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Aquaculture
October 2013, Volumes 410–411, Pages 236–244
http://dx.doi.org/10.1016/j.aquaculture.2013.06.016
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Archimer
http://archimer.ifremer.fr

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*) ☆

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Abstract:

Selection to improve processing yields relies on sib selection, in which live candidates are ranked according to their family breeding value. This approach limits genetic progress, as it only exploits genetic variability between families and not within them. Indirect criteria measured on live candidates could overcome this limitation. The present study (1) proposes a procedure to identify indirect criteria to predict processing yields in rainbow trout (head, carcass and fillet yields), (2) estimates genetic parameters of these indirect criteria, and (3) predicts relative genetic gains in processing yields using full-sib selection or indirect individual selection on those indirect criteria.

DNA-pedigreed all-female rainbow trout *Oncorhynchus mykiss* (n = 2029, 1631.0 ± 355.6 g) from 600 families produced from 100 sires and 60 dams were characterized by external and internal non-lethal morphological measures using digital pictures and real time ultrasound tomography. Nineteen landmarks were recorded on the digital pictures to define the outline of the body, head and lateral line. Their coordinates were used to calculate different lengths, heights and areas. Five different internal thicknesses were measured by ultrasound tomography.

In the first phase of this study, processing yields were predicted using multiple linear regressions including both external and internal morphometric variables. In a second phase, the heritability of the predicted values and their genetic correlations with real processing yields were estimated using animal models. Predicted yields exhibited intermediate heritabilities (0.25–0.28) that were half the value of heritabilities for real processing yields (0.47–0.55), but had high genetic correlations with these real yields (0.87–0.90). The relative efficiency of indirect selection (IS) on these indirect criteria was compared to theoretical mass selection (MS) or sib selection (FS) with different family sizes (10 or 100) and two different selection pressures (10% or 40%). At the same selection pressure (10%, with 100 sibs per family %), full-sib selection created genetic progress 49.6% to 60.5% higher than indirect selection according to the processing yield targeted. However, when sib-selection pressure was limited to a more realistic between family selection pressure (40% and 10 sibs per family), indirect selection with 10% selection pressure was 21.9% to 32.7% more efficient than sib selection.

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Highlights

► Application of ultrasound and 2D imagery to predict processing yields in rainbow trout. ► Estimation of genetic parameters and genetic correlations with yields to predict. ► Comparison of different strategy of selection.

Keywords: Salmonids ; Heritability ; Fillet yield ; Selection ; Aquaculture ; Morphometry

☆ Paper presented at the International Symposium on Genetics in Aquaculture XI, Auburn, AL, USA, June 24–30, 2012.

1. Introduction

During the last twenty years (1987-2007), the proportion of rainbow trout *Oncorhynchus mykiss* slaughtered at a higher body weight than 300 g increased from 9 % to 65 % in France (Agreste, 2009). This increase in slaughtering weight up to 1-3.5 kg was driven by the consumer's demand for fresh or smoked fillet. It was allowed by important technological investments such as water oxygenation, use of extruded feed, vaccination, all-female monosexing, sterilization by triploid induction and selective breeding. Initially validated experimentally in brown trout *Salmo trutta* to improve growth (Chevassus et al., 2004), the optimized PROSPER procedure of mass selection was transferred to the farmers of rainbow trout starting in 1993 (Haffray et al., 2004). In 1996, gutted carcass yield was included in the selected traits based on individual scoring of fish morphology for more "salmon like" and elongated body shape. DNA parentage assignment with microsatellite markers was introduced in 1998 to optimize mating and to manage inbreeding. Since 2004, DNA fingerprinting was used to initiate sib selection on carcass yield based on intermediate heritability estimated with families mixed together since eyed stage and a posteriori DNA-pedigreed (Haffray et al., 2012b).

In the absence of high density SNP information that would allow within-family genomic selection, selection to improve processing yields is for the time being limited in practice to sib-selection to rank live candidates on their family breeding value estimated on slaughtered sibs. However, such a selection limits genetic progress as it uses only between-sire and between-dams additive variation and not within-family variation. The development of indirect criteria measured on live candidates could overcome this limit through the use of within-family variation to increase genetic gains through indirect selection with higher selection intensity than sib-selection. However, the relative advantage of sib- or indirect- selection depends on the genetic parameters of the traits but also on the number of sibs measured (Falconer and Mackay, 1996).

