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

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Running head : Estimating selection gain for fillet yield

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Abstract:

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

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

1. Introduction

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

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

The fact that selection gain on fillet yield can be obtained by those methods does not imply however, that such selection gains can easily be predicted from their genetic parameters. Indeed, it was previously shown that the heritability of a ratio trait, estimated from the analysis of covariance between relatives, was substantially different from the estimate obtained from simulated genetic gains (Gunsett, 1987), thus showing that the heritability of the ratio cannot be used to predict genetic gain. The same study showed that a method using selection index theory to approximate the process of selection on a ratio was more efficient, but still did not provide an exact estimate of genetic gain in all situations. On the contrary, when selection is done not on the ratio but on a linear index combining the numerator and the denominator in an optimal way, as proposed by Lin (1980) the genetic gain is expected to be perfectly predictable using standard selection index theory as long as the heritability, genetic and phenotypic correlations, and the phenotypic variance of both component traits are known (Lin and Aggrey, 2013).

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

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

To this end, we estimated the genetic parameters of body weight, fillet weight and waste weight (defined as waste weight= body weight – fillet weight) in nine field datasets from four important aquaculture species (rainbow trout *Oncorhynchus mykiss*, European sea bass *Dicentrarchus labrax*, gilthead sea bream *Sparus aurata* and common carp *Cyprinus carpio*). In the same datasets, we also estimated the genetic parameters of fillet yield and of residual fillet weight. Then, we performed stochastic simulation of selection using different selection indices to determine the expected genetic gain in the first generation, and compared this simulated gain with estimates derived from the genetic parameters of the traits using standard quantitative genetics theory for single traits (fillet yield and residual fillet weight) and linear indices.

2. Materials and methods

2.1. Estimation of genetic parameters for fillet traits

In order to perform simulations of fillet weight, body weight and waste weight with realistic values, we first estimated their genetic and phenotypic parameters. The database used was composed of carcass traits recorded on nine commercial stocks from four species: European sea bass (*Dicentrarchus labrax*), gilthead sea bream (*Sparus aurata*), common carp (*Cyprinus carpio*) and rainbow trout (*Oncorhynchus mykiss*). All fish used to estimate parameters were from factorial or partly factorial designs, with the pedigree identified by genotyping of microsatellite markers. All families were mixed, in order to minimize the environmental effect common to full siblings or half siblings. Number of offspring, of parents and of families as well as the age of the fish are given in Table 1. In all cases, the pedigree used comprised only the parental and the offspring generation. The estimations of genetic parameters were performed using an animal model with VCE (version 6.0.2, Groeneveld *et al.,* 2010), using specific fixed effects for each population. For fillet yield, a single trait model was used. For residual fillet weight the same model was used with the addition of a linear regression term with body weight. Then we used two bivariate models 1) with fillet weight and waste weight and 2) with fillet weight and body weight in order to estimate the heritability, genetic and phenotypic correlations of the component traits. Genetic parameters for sea bass were estimated separately in two batches from the same population, the first one fed a standard diet with marine ingredients (Dla1_M), and the second one (Dla1_V) fed a plant-based diet (Bestin et al., 2014), with sex (568 males and 289 females in Dla1_M, 550 males and 307 females in Dla1_V) and dam batch (corresponding to 3 different subpopulations in the breeding nucleus, with N=301, 371 and 185 in Dla1_M and N=281, 376 and 200 in Dla1_V) as fixed effects. We chose to estimate genetic parameters separately in the two batches because we anticipated different heritability estimates in the two batches, as already seen before for growth on marine vs. plant-based diets in the same species (Le Boucher et al., 2013). In a third batch from a different breeding population (Dla2), only sex (893 males, 482 females) was used as fixed effect. For sea bream, three datasets were available: two with fish reared in tanks and one with fish reared in sea cages. For the first batch of tank-farmed sea bream (Sau_T1), tank (the group was reared in two different tanks, N=1249 and 751) and presence-absence of vertebral deformities were used as fixed effects (48 present, 1952 absent), while only presence-absence of vertebral deformities (478 present, 1509 absent) was used for cage-farmed sea bream (Sau_C). For the second batch of tank-farmed sea bream

(Sau_T2), no fixed effects were included as the fish were all reared in a single tank, and the very few fish with vertebral deformities were discarded from the dataset. For the first batch of rainbow trout (Omy1), fixed effects were processing day (5 days, N= 379, 452, 457, 489, 240) and filleting operator (2 operators, N=414 and 1603). For the second batch (from a different population, Omy2) no fixed effects were included, as there was no effect of processing day and there was only one filleting operator. For common carp (Cca1), the only fixed effect included was sex (751 males, 754 females, 48 unknown). Maternal effects were tested in all populations and found non-significant, so they were not included in the models. Note that populations Dla1_M, Dla1_V, Sau_T, Sau_C and Omy1 were already used to obtain genetic parameters in our previous simulation work (Fraslin et al., 2018) with a different objective, identifying selection indices that can efficiently be used to improve for fillet yield. Population Cca1 is the same as the one used by (Prchal et al., 2018), and population Omy2 is the SIBS population in Vandeputte et al. (in press). As it was key for the present study to have the different genetic and phenotypic parameters shown in Table 1 estimated with the same models, on exactly the same fish and with the same fixed effects, we chose to re-estimate all of them starting from the base data, although some of those estimates have already been published before (but never the whole set of parameters that we use here, for any of those populations). The use of different software and of different rules to include/exclude animals may result in small changes compared to the initial publications.

