2018; Vandeputte et al., 2017, 2014). Here we showed that the heritability of fillet yield  
392 only enables a very approximate estimation of potential gains in fillet yield (Fig. 3), thus  
393 questioning their usefulness to decide on future breeding programs. The populations where  
394 the estimate was the worst were among those with very high genetic correlations of fillet  
395 weight and body weight (0.990 or higher), but the bias could be in either direction (over  
396 estimation for Dla1\_V and Omy2, under estimation for Dla2 and Sau\_T2). However, one of  
397 the best estimates of genetic gain using the genetic parameters of fillet yield was for Omy1,  
398 for which the genetic correlation of fillet weight and body weight was also very high (0.9915).  
399 Thus, there seems to be no simple way to identify meaningful estimates of heritability for  
400 fillet yield. The fact that the heritability of a ratio, estimated from correlation between  
401 relatives, differs from the “realized “ heritability estimated from simulated selection had  
402 already been demonstrated by Gunsett (1987) in the context of selection for feed conversion  
403 ratio. The range of parameter values that Gunsett tested for the numerator and the  
404 denominator of the ratio was similar to our values for heritability (0.1 to 0.7, vs. 0.2 to 0.7 in  
405 our data), but very different for the genetic correlation which was 0 or 0.5 (0.982 to 0.996 for  
406 FW and BW in our data). Still, we see the same type of discrepancies between predicted and  
407 simulated values, but with higher biases in the present study: when both numerator and  
408 denominator heritability values were equal and the genetic correlation is 0.5, the genetic gain  
409 predicted by the ratio heritability was 95 to 121% of the simulated gain in Gunsett (1987), and  
410 this difference ranged from 65 to 142% in our case.

411 The solution proposed by several authors (Gunsett, 1987; Lin and Aggrey, 2013) to overcome  
412 this difficulty is to use selection index theory to predict genetic gain on a linear index  
413 combining the numerator (fillet yield) and the denominator trait (body weight or waste  
414 weight). We showed that this was very efficient, as linear predictions based on the covariation  
415 of fillet weight or waste weight or of fillet weight and body weight led to an almost perfect  
416 prediction of the simulated gain in fillet yield (Fig. 2). This confirms the observations by  
417 Gunsett (1987), who showed that the linear index enabled excellent prediction of the genetic  
418 change for the numerator and the denominator, and thus that of the ratio itself (here, fillet  
419 yield). This works well even though in our case, the heritability of numerator and  
420 denominator are very similar to each other, and the correlations between them extremely high,  
421 a case not tested by Gunsett.

422 While modelling the joint genetic change in numerator and denominator values is less  
423 practically convenient than a simple prediction of one trait (the ratio of interest, fillet yield)  
424 with the breeder's equation, it is remarkably efficient and more satisfying as it also shows by  
425 which combination of increase or decrease of the numerator and denominator traits the ratio  
426 changes. Thus, as the published literature on selection for fillet yield in fish almost always  
427 includes genetic parameters of fillet weight and body weight, this could be used to evaluate  
428 potential gains. However, in all of the twenty previously cited studies on the subject,  
429 heritability estimates, phenotypic and genetic correlations were reported with (and thus  
430 rounded to) two decimals. We showed that given the very high correlations implied, rounding  
431 genetic and phenotypic correlations of FW and BW to two decimals may create large biases in  
432 the estimations of genetic gains, using the otherwise optimal selection index theory (Fig. 5a).  
433 One typical case in our data is population D1a2, where the genetic correlation of 0.9959 would  
434 be rounded to 1.00, leading to 0.00-0.01% predicted gain depending on selection intensity,  
435 while the expected gain with 0.9959 would range between 0.26 and 0.73%. A possible  
436 alternative is to use the genetic parameters of fillet weight and waste weight, as previously  
437 suggested (Fraslin et al., 2018), as they are less sensitive to this rounding issue (Fig. 5b). If  
438 genetic parameters of fillet weight and body weight are to be used, but they should be  
439 reported with 3 decimals, at least for what concerns genetic and phenotypic correlations.