Across fish species, some authors have estimated heritability of single or combined external or internal body shape traits and their genetic correlations with weights or yields of carcass or fillets (Gjerde and Shaeffer, 1989; Rye and Refstie, 1995; Neira et al., 2004; Rutten et al., 2005; Kocour et al., 2007). However, heritabilities for these criterias and their genetic correlations with the yields to predict were in general limited. Moreover, internal measures were done on slaughtered sib and could not be used on live candidates. Ultrasound imagery presents a high potential for the *in-vivo* internal morphometric measures and prediction of processing yields in fish (Bosworth et al., 2001) but, as far as we know, there is no publication reporting its application to fish breeding to improve processing yields.

The present publication reports 1) a procedure to identify external and internal traits (measured by ultrasounds) to be combined by linear regression in indirect criteria to predict processing yields (head, carcass or fillet yields) 2) heritability of these criteria and their genetic correlation with the yield to predict. 3) predicted genetic progress according to sib or indirect selection on theses indirect criteria. This study used large all-female rainbow trout reared in fresh water in commercial French conditions of production. The results are expected to be useful to increase the efficiency of selection on processing yields.

2. Material and methods

2.1. Production of experimental fish and DNA collection

The fish are the same as those reported in Haffray et al. (2012a, b). Briefly, they were derived from a commercial line from the Aqualande breeding company (France), already mass selected for growth for three generations using PROSPER procedure principles (Chevassus et al., 2004) and on external morphology (individual visual scoring). Pedigree was known with DNA parentage assignment. Inbreeding (F) level estimated during three generations with the "pedigree" package of the R software was 0.45%.

Briefly and as reported previously (Haffray et al., 2012a and b), 600 full-sib families were produced at the Aqualande breeding centre (Pissos, France). Sixty dams (two years old) were crossed with 100 sex-reversed females (defined as sires) in 10 full factorial crosses of six dams by 10 sires following the recommendations of Dupont-Nivet et al. (2006). At the eyed stage, 12 groups of five spawns each were created based on homogeneity for mean eyed egg size. The initial differences of mean weight between groups were progressively decreased by using different feeding ratios for each group (Haffray et al., 2012a). When groups achieved the same mean body length (147 days post fertilization, dpf), 250 individuals per group were pooled (in total 3000 fish). At 198 dpf, fish were individually tagged with RFID transponders. Their DNA was collected through a fin sample preserved in 95% ethanol. At 220 dpf, fish were transferred to the “Viviers de la Hountine” fish farm (Belin-Béliet, France) located 12 km downstream the Pissos hatchery. Fish were reared in fibreglass tanks until they reached 0.5 g and then in concrete raceways until the end of the experiment. The water temperature varies from 3 to 20°C and oxygen concentration was not limiting (> 80% saturation). During growth, fish were fed to satiation using extruded commercial feed (Le Gouessant, Lamballe, France). Density increased progressively to reach 70 kg/m^3. Survival rate was 92.6 % from tagging (d198) to slaughtering (d509).

2.2. Processing trait recording

The slaughtering protocol detailed in Haffray et al. (2012b) limited the post-mortem storage duration to less than five days. Fish (*n* = 2042) were randomly slaughtered at 509 or 511 dpf. The two sub-groups were treated in the same way: three days of fasting, live transportation by truck to the Aqualande processing plant (Roquefort, France, 50 km from the fish farms) for slaughter (CO_2 anaesthesia, followed by bleeding in icy water), and then transportation by refrigerated truck to IFREMER (Nantes, France) for processing and data collection. Data collection at fish processing was done between two to four days after slaughter. Malformed fish (*n* = 18) evaluated by visual examination of the vertebral axis after filleting were excluded from the measurements. Four other fish were discarded due to errors in data collection.

Non malformed fish (*n* = 2020) were assigned to their parents by the French laboratory for livestock genotyping LABOGENA (ISO 17025 accredited, Jouy-en-Josas, France) using microsatellites markers. The rate of correct assignment to one unique parental pair with a maximum of one mismatch authorized was 99.5 % and 559 full-sib families were represented out of the 600 expected (Haffray et al., 2012 b). All sires and all dams were represented. Spontaneous triploids (*n* = 48), identified from their DNA-fingerprint signature, were removed from the statistical analysis (see Haffray et al., 2012a).