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

2.2. Stochastic simulations

2.2.1. Model used

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

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

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

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

with $\boldsymbol{p}$, $\boldsymbol{a}$ and $\boldsymbol{e}$ following bivariate normal distributions, $\boldsymbol{p} = \begin{bmatrix} p_{FW0} \\ p_{WW0} \end{bmatrix} \sim N \ \left(\boldsymbol{\mu_p}\ ;\ \boldsymbol{V_p}\right)$ with $\boldsymbol{\mu_p} = \begin{bmatrix} \mu_{FW0} \\ \mu_{WW0} \end{bmatrix}$ and $\boldsymbol{V_p} = \begin{bmatrix} \sigma^2{}_{P_{FW}} & \sigma_{P_{FW}P_{WW}} \\ \sigma_{P_{FW}P_{WW}} & \sigma^2{}_{P_{WW}} \end{bmatrix}$, $\boldsymbol{a} = \begin{bmatrix} a_{FW0} \\ a_{WW0} \end{bmatrix} \sim N \ (\boldsymbol{\mu_a}\ ;\ \boldsymbol{V_a})$ with $\boldsymbol{\mu_a} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ and $\boldsymbol{V_a} = \begin{bmatrix} \sigma^2{}_{A_{FW}} & \sigma_{A_{FW}A_{WW}} \\ \sigma_{A_{FW}A_{WW}} & \sigma^2{}_{A_{WW}} \end{bmatrix}$, and $\boldsymbol{e} = \begin{bmatrix} e_{FW0} \\ e_{WW0} \end{bmatrix} \sim N \ (\boldsymbol{\mu_e}\ ;\ \boldsymbol{V_e})$ with $\boldsymbol{\mu_e} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ and $\boldsymbol{V_e} = \begin{bmatrix} \sigma^2{}_{E_{FW}} & \sigma_{E_{FW}E_{WW}} \\ \sigma_{E_{FW}E_{WW}} & \sigma^2{}_{E_{WW}} \end{bmatrix}$

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

2.2.2. Selection indices

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

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

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

$$\boldsymbol{b} = \begin{bmatrix} b_{FW} \\ b_{WW} \end{bmatrix} = \mathbf{V}_{\boldsymbol{p}}^{-1}\mathbf{V}_{\boldsymbol{a}} \begin{bmatrix} 1/\mu_{FW0} \\ -\mu_{FW0}/\mu_{WW0}^{2} \end{bmatrix} \quad [3]$$

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

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

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

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

2.2.4. Comparison of indices

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

2.2.5. Prediction of gains with linear indices

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

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

With $\begin{bmatrix}\widehat{a_{FW}}\\ \widehat{a_{WW}}\end{bmatrix} = \boldsymbol{V_a b}(i/\sqrt{\boldsymbol{b'V_p b}})$ [7]

where i is the standardized selection intensity. See 2.2.1 and 2.2.2 for the definitions of $\boldsymbol{V_a}$, $\boldsymbol{V_p}$ and $\boldsymbol{b}$.

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

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

Where $\widehat{a_{FW}}$ and $\widehat{a_{BW}}$ are estimated in the same way as with I_{LFWR}, using the genetic and phenotypic parameters of fillet weight and body weight (instead of fillet weight and waste weight) to establish $\boldsymbol{V_a}$, $\boldsymbol{V_p}$ and $\boldsymbol{b}$..

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

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

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

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

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

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

$$\Delta rFW = ih^2_{rFW}\sigma_{P_{rFW}} \quad [10]$$

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

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

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

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

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

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

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

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

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

2.2.9. Statistical analyses

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

3. Results

3.1. Estimation of genetic and phenotypic parameters

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

3.2. Comparison of selection indices

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

3.3. Prediction of gains with linear indices

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

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

When the simulated gain $\Delta FY_{sim}(I_Y)$ was predicted with $\Delta FY_{pred}(I_Y)$, using the breeder's equation with the genetic parameters of fillet yield, the prediction was by far less efficient. The coefficient of determination of the simulated gain by the predicted gain was 0.70, and the average simulated gain was only 84% of the predicted gain (Fig. 3a). However, this was very much dependent on the batch of fish: the average simulated gain was up to 142% of the predicted gain in the Dla2 stock of sea bass, while it could be as low as 65% of the predicted gain in the Dla1_V stock of sea bass (Fig. 3b). For each population, while the relation between the average simulated gain and the predicted gain could be very biased (as expresses by the slope of the regression), this bias did not depend strongly on the selection intensity, as the simulated response was highly linear with the predicted response (individual regressions within each population had a r^2 between 0.936 and 0.998)

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

When the simulated gain $\Delta FY_{sim}(I_{res})$ was predicted with $\Delta FY_{pred}(I_{res})$, the prediction was not perfect but reasonably accurate. The coefficient of determination of the simulated gain by the predicted gain was 0.952 on average, and the simulated gain was on average 92.7% of the predicted gain (Fig. 4a). This was also dependent on the batch of fish: the average simulated gain was up to 102% of the predicted gain in the Dla1_V stock of sea bass, and down to 80% of the predicted gain in the CCa1 stock of common carp (Fig. 4b)

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

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

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

4. Discussion

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

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

In order to plan selection for fillet yield, it is essential to be able to project potential gains from genetic parameters. Many studies have been conducted to estimate the genetic parameters of fillet traits in fish (Gjerde et al., 2012; Haffray et al., 2012; Kause et al., 2007, 2002; Kocour et al., 2007; Navarro et al., 2009; Nguyen et al., 2010; Powell et al., 2008; Prchal et al., 2018; Rutten et al., 2005b; Saillant et al., 2009; Sang et al., 2012; Schlicht et al., 2019; Thodesen et al., 2012; Tsai et al., 2015; Turra et al., 2018; Vandeputte et al., 2017, 2014). All of them estimated genetic parameters of fillet yield, and only a few estimated genetic parameters for (log-transformed) residual fillet yield (Haffray et al., 2012; Prchal et al., 2018; Vandeputte et al., 2017, 2014). Here we showed that the heritability of fillet yield only enables a very approximate estimation of potential gains in fillet yield (Fig. 3), thus questioning their usefulness to decide on future breeding programs. The populations where the estimate was the worst were among those with very high genetic correlations of fillet weight and body weight (0.990 or higher), but the bias could be in either direction (over estimation for Dla1_V and Omy2, under estimation for Dla2 and Sau_T2). However, one of the best estimates of genetic gain using the genetic parameters of fillet yield was for Omy1, for which the genetic correlation of fillet weight and body weight was also very high (0.9915). Thus, there seems to be no simple way to identify meaningful estimates of heritability for fillet yield. The fact that the heritability of a ratio, estimated from correlation between relatives, differs from the “realized “ heritability estimated from simulated selection had already been demonstrated by Gunsett (1987) in the context of selection for feed conversion ratio. The range of parameter values that Gunsett tested for the numerator and the denominator of the ratio was similar to our values for heritability (0.1 to 0.7, vs. 0.2 to 0.7 in our data), but very different for the genetic correlation which was 0 or 0.5 (0.982 to 0.996 for FW and BW in our data). Still, we see the same type of discrepancies between predicted and simulated values, but with higher biases in the present study: when both numerator and denominator heritability values were equal and the genetic correlation is 0.5, the genetic gain predicted by the ratio heritability was 95 to 121% of the simulated gain in Gunsett (1987), and this difference ranged from 65 to 142% in our case.