440 A few previous studies used regression residuals of fillet weight on body weight as surrogates  
441 for fillet yield (Haffray et al., 2013, 2012; Prchal et al., 2018; Vandeputte et al., 2017, 2014).  
442 Our results show that such an approach should be more satisfying than using the genetic  
443 parameters of fillet yield, most of the time providing a reasonable estimate of potential gains  
444 in fillet yield (Fig. 4). It has to be noted that the above-cited studies did not use simple  
445 regression residuals, but regression residuals on log-log transformed data. The main  
446 advantage of log-log transformed data is that they reduce scaling effects and take into account  
447 possible non-linear allometric development of body parts. In the data sets we used here,  
448 although fillet weight and waste weight were in general not normally distributed, their  
449 bivariate distribution was closer to the bivariate normal distribution than the log-log  
450 distribution was. As we used bivariate normal distributions to run the simulations, we chose to  
451 use simple regression residuals and not log-residuals. Still, if the bivariate log-log distribution  
452 of the data fits more with a bivariate normal, there should be no reason for the use of log-  
453 residuals not to be equally good to predict gains in fillet yield as the simple residuals used in  
454 the present study. The fact that residual fillet weight is a single trait, easily managed with the

455 breeder's equation, is a clear advantage, as knowing the heritability and the phenotypic  
456 variance, it is very easy to project genetic gains, more than with the two-traits linear index. A  
457 second advantage of this method is that it is little affected by the rounding of genetic  
458 parameters, as the usual two decimals are appropriate (Fig. 5c).

459 When the estimated genetic parameters were resampled from the distribution of their  
460 estimates, we saw that the uncertainty in predicted gains was rather similar among methods  
461 ( $I_{FY}$ ,  $I_{FWR}$  and  $I_{res}$ ), with a slight disadvantage for  $I_{res}$  in terms of both bias and precision. This  
462 shows that although  $I_{res}$  is less sensitive to rounding of the genetic parameters to two  
463 decimals, it is not more precise in a given design, with a given level of precision of the  
464 estimates.

465 To conclude, the genetic parameters of fillet yield were shown not to adequately reflect the  
466 potential of selective breeding for this trait, and should therefore not be used anymore. The  
467 most precise method to predict genetic gain is the linear index theory, using the joint genetic  
468 and phenotypic variation of fillet weight and body weight, but the precision of this method is  
469 highly dependent on the precision of the estimates of genetic and phenotypic correlations.  
470 These correlations should not be rounded to less than three decimals. Alternatively, a simple  
471 and reasonably precise method to project genetic gains in fillet yield is the use of residual  
472 fillet weight as a surrogate of fillet yield.

473

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Table 1: Phenotypic means ( $\pm$  standard deviation) and genetic parameters ( $\pm$  standard error of the estimate, SEE) of fillet traits in nine population batches of five fish species. Fillet weight is the untrimmed, skin-on, ribs-on fillet weight. Waste weight is the difference between body weight and fillet weight. Residual fillet weight is the residual of the regression of fillet weight on body weight. Standard deviations of the traits are estimated after adjustment for the appropriate fixed effects (see § 2.1).