Body length (BL), body weight (BW), Fulton coefficient K (= BW (g) * 100 / BL^3 (cm)), head yield (*Head%*), gutted carcass yield (*Carc%*), fillet yield (*Fil%*) and headless gutted carcass yield (*HGCarc%*) already reported by Haffray et al. (2012b) are presented Table 1. *HGCarc%* was preferred to *Fil%* to express fillet yield as it exhibited very high genetic correlation with

fillet yield (0.97 ± 0.01) and a higher heritability (0.54 ± 0.04 *vs* 0.35 ± 0.04) making indirect selection on this trait more efficient than direct selection on fillet yield (see Haffray et al., 2012b).

2.3. External and internal body shape traits recording

Each individual was photographed using a digital camera (Canon PowerShot S50 2592X1944 pixels) at processing in Nantes. Coordinates of nineteen morphometric points (landmarks) were digitized using Visilog 6.7 software (Figure 1a). Theses coordinates allowed calculating twenty three variables (Figure 1b to 1d): seven heights (Ht and H1 to H6), the head perimeter (P), seven lengths (L1 to L7), six surfaces (A1 to A6) and two angles (β1 and β2). The distances between two landmarks A (x_A, y_A) and B (x_B, y_B) were calculated by $d = \sqrt{(x_B - x_A)^2 + (y_B - y_A)^2}$. Surfaces were calculated based on angle estimation with Al-Kashi theorem in a triangle between three landmarks A, B and C for which $AB^2=AC^2+BC^2-2.AC.BC.\cos(A\hat{C}B)$. Each of the six surfaces was first divided in two triangles for which heights were also estimated using Al-Kashi theorem. Then surface of each triangle was calculated, as Surface = (base * height) / 2, and added to get the total surface of each two triangles.

Four thicknesses and one internal depth measured with ultrasound imagery (Hospimedi, LC100, 7.5 MHz) were represented in Figure 2: Echo4, Echo5, Echo8, Echo11 and Echo 23.

Eighty four new variables were calculated by the division of the previously measured twenty eight variables by BW, BL and LogBW. Twenty one additional variables which we considered as having some biological meaning were also calculated as differences between sums, subtraction and ratios of the calculated variables. The total number of variables was one hundred twenty eight. Only variables with significant effect in the model to predict processing yields were kept for the publication.

2.4. Selection of variables and definition of models to predict yields

Among the high number of variables used to describe the fish morphology, a challenging task was to find the best ones to predict yields. Geometric morphometric is a powerful statistic method used to describe and analysis shape changes (Rohlf and Markus, 1993). In order to identify the morphology associated to high or low processing yields, two groups of 100 fish each with the 10% highest or the 10% lowest yields were randomly chosen with no significant difference in mean BW.

Shape variations of these 200 fishes were analysed using APS software (Penin, 2007). Briefly the method consists to a Procrustes superimposition of landmarks. The principal components of shape (PCs) are computed from a principal component analysis of the Procrustes residuals. Finally the low and high yields groups were defined in the overall population and a discriminant analysis was performed to obtain the shape vector which discriminates the two groups. The statistical tests were calculated with a reduced number of PCs corresponding to the high value of R^2 and F-test. APS allows a graphical visualization of the discriminant function, the shape differences obtain along the discriminant vector contribute and thus contributing to identify pertinent variables to introduce in a prediction model.

Finally these variables were used in a multiple linear regression (Reg.best, R software package) to find the best prediction model with highest R^2 and F value to predict *Carc%* (*ModCarc%*), *Head%* (*ModHead%)* and *HGCarc%* (*ModHGCarc%*).

2.5. Validation of the models

Models were validated by the cross validation technique, for assessing how the results will generalize to an independent data. First the dataset is divided into *K* subsets, and then the analysis is performed on the data of the *K-1* subsets called "training sets" and validated on the data of the left apart set, called the "validation set". Multiple rounds are performed and each set is used for training and for validation.

The validation result is The Root Mean Square Error of Prediction (RMSEP). It is calculated at each round and final result is RMSEP averaged over the rounds.

Cross validation was realised with cv.glm function of the Boot packages in R software with *K*= 20.