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

While modelling the joint genetic change in numerator and denominator values is less practically convenient than a simple prediction of one trait (the ratio of interest, fillet yield) with the breeder's equation, it is remarkably efficient and more satisfying as it also shows by which combination of increase or decrease of the numerator and denominator traits the ratio changes. Thus, as the published literature on selection for fillet yield in fish almost always includes genetic parameters of fillet weight and body weight, this could be used to evaluate potential gains. However, in all of the twenty previously cited studies on the subject, heritability estimates, phenotypic and genetic correlations were reported with (and thus rounded to) two decimals. We showed that given the very high correlations implied, rounding genetic and phenotypic correlations of FW and BW to two decimals may create large biases in the estimations of genetic gains, using the otherwise optimal selection index theory (Fig. 5a). One typical case in our data is population Dla2, where the genetic correlation of 0.9959 would be rounded to 1.00, leading to 0.00-0.01% predicted gain depending on selection intensity, while the expected gain with 0.9959 would range between 0.26 and 0.73%. A possible alternative is to use the genetic parameters of fillet weight and waste weight, as previously suggested (Fraslin et al., 2018), as they are less sensitive to this rounding issue (Fig. 5b). If genetic parameters of fillet weight and body weight are to be used, but they should be reported with 3 decimals, at least for what concerns genetic and phenotypic correlations.

A few previous studies used regression residuals of fillet weight on body weight as surrogates for fillet yield (Haffray et al., 2013, 2012; Prchal et al., 2018; Vandeputte et al., 2017, 2014). Our results show that such an approach should be more satisfying than using the genetic parameters of fillet yield, most of the time providing a reasonable estimate of potential gains in fillet yield (Fig. 4). It has to be noted that the above-cited studies did not use simple regression residuals, but regression residuals on log-log transformed data. The main advantage of log-log transformed data is that they reduce scaling effects and take into account possible non-linear allometric development of body parts. In the data sets we used here, although fillet weight and waste weight were in general not normally distributed, their bivariate distribution was closer to the bivariate normal distribution than the log-log distribution was. As we used bivariate normal distributions to run the simulations, we chose to use simple regression residuals and not log-residuals. Still, if the bivariate log-log distribution of the data fits more with a bivariate normal, there should be no reason for the use of log-residuals not to be equally good to predict gains in fillet yield as the simple residuals used in the present study. The fact that residual fillet weight is a single trait, easily managed with the breeder's equation, is a clear advantage, as knowing the heritability and the phenotypic variance, it is very easy to project genetic gains, more than with the two-traits linear index. A second advantage of this method is that it is little affected by the rounding of genetic parameters, as the usual two decimals are appropriate (Fig. 5c).

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

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

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References cited

Acosta Alba, I., Aubin, J., Cariou, S., Haffray, P., Quittet, B., Vandeputte, M., 2015. Le programme FilDor: associer sélection génétique et analyse d'impact environnemental des élevages de poissons. Courr. l'environnement l'Inra 65, 49–57.

Bestin, A., Dupont-Nivet, M., Haffray, P., Médale, F., Quillet, E., Vandeputte, M., Cariou, S., Desgranges, A., Laureau, S., Ricoux, R., Beutin, C., 2014. Genotype by diet interactions on growth and processing traits in rainbow trout (Oncorhynchus mykiss), European sea bass (Dicentrarchus labrax), gilthead sea bream (Sparus aurata) and meagre (Argyrosomus regius) fed diets with almost complete substitution, in: Proceedings, 10th World Congress of Genetics Applied to Livestock Production.

Campos-Montes, G.R., Montaldo, H.H., Armenta-Córdova, M., Martínez-Ortega, A., Caballero-Zamora, A., Castillo-Juárez, H., 2017. Incorporation of tail weight and tail percentage at harvest size in selection programs for the Pacific white shrimp Penaeus (Litopenaeus) vannamei. Aquaculture 468, 293–296. https://doi.org/10.1016/j.aquaculture.2016.10.034

Chevassus, B., Quillet, E., Krieg, F., Hollebecq, M.-G.G., Mambrini, M., Fauré, A., Labbé, L., Hiseux, J.-P.P., Vandeputte, M., Faure, A., Labbe, L., Hiseux, J.-P.P., Vandeputte, M., 2004. Enhanced individual selection for selecting fast growing fish: the “PROSPER” method, with application on brown trout (Salmo trutta fario). Genet. Sel. Evol. 36, 643–661. https://doi.org/10.1186/1297-9686-36-6-643

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to quantitative genetics. Longman, Harlow, England.