Species	<i>Dicentrarchus labrax</i>			<i>Sparus aurata</i>			<i>Oncorhynchus mykiss</i>		<i>Cyprinus carpio</i>
Batch	Dla1_V	Dla1_M	Dla_2	Sau_T1	Sau_C	Sau_T2	Omy1	Omy2	Cca1
Age (days)	715	715	690	417	620	528	509	551	907
Nsires, Ndams	45♂ 15♀	45♂ 15♀	48♂ 17♀	82♂ 26♀	82♂ 19♀	77♀ 26♂	100♂ 60♀	98♂ 70♀	40♂ 20♀
N full-sib families	190	191	135	238	158	188	558	539	197
N half-sib families	60	60	65	108	101	103	160	168	60
N offspring	857	857	1375	2000	1987	1495	2017	1715	1553
Body weight - BW(g)	734.0 $\pm$ 194.1	869.2 $\pm$ 169.2	285.0 $\pm$ 65.0	321.0 $\pm$ 44.6	381.8 $\pm$ 63.3	250.4 $\pm$ 59.3	1622.4 $\pm$ 358.4	1923.3 $\pm$ 376.0	1910.5 $\pm$ 284.6
Fillet weight -FW (g)	411.6 $\pm$ 116.4	496.0 $\pm$ 101.0	166.7 $\pm$ 39.1	187.8 $\pm$ 28.1	230.2 $\pm$ 41.4	143.6 $\pm$ 36.2	1047.1 $\pm$ 240.8	1317.4 $\pm$ 268.6	952.3 $\pm$ 155.6
Waste weight - WW (g)	322.4 $\pm$ 81.8	373.2 $\pm$ 74.2	118.3 $\pm$ 26.4	133.2 $\pm$ 18.5	151.6 $\pm$ 23.9	106.8 $\pm$ 24.1	575.3 $\pm$ 122.5	605.9 $\pm$ 113.5	958.2 $\pm$ 136.6
Residual FW - rFW (g)	0 $\pm$ 19.74	0 $\pm$ 22.53	0 $\pm$ 4.40	0 $\pm$ 6.63	0 $\pm$ 7.67	0 $\pm$ 5.48	0 $\pm$ 29.46	0 $\pm$ 30.78	0 $\pm$ 33.24
Fillet yield - FY	0.557 $\pm$ 0.035	0.571 $\pm$ 0.027	0.584 $\pm$ 0.016	0.584 $\pm$ 0.021	0.601 $\pm$ 0.023	0.571 $\pm$ 0.026	0.644 $\pm$ 0.019	0.683 $\pm$ 0.020	0.497 $\pm$ 0.019
h <sup>2</sup> BW	0.395 $\pm$ 0.083	0.213 $\pm$ 0.061	0.357 $\pm$ 0.046	0.403 $\pm$ 0.056	0.334 $\pm$ 0.062	0.212 $\pm$ 0.056	0.350 $\pm$ 0.052	0.382 $\pm$ 0.068	0.632 $\pm$ 0.094
h <sup>2</sup> FW	0.413 $\pm$ 0.086	0.226 $\pm$ 0.064	0.342 $\pm$ 0.046	0.419 $\pm$ 0.057	0.322 $\pm$ 0.060	0.184 $\pm$ 0.053	0.339 $\pm$ 0.050	0.375 $\pm$ 0.067	0.539 $\pm$ 0.086
h <sup>2</sup> WW	0.359 $\pm$ 0.079	0.179 $\pm$ 0.057	0.374 $\pm$ 0.046	0.351 $\pm$ 0.057	0.343 $\pm$ 0.063	0.253 $\pm$ 0.061	0.353 $\pm$ 0.050	0.399 $\pm$ 0.066	0.723 $\pm$ 0.091
h <sup>2</sup> rFW	0.270 $\pm$ 0.075	0.101 $\pm$ 0.053	0.256 $\pm$ 0.064	0.280 $\pm$ 0.050	0.271 $\pm$ 0.052	0.209 $\pm$ 0.053	0.395 $\pm$ 0.050	0.399 $\pm$ 0.052	0.542 $\pm$ 0.089
h <sup>2</sup> FY	0.316 $\pm$ 0.073	0.111 $\pm$ 0.054	0.148 $\pm$ 0.037	0.310 $\pm$ 0.052	0.224 $\pm$ 0.048	0.110 $\pm$ 0.040	0.384 $\pm$ 0.053	0.460 $\pm$ 0.077	0.356 $\pm$ 0.071
r <sub>a</sub> (FW, WW)	0.942 $\pm$ 0.022	0.935 $\pm$ 0.040	0.976 $\pm$ 0.007	0.874 $\pm$ 0.031	0.895 $\pm$ 0.031	0.948 $\pm$ 0.023	0.925 $\pm$ 0.016	0.925 $\pm$ 0.019	0.932 $\pm$ 0.020
r <sub>p</sub> (FW, WW)	0.915	0.861	0.962	0.823	0.871	0.929	0.934	0.925	0.897
r <sub>a</sub> (FW, BW)	0.9909 $\pm$	0.9898 $\pm$	0.9959 $\pm$	0.9821 $\pm$	0.9854 $\pm$	0.9899 $\pm$	0.9915 $\pm$	0.9931 $\pm$	0.9824 $\pm$
r <sub>p</sub> (FW, BW)	0.0036	0.0064	0.0012	0.0046	0.0044	0.0043	0.0020	0.0019	0.0055
r <sub>p</sub> (FW, BW)	0.9856	0.9749	0.9937	0.9718	0.9827	0.9885	0.9925	0.9934	0.9773