2.6. Statistical analysis and estimation of genetic parameters

Mean and standard deviation for each trait and fixed effects were estimated using the SAS software package. Maternal common environment effect, with dams considered as a random effect (n = 60), and fixed effects (day of slaughtering, day of measurement) were not significant for the traits considered (Haffray et al., 2012b).

Heritability was estimated using VCE 6 software (Groeneveld et al., 2008) with a univariate animal model for each trait:

$$Y = \mu + Za + \varepsilon$$

where Y is the vector of observations, μ the mean of the performance, Z the incidence matrice, a the vector of random additive genetic effects and ε the vector of random residual effects. Genetic correlations between traits were estimated with bivariate animal models.

The expected genetic gains of full-sib selections (FS) or indirect individual selection (IS) on the models were compared to direct individual mass selection (MS), which is a theoretical point since this is not possible to carry out a mass selection on lethal traits, using Falconer and McKay (1996) formulas:

- Expected genetic gain (ΔG) in the case of direct individual mass selection (MS) was calculated as following: $\Delta G = i\, h^2\, \sigma_x$ where h^2_x is the heritability of the trait X, i is the selection intensity on X and σ_x is the phenotypic standard deviation of the trait X selected.
- Expected correlated response (CR) to indirect individual selection (IS) on the models (criteria) was calculated as following: $CR = i_x\, h_x\, \sigma_y\, h_y\, r_g$ where i is the selection intensity, h_x and h_y are the square roots of heritability of the trait X selected and Y the trait targeted for improvement, σ_y is the phenotypic standard deviation of the correlated trait to improve and r_g is the genetic correlation between the traits X and Y.
- Expected genetic gain in the case of full-sib family selection (FS) was calculated as follows: $R_s = \frac{i\sigma_p h^2 nr}{\sqrt{n(1+(n-1)t)}}$, where i is the selection intensity, σ_p is the phenotypic standard deviation of the trait selected, h^2 is its heritability, n is the number of sibs measured per family, r is the correlation between additive genetic values of sibs (here r = 0.5 within full-sib families) and t is the phenotypic intra class correlation(with $t=rh^2$, assuming common environmental effects (c^2) to be zero as all fish are reared in common garden conditions). Selection methods (MS, FS, IS) were computed with 10 % selection pressure (i = 1.755) on the selected trait or indirect criteria for the three yields to improve. As family selection efficiency depends on the number of sibs measured per family and on between family selection pressure, two scenarii of full-sib

selection (FS) were calculated with 10 % selection pressure and 100 or 10 sibs per family (FS(10 %, 100); FS(10%, 10)). However, as selection efficiency depends also on economic constraints, a third scenario of sib-selection more in agreement with technical and economical practices (see Gjerde et al., 2012; i = 0.47 to 0.98) was also considered with 40 % selection pressure (i = 0.966) and 10 sibs per family (FS(40 %, 10)).

3. Results

3.1. Morphology of low and high processing yields rainbow trout

The graphical visualization of shape differences obtained with the discriminant function for low and high yield fish for *Carc%, Head%* and *HGCarc%* were represented on Figure 3.

The discriminant functions were highly significant with three PCs for *Carc%* (R^2 = 0.37 and F = 38.5, $P < 10^{-6}$), *Head%* (R^2 = 0.5, F = 197, $P < 10^{-6}$) and *HGCarc%* (R^2 = 0.19, F = 23.5, $P < 10^{-6}$).

The graphical visualization of shape with the highest *Carc%* was more oblong (or salmon like). The visualization with highest *Carc%* exhibited nearly equal dorsal and ventral heights above and under the lateral line. Fish with the lowest *Carc%* exhibited higher belly heights than dorsal heights. The anal fin of the fish with the highest *Carc%* was advanced (due to smaller belly cavity) and their tail began after the tail of the fish with the lowest *Carc%*. The highest *Carc%* also corresponded to a smaller head angle than the lower ones.

The two groups differed mainly by their relative head development, the group with the highest *Head%* having a higher head surface, a smaller trunk and a higher head height and length.

The conformation corresponding to the highest *HGCarc%* was the same as the conformation for the fish with the highest *Carc%* but with a smaller head development.

The variables selected in the models for the three prediction equations are presented in Table 2.