Famula, T.R., 1990. The equivalence of two linear methods for the improvement of traits expressed as ratios. TAG Theor. Appl. Genet. 79, 853–856. https://doi.org/10.1007/BF00224256

Fraslin, C., Dupont-Nivet, M., Haffray, P., Bestin, A., Vandeputte, M., 2018. How to genetically increase fillet yield in fish: New insights from simulations based on field data. Aquaculture 486, 175–183. https://doi.org/10.1016/j.aquaculture.2017.12.012

Gjedrem, T., 2012. Genetic improvement for the development of efficient global aquaculture: A personal opinion review. Aquaculture 344–349, 12–22. https://doi.org/10.1016/j.aquaculture.2012.03.003

Gjerde, B., Mengistu, S.B., Ødegård, J., Johansen, H., Altamirano, D.S., 2012. Quantitative genetics of body weight, fillet weight and fillet yield in Nile tilapia (Oreochromis niloticus). Aquaculture 342–343, 117–124. https://doi.org/10.1016/j.aquaculture.2012.02.015

Gunsett, F.C., 1987. Merit of utilizing the heritability of a ratio to predict the genetic change of a ratio. J. Anim. Sci. 65, 936–942.

Gunsett, F.C., 1984. Linear Index Selection to Improve Traits Defined as Ratios. J. Anim. Sci. 59, 1185–1193.

Haffray, P., Bugeon, J., Pincent, C., Chapuis, H., Mazeiraud, E., Rossignol, M.N.M.-N., Chatain, B., Vandeputte, M., Dupont-Nivet, M., 2012. Negative genetic correlations between production traits and head or bony tissues in large all-female rainbow trout (Oncorhynchus mykiss). Aquaculture 368–369, 145–152. https://doi.org/10.1016/j.aquaculture.2012.09.023

Haffray, P., Bugeon, J., Rivard, Q., Quittet, B., Puyo, S., Allamelou, J.M., Vandeputte, M., Dupont-Nivet, M., 2013. Genetic parameters of in-vivo prediction of carcass, head and fillet yields by internal ultrasound and 2D external imagery in large rainbow trout (Oncorhynchus mykiss). Aquaculture 410–411, 236–244. https://doi.org/10.1016/j.aquaculture.2013.06.016

Kankainen, M., Setälä, J., Kause, A., Quinton, C., Airaksinen, S., Koskela, J., 2016. Economic values of supply chain productivity and quality traits calculated for a farmed European whitefish breeding program. Aquac. Econ. Manag. 20, 131–164. https://doi.org/10.1080/13657305.2016.1155961

Kause, A., Paananen, T., Ritola, O., Koskinen, H., 2007. Direct and indirect selection of visceral lipid weight, fillet weight, and fillet percentage in a rainbow trout breeding program. J. Anim. Sci. 85, 3218–3227.

Kause, A., Ritola, O., Paananen, T., Mantysaari, E., Eskelinen, U., 2002. Coupling body weight and its composition: a quantitative genetic analysis in rainbow trout. Aquaculture 211, 65–79.

Kocour, M., Mauger, S., Rodina, M., Gela, D., Linhart, O., Vandeputte, M., 2007. Heritability estimates for processing and quality traits in common carp (Cyprinus carpio L.) using a molecular pedigree. Aquaculture 270, 43–50. https://doi.org/10.1016/j.aquaculture.2007.03.001

Le Boucher, R., Vandeputte, M., Dupont-Nivet, M., Quillet, E., Ruelle, F., Vergnet, A., Kaushik, S., Allamellou, J.M., Médale, F., Chatain, B., 2013. Genotype by diet interactions in European sea bass (Dicentrarchus labrax L.): Nutritional challenge with totally plant-based diets. J. Anim. Sci. 91, 44–56. https://doi.org/10.2527/jas.2012-5311

Lin, C.Y., 1980. Relative Efficiency of Selection Methods for Improvement of Feed Efficiency. J. Dairy Sci. 63, 491–494. https://doi.org/10.3168/jds.S0022-0302(80)82960-2

Lin, C.Y., Aggrey, S.E., 2013. Incorporation of economic values into the component traits of a ratio : Feed efficiency. Poult. Sci. 92, 916–922. https://doi.org/10.3382/ps.2012-02688

Lynch, M., Walsh, B., 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, MA.

Navarro, A., Zamorano, M.J., Hildebrandt, S., Ginès, R., Aguilera, C., Afonso, J.M., 2009. Estimates of heritabilities and genetic correlations for growth and carcass traits in gilthead seabream (Sparus auratus L.), under industrial conditions. Aquaculture 289, 225–230.

Nguyen, N.H., Ponzoni, R.W., Abu-Bakar, K.R., Hamzah, A., Khaw, H.L., Yee, H.Y., Bu-Bakar, K.R., 2010. Correlated response in fillet weight and yield to selection for increased harvest weight in genetically improved farmed tilapia (GIFT strain), Oreochromis niloticus. Aquaculture 305, 1–5. https://doi.org/10.1016/j.aquaculture.2010.04.007

Nguyen, T.T.T., Hayes, B.J., Guthridge, K., Ab Rahim, E.S., Ingram, B.A., 2011. Use of a microsatellite-based pedigree in estimation of heritabilities for economic traits in Australian blue mussel, Mytilus galloprovincialis. J. Anim. Breed. Genet. 128, 482–490. https://doi.org/10.1111/j.1439-0388.2011.00948.x

Powell, J., White, I., Guy, D., Brotherstone, S., 2008. Genetic parameters of production traits in Atlantic salmon (Salmo salar). Aquaculture 274, 225–231.

Prchal, M., Bugeon, J., Vandeputte, M., Kause, A., Vergnet, A., Zhao, J., Gela, D., Genestout, L., Bestin, A., Haffray, P., Kocour, M., 2018. Potential for Genetic Improvement of the Main Slaughter Yields in Common Carp With in vivo Morphological Predictors. Front. Genet. 9, 1–13. https://doi.org/10.3389/fgene.2018.00283

Roff, D.A., 1995. The estimation of genetic correlations from phenotypic correlations: A test of Cheverud's conjecture. Heredity (Edinb). 74, 481–490. https://doi.org/10.1038/hdy.1995.68

Rutten, M.J.M., Bovenhuis, H., Komen, H., 2005a. Genetic parameters for fillet traits and body measurements in Nile tilapia (Oreochromis niloticus L.). Aquaculture 246, 125–132.

Rutten, M.J.M., Komen, H., Bovenhuis, H., 2005b. Longitudinal genetic analysis of Nile tilapia (Oreochromis niloticus L.) body weight using a random regression model. Aquaculture 246, 101–113.