## Figure captions

Figure 1: Simulated gains in fillet yield in the first generation using a linear index  $I_{LFWR}$ , compared with the simulated gains obtained by selection on fillet yield  $I_Y$  (a) and on residual fillet weight  $I_{res}$  (b). The 27 data points are the combination of nine populations of sea bass, sea bream, rainbow trout and common carp with three selection intensities of 50%, 20% and 5%.

Figure 2: Comparison of simulated gains in fillet yield in the first generation using a linear index  $I_{LFWR}$  with their predicted values using selection index theory, either (a) with the genetic parameters of fillet weight and waste weight  $\Delta FY_{pred}(I_{LFWR})$ , or (b) using the genetic parameters of fillet weight and body weight  $\Delta FY_{pred}(I_{LFY})$ . The 27 data points are the combination of nine populations of sea bass, sea bream, rainbow trout and common carp with three selection intensities of 50%, 20% and 5%.

Figure 3: Comparison of simulated gains in fillet yield in the first generation by selection on fillet yield  $I_Y$  with their predicted values using the genetic parameters of fillet yield. (a) Global view, with all populations and selection intensities mixed. (b) With populations identified.

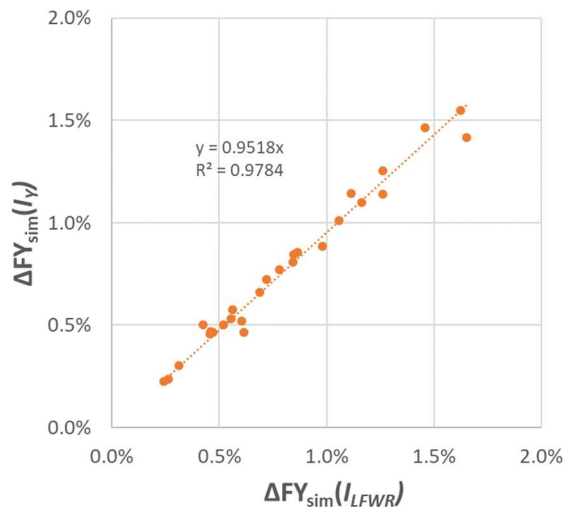
Figure 4: Comparison of simulated gains in fillet yield in the first generation by selection on residual fillet yield  $I_{res}$  with their predicted values using the genetic parameters of residual fillet weight. (a) Global view, with all populations and selection intensities mixed. (b) With populations identified.

Figure 5: Impact of the rounding of the genetic parameters used in the prediction equations (left panel: 3 decimals and right panel: 2 decimals for heritability and genetic correlations) to predict simulated gain with (a) selection index theory with genetic parameters of fillet weight and body weight (b) selection index theory with genetic parameters of fillet weight and waste weight and (c) breeder's equation using residual fillet yield.

Figure 6: Analysis of the sensitivity of the predicted genetic gain in fillet yield to the errors of the estimates of genetic parameters. Each boxplot represents a sample of 1000 values where the relevant genetic parameters were sampled in normal distributions representative of the precision of the estimates from Table 1 (see §2.2.8). Each of the 9 populations is represented with a specific colour, the full boxplot represents  $\Delta FY_{pred}(I_{LFY})$ , the one with diagonal lines  $\Delta FY_{pred}(I_{LFWR})$  and the one with vertical lines  $\Delta FY_{pred}(I_{res})$ .