Carc% could be predicted with three variables (X1, X2 and X3) that associated the homogeneity of body shape from the middle part of the fish to its tail (X1) and the two ratios of abdominal fillet thickness to the development of the belly depth (X2) and the visceral surface reported to the complementary surface of the whole body (X3).

Head % could be predicted with four variables (X4, X5, X6 and X7) that associated the head surface (A1) reported to the fish thickness (E5) at constant BW, the head height reported to the total body length measures as the total lateral line length (L5 + L6), the condition coefficient K and the head surface reported to BW.

HGCarc% could be predicted with the five variables that explained the best *Carc%* (X1, X2 and X3) and inversely *Head%* (X4; X5 and X7).

The mean predicted values were 88.39 % ± 0.99 for *ModCarc%,* 14.17 % ± 0.90 for *ModHead%* and 72.38 % ± 1.14 for *ModHGCarc%*.

The phenotypic correlations between yields predicted by the models and real yields to predict calculated from the whole data set ranged from 0.56 to 0.68 (Table 4).

RMSEPs of the models were respectively 1.07 for *Carc%,* 0.64 for *Head%,* 1.18 for *HGCarc%.* These values are systematically inferiors to the standard errors of the values measured for these parameters (sd(*Carc%*) = 1.4, sd(*Head%*)=0.9, sd(*HGCarc%*)=1.5).

3.2. Heritabilities and genetic correlations

Heritabilities of the morphological traits measured (lengths, heights, ultrasound measures, surfaces and angles) are represented in Figure 4. Heritabilities were intermediate and ranged from 0.26 ± 0.05 (L6) to 0.46 ± 0.06 (L6), excepted L3 (0.05 ± 0.02) and the angle β2 (0.12 ± 0.03)

Heritabilities of the composite variables X1 to X7 and their genetic and phenotypic correlations with the yields to predict are given in Table 2. The heritabilities were lower (0.23-0.33) than those of the traits to predict (Table 3).

Heritabilities of the predicted yields (*ModCarc%, ModHead%* and *ModHGCarc%*) ranged from 0.25 to 0.28 (Table 3).

Several variables of the models exhibited high genetic correlation with yields to predict or between them: X2 and X3 with *Carc%* (0.85 and -0.75), X4 and X7 with *Head%* (0.80 and 0.85), X2 with *HGCarc%* (0.72), X4 with X7 (0.96 ± 0.01).

The prediction models tended to present higher genetic correlations with growth and conformation (BW, BL, K) than the real yields to predict (e.g. -0.68 ± 0.07 between Mod *Head%* and BW *vs* -0.51 ± 0.10 between *Head%* and BW).

Each predicted yield was highly genetically correlated with real yield : 0.88 ± 0.04 for *ModCarc%*, 0.90 ± 0.03 for *ModHead%* and 0.87 ± 0.05 for *ModHGCarc%.*

3.3. Comparative expected genetic gains

Sib-selection with 100 or 10 sibs per full-sibs family [FS(10%, 100); FS(10%, 10)] created the same range of genetic progress for a 10% selection pressure (Figure 5). The genetic gains of FS (10%, 10) were slightly lower when compared to MS selection: 88.3%, 89.6% and 84.8% for *Carc%*, *Head%* and *HGCarc%*. FS (40%, 10) selection with 40% selection pressure decreased genetic gain to 50.1%, 50.8% and 48.1% of theoretical MS selection efficiency.

IS selection progress for *Car%*, *Head%* and *HGCarc%* was 66.5%, 66.9% and 58.7% of the theoretical progress that could be achieved by MS selection but IS selection was 32.7%, 31.7% and 21.9% more efficient than FS(40%, 10) for same targeted processing yields.

4. Discussion

The study investigated a new procedure to identify external and/or internal morphological variables phenotypically correlated with different processing yields in large rainbow trout. The application of geometric morphometrics tools provided a visual support to better understand phenotypic differences between high and low yields and to define pertinent combinations between variables to objective differences observed intuitively by human eyes. These

variables were combined in a linear regression model. Heritabilities of indirect criteria were estimated and the relative efficiency of indirect selection (IS) on these indirect criteria was compared to theoretical mass selection (MS) or sib-selection (FS) with different family sizes (10 or 100) and two different selection pressures (10% or 40%).