Saillant, E., Dupont-Nivet, M., Sabourault, M., Haffray, P., Laureau, S., Vidal, M.-O.O., Chatain, B., 2009. Genetic variation for carcass quality traits in cultured sea bass (Dicentrachus labrax). Aquat. Living Resour. 22, 105–112. https://doi.org/10.1051/alr/2009010

Sang, N. Van, Klemetsdal, G., Odegard, J., Gjoen, H.M., 2012. Genetic parameters of economically important traits recorded at a given age in striped catfish (Pangasianodon hypophthalmus). Aquaculture 344–349, 82–89.

Schlicht, K., Krattenmacher, N., Lugert, V., Schulz, C., Thaller, G., Tetens, J., 2019. Estimation of genetic parameters for growth and carcass traits in turbot (*Scophthalmus maximus*). Arch. Anim. Breed. 62, 265–273. https://doi.org/10.5194/aab-62-265-2019

Shirali, M., Varley, P.F., Jensen, J., 2018. Bayesian estimation of direct and correlated responses to selection on linear or ratio expressions of feed efficiency in pigs. Genet. Sel. Evol. 50, 33. https://doi.org/10.1186/s12711-018-0403-0

Thodesen, J., Rye, M., Wang, Y.-X., Bentsen, H.B., Gjedrem, T., 2012. Genetic improvement of tilapias in China: Genetic parameters and selection responses in fillet traits of Nile tilapia (Oreochromis niloticus) after six generations of multi-trait selection for growth and fillet yield. Aquaculture 366–367, 67–75. https://doi.org/10.1016/j.aquaculture.2012.08.028

Tsai, H.Y., Hamilton, A., Guy, D.R., Tinch, A.E., Bishop, S.C., Houston, R.D., 2015. The genetic architecture of growth and fillet traits in farmed Atlantic salmon (Salmo salar). BMC Genet. 16. https://doi.org/10.1186/s12863-015-0215-y

Turra, E.M., Fernandes, A.F.A., De Alvarenga, E.R., Teixeira, E.A., Alves, G.F.O., Manduca, L.G., Murphy, T.W., Silva, M.A., 2018. Longitudinal analyses of correlated response efficiencies of fillet traits in Nile tilapia. Animal 12, 445–453. https://doi.org/10.1017/S1751731117001768

Vandeputte, M., Garouste, R., Dupont-Nivet, M., Haffray, P., Vergnet, A., Chavanne, H., Laureau, S., Ron, T.B.T.B., Pagelson, G., Mazorra, C., Ricoux, R., Marques, P., Gameiro, M., Chatain, B., 2014. Multi-site evaluation of the rearing performances of 5 wild populations of European sea bass (Dicentrarchus labrax). Aquaculture 424–425, 239–248. https://doi.org/10.1016/j.aquaculture.2014.01.005

Vandeputte, M., Puledda, A., Tyran, A.S.A.S., Bestin, A., Coulombet, C., Bajek, A., Baldit, G., Vergnet, A., Allal, F., Bugeon, J., Haffray, P., 2017. Investigation of morphological predictors of fillet and carcass yield in European sea bass (Dicentrarchus labrax) for application in selective breeding. Aquaculture 470, 40–49. https://doi.org/10.1016/j.aquaculture.2016.12.014

Varkoohi, S., Moradi Shahr Babak, M., Pakdel, A., Nejati Javaremi, A., Zaghari, M., Kause, A., 2010. Response to selection for feed conversion ratio in Japanese quail. Poult. Sci. 89, 1590–1598. https://doi.org/10.3382/ps.2010-00744

Table 1: Phenotypic means (± standard deviation) and genetic parameters (± 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	*Dicentrarchus labrax*			*Sparus aurata*			*Oncorhynchus mykiss*		*Cyprinus carpio*
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 ± 194.1	869.2 ± 169.2	285.0 ± 65.0	321.0 ± 44.6	381.8 ± 63.3	250.4 ± 59.3	1622.4 ± 358.4	1923.3 ± 376.0	1910.5 ± 284.6
Fillet weight -FW (g)	411.6 ± 116.4	496.0 ± 101.0	166.7 ± 39.1	187.8 ± 28.1	230.2 ± 41.4	143.6 ± 36.2	1047.1 ± 240.8	1317.4 ± 268.6	952.3 ±155.6
Waste weight - WW (g)	322.4 ± 81.8	373.2 ± 74.2	118.3 ± 26.4	133.2 ± 18.5	151.6 ± 23.9	106.8 ± 24.1	575.3 ± 122.5	605.9 ± 113.5	958.2 ±136.6
Residual FW - rFW (g)	0 ± 19.74	0 ± 22.53	0 ± 4.40	0 ± 6.63	0 ± 7.67	0 ± 5.48	0 ± 29.46	0 ± 30.78	0 ± 33.24
Fillet yield - FY	0.557 ± 0.035	0.571 ± 0.027	0.584 ± 0.016	0.584 ± 0.021	0.601 ± 0.023	0.571 ± 0.026	0.644 ± 0.019	0.683 ±0.020	0.497 ± 0.019
h^2 BW	0.395 ± 0.083	0.213 ± 0.061	0.357 ± 0.046	0.403 ± 0.056	0.334 ± 0.062	0.212 ± 0.056	0.350 ± 0.052	0.382 ± 0.068	0.632 ± 0.094
h^2 FW	0.413 ± 0.086	0.226 ± 0.064	0.342 ± 0.046	0.419 ± 0.057	0.322 ± 0.060	0.184 ± 0.053	0.339 ± 0.050	0.375 ± 0.067	0.539 ± 0.086
h^2 WW	0.359 ± 0.079	0.179 ± 0.057	0.374 ± 0.046	0.351 ± 0.057	0.343 ± 0.063	0.253 ± 0.061	0.353 ± 0.050	0.399 ± 0.066	0.723 ± 0.091
h^2 rFW	0.270 ± 0.075	0.101 ± 0.053	0.256 ± 0.064	0.280 ± 0.050	0.271 ± 0.052	0.209 ± 0.053	0.395 ± 0.050	0.399 ± 0.052	0.542 ± 0.089
h^2 FY	0.316 ± 0.073	0.111 ± 0.054	0.148 ± 0.037	0.310 ± 0.052	0.224 ± 0.048	0.110 ± 0.040	0.384 ± 0.053	0.460 ± 0.077	0.356 ± 0.071
r_a (FW,WW)	0.942 ± 0.022	0.935 ± 0.040	0.976 ± 0.007	0.874 ± 0.031	0.895 ± 0.031	0.948 ± 0.023	0.925 ± 0.016	0.925 ± 0.019	0.932 ±0.020
r_p (FW, WW)	0.915	0.861	0.962	0.823	0.871	0.929	0.934	0.925	0.897
r_a (FW, BW)	0.9909 ± 0.0036	0.9898 ± 0.0064	0.9959 ± 0.0012	0.9821 ± 0.0046	0.9854 ± 0.0044	0.9899 ± 0.0043	0.9915 ± 0.0020	0.9931 ± 0.0019	0.9824 ± 0.0055
r_p (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