Figure 1

**a**



**b**

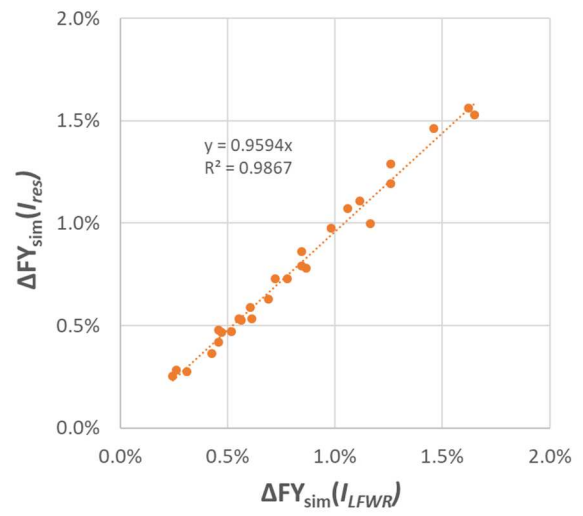
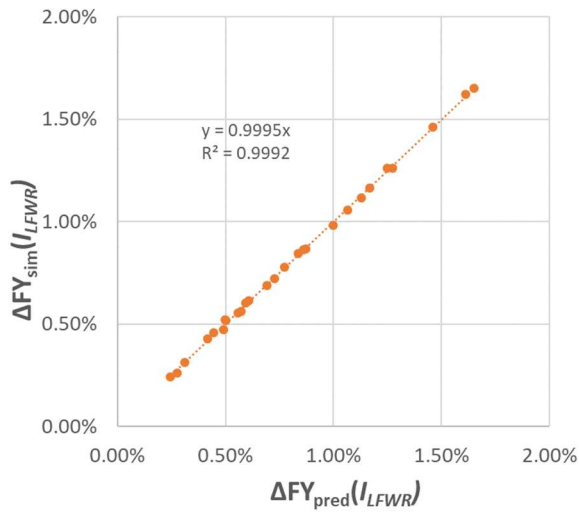