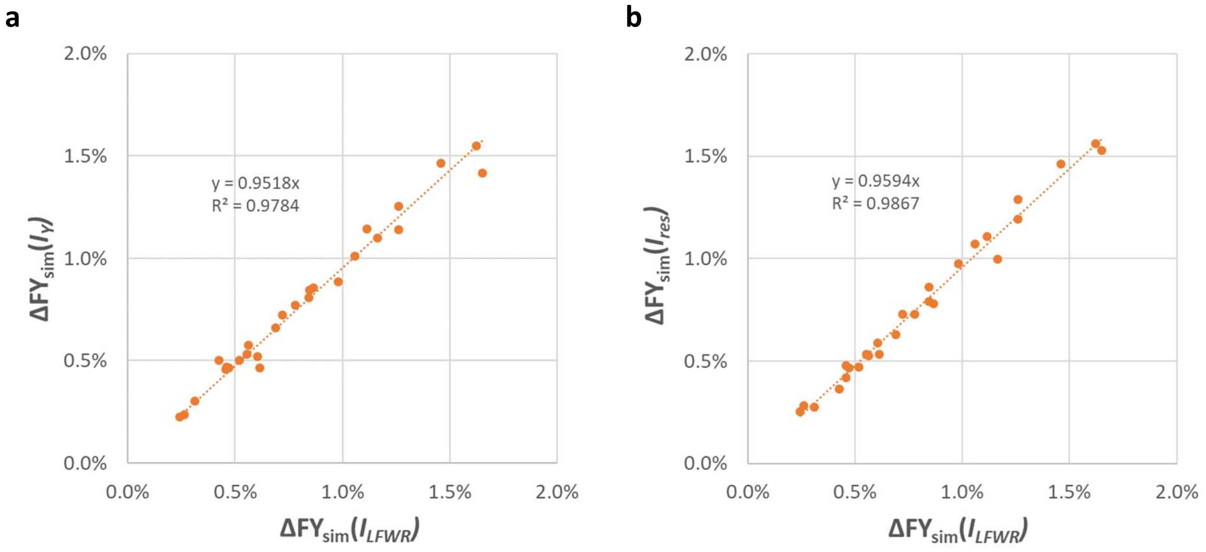


Figure 2

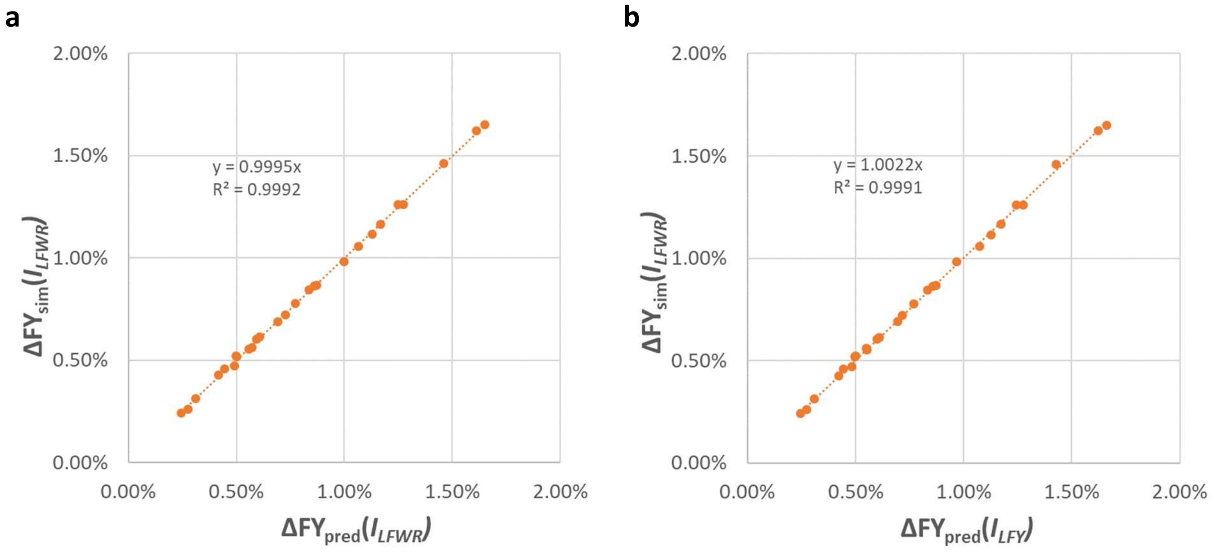


Figure 3

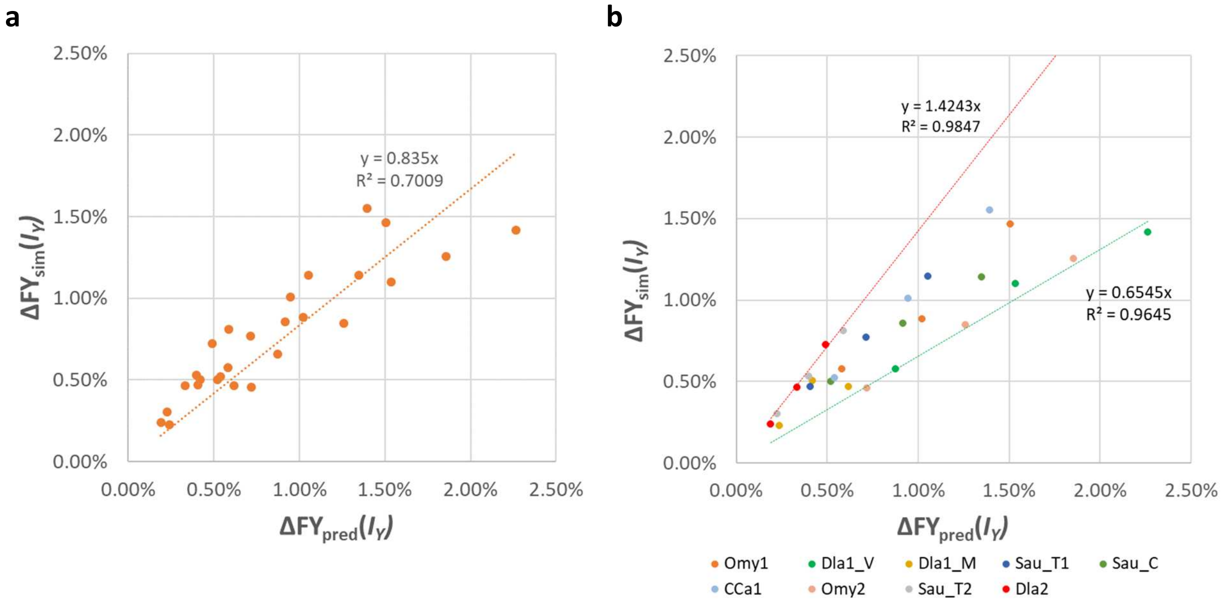


Figure 4

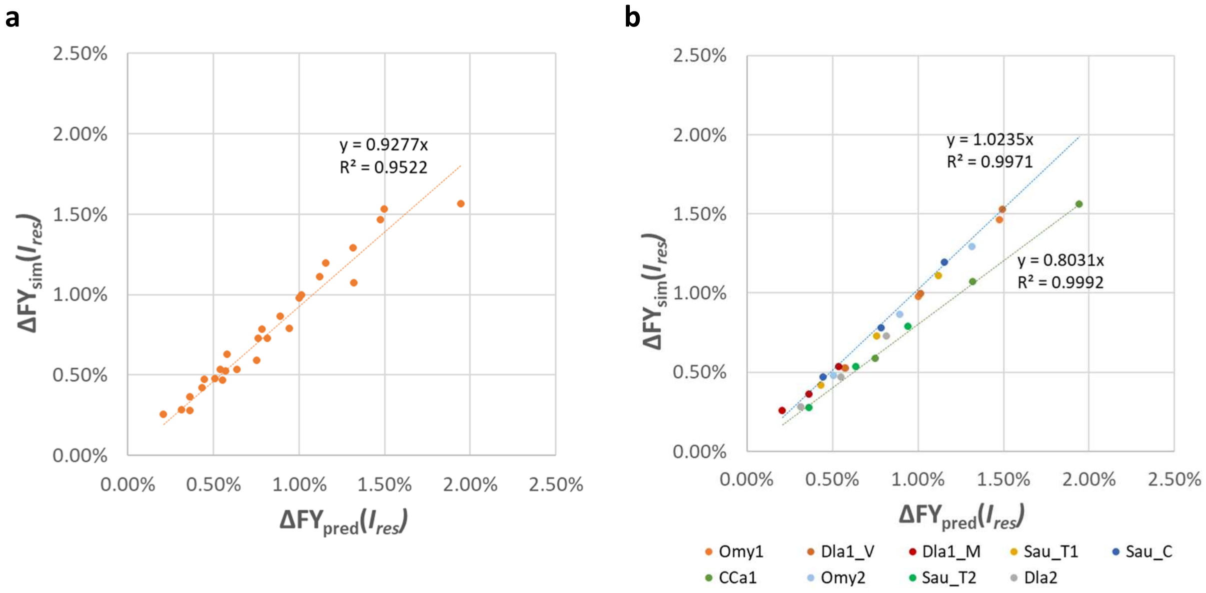


Figure 5

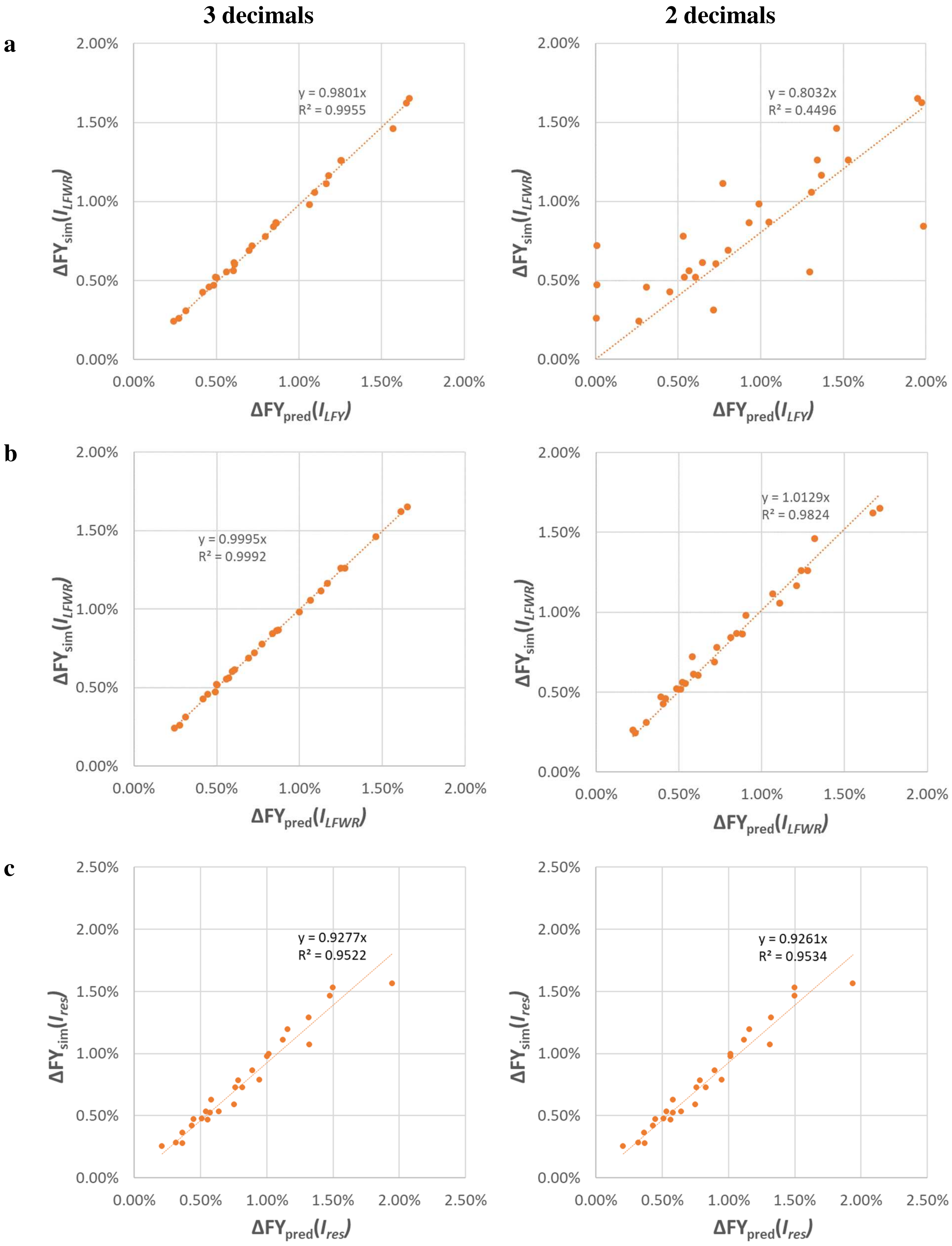
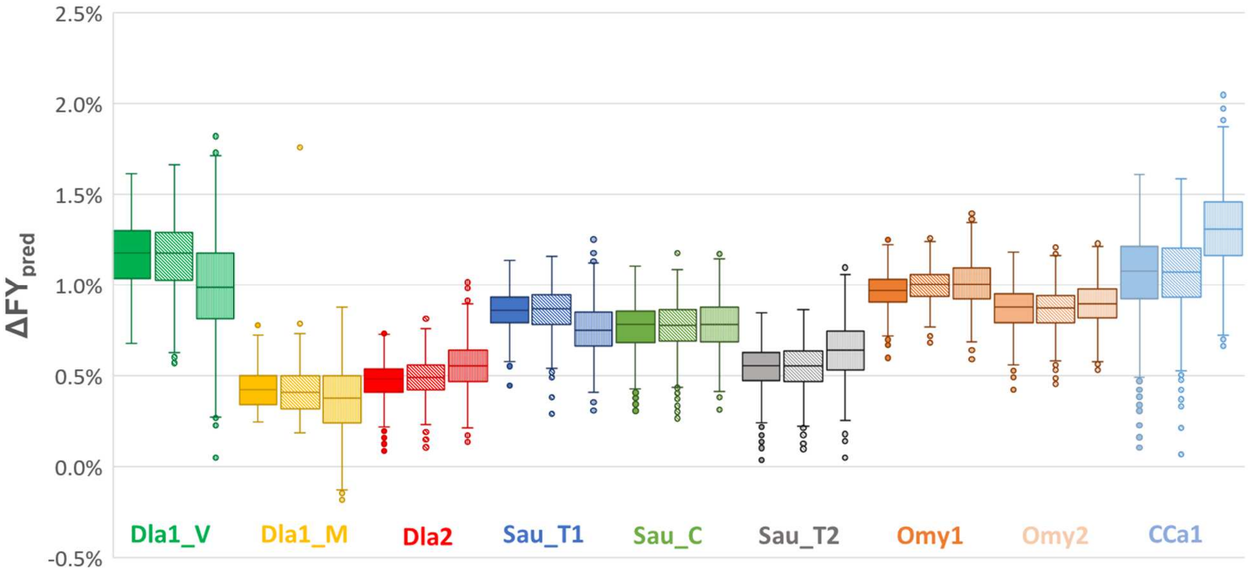

3 decimals
2 decimals