Figure 2

**a**



**b**

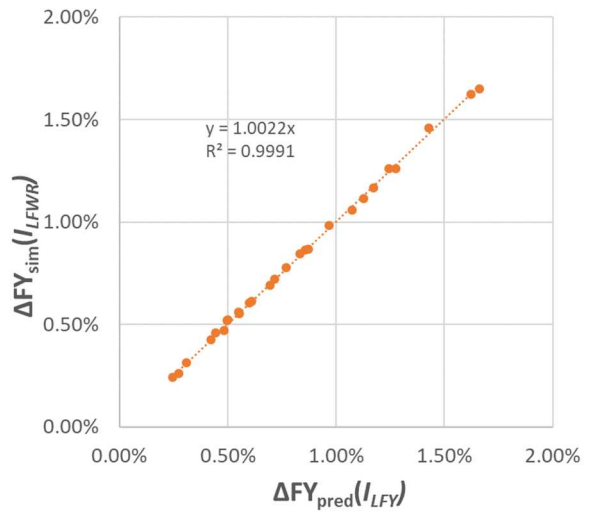


Figure 3

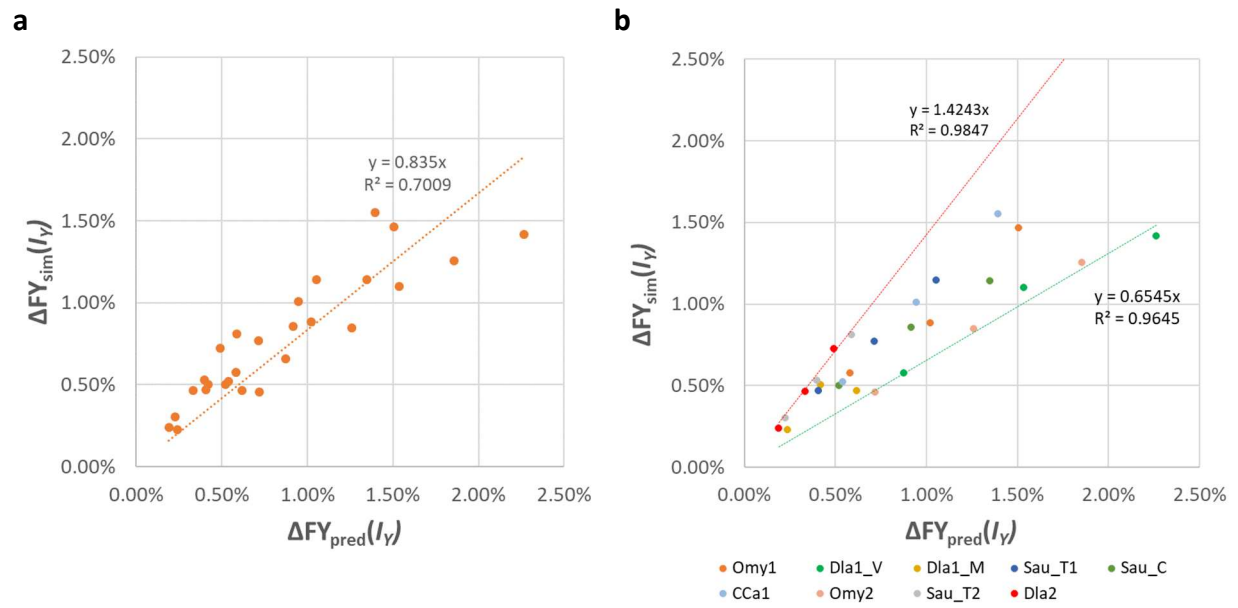


Figure 4

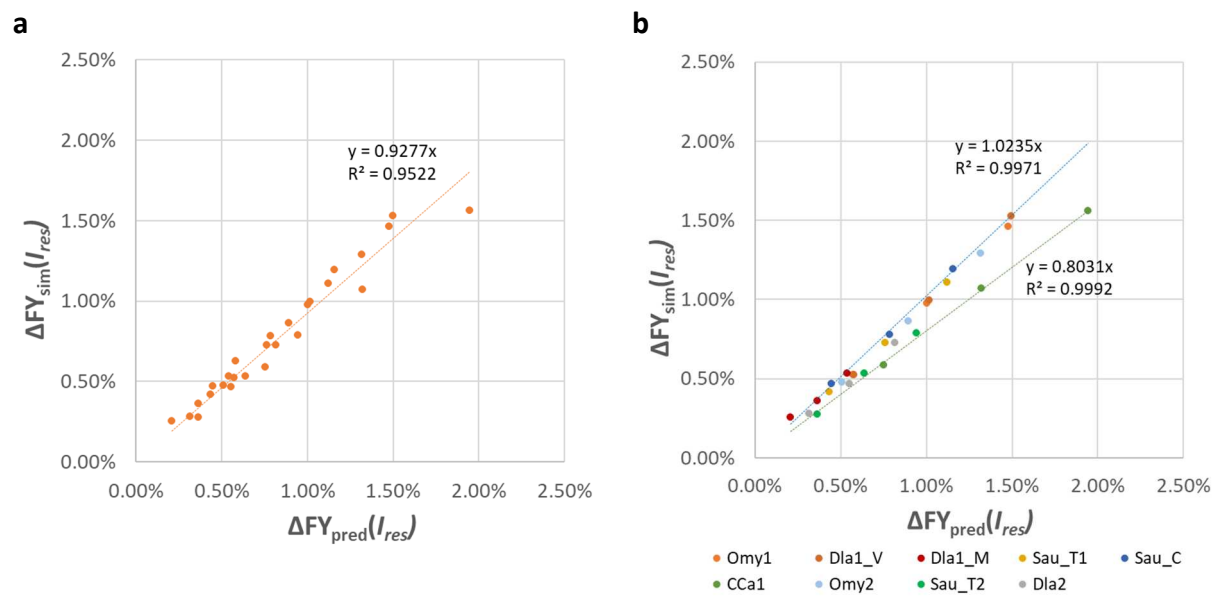


Figure 5

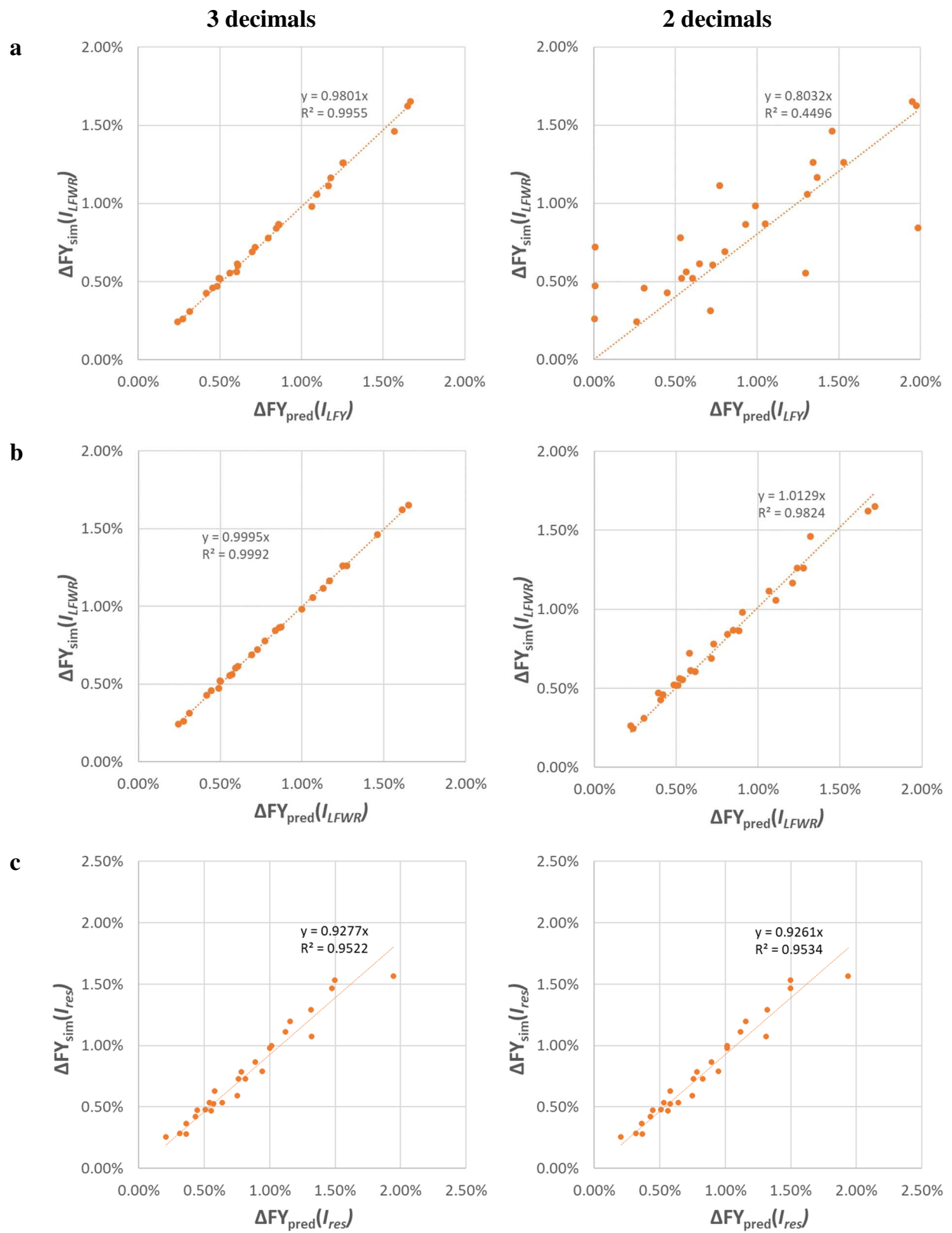


Figure 6