a
y = 0.9801x
R² = 0.9955
$\Delta FY_{sim}(I_{LFWR})$
$\Delta FY_{pred}(I_{LFY})$
y = 0.8032x
R² = 0.4496
$\Delta FY_{sim}(I_{LFWR})$
$\Delta FY_{pred}(I_{LFY})$
b
y = 0.9995x
R² = 0.9992
$\Delta FY_{sim}(I_{LFWR})$
$\Delta FY_{pred}(I_{LFWR})$
y = 1.0129x
R² = 0.9824
$\Delta FY_{sim}(I_{LFWR})$
$\Delta FY_{pred}(I_{LFWR})$
c
y = 0.9277x
R² = 0.9522
$\Delta FY_{sim}(I_{res})$
$\Delta FY_{pred}(I_{res})$
y = 0.9261x
R² = 0.9534
$\Delta FY_{sim}(I_{res})$
$\Delta FY_{pred}(I_{res})$
0.00%
0.50%
1.00%
1.50%
2.00%
2.50%

Figure 6


2.5%
2.0%
1.5%
1.0%
0.5%
0.0%
-0.5%
ΔFY_{pred}
Dla1_V
Dla1_M
Dla2
Sau_T1
Sau_C
Sau_T2
Omy1
Omy2
CCa1