4.1. Phenotypic linear models

Phenotypic correlations between predicted yields and real yields were intermediate (0.56-0.68). A limited number of studies had reported the application of linear combinations of morphological variables to predict phenotypic processing yields in fish (Bosworth et al., 2001; Rutten et al., 2004; Van Sang et al., 2009). The present study estimated 0.56 as correlation coefficient between *HGCarc%* (highly correlated with *Fil%*), estimation in the range of prediction of fillet yield by previous authors: 0.16 to 0.50 in females and males catfish (Bosworth et al., 2001), 0.38 in Nile tilapia (Rutten et al., 2004) and 0.77 in river catfish (Van Sang et al., 2008). None of them investigated *Carc%* or *Head%* and results on these last two traits cannot be compared with previous work. The values estimated for RMSEP are quite low and inferior to standard errors, which validate the ability of the models to predict yields with acceptable precision for new data.

Fish with the highest *Carc%* had a homogeneous antero-posterior body shape, a smaller visceral depth combined to a high abdominal muscle thickness and a smaller relative visceral surface. Fish with the lowest *Head%* were those with a smaller head surface and height and the highest body thickness. Those with the highest *HGCarc%*, and therefore fillet yield, were fish that combined traits defined in the previous two models. These results confirmed that differences in body shape can be phenotypically link to muscle and adipose tissue development and associated with processing yields in fish (Bosworth et al., 2001; Rutten et al., 2004; Van Sang et al., 2008).

4.2. Genetic parameters of the predicted yields

Heritabilities of the combined variables that were used for the models were moderate (0.23-0.33), or intermediate for K (X6, 0.56). These moderate values, lower than some of the heritabilities estimated for some traits that composed these variables may be explained by intermediate genetic correlations between these traits and some antagonistic relationship.

The predicted yields exhibited moderate heritabilities (0.25-0.28). The intermediate genetic correlations between the combined traits included in the models could also contribute to these limited heritabilities.

Genetic correlations of predicted yields with real yields were high (0.87-0.90). Some of the variables that composed the models exhibited very high genetic correlations with the yields to predict (X2 and X3 with *Carc%,* X4 and X7 to Head % and X2 with *HGCarc%)* making some of these variables (like X2) nearly equally genetically correlated with the trait to predict. However, none of the variables included in the models exhibited as high a genetic correlation as the predicted yields, which were then preferred.

Previous authors that used single morphometric variables (Gjerde and Shaeffer, 1989; Neira et al., 2004; Rutten et al., 2005) or linearly combined variables (Van Sang et al., 2012) did not find added value to these variables when compared to the measurement of the yield to predict on sibs. However, none of them investigated such a large number of variables combining lengths, height and surfaces or body thicknesses or belly depth.

The variable X2 was highly genetically correlated with *Carc%.* X2 is partly composed by Echo8 already reported as moderately genetically correlated (0.46-0.63) with dressing percentage (refered as *Carc%* here) by Gjerde and Shaeffer (1989) in rainbow trout. However, the measurement of Echo23, the other component of X2, was never reported before. X2 is highly genetically correlated (0.85) with *Carc%* and is the first variable selected in the *Carc%* and *HGCarc%* models. The additional external morphometric variable allowed increasing genetic correlations with the model to 0.88. The gain in genetic correlation is limited when comparing predicted yields to X2. The predicted yield added information on different relative body compartments and integrated other sources of morphological variations than X2.

Curiously, fillet thickness at different locations (Echo4 and Echo5) were not selected in *ModHGCarc%* that is highly genetically correlated with *HGCarc%* and highly genetically correlated to Fil% (0.87). As also proposed by Kause et al. (2004), the visceral fat deposit variation may mostly determine *HGCarc%* variation, and higher here than fillet thickness.

The present study confirmed the potential of ultrasound tomography as initially investigated phenotypically in the American catfish (Bosworth et al., 2001). This technology is routinely used in livestock breeding programs to predict backfat thickness and increase percentage of lean cuts in pig (Lo et al., 1992), backfat thickness and *longissimus* muscle area or lean meat yield in beef cattle (Crew and Kemp, 2001; Nalaila et al., 2012) or breast meat yield in broiler and turkey (Gaya et al., 2006; Case et al., 2011). The genetic correlations estimated with the yield to predict (0.87-0.90) in this study are in the same range as the trait measured to predict *longissimus* muscle area (0.87) in pig (Lo et al., 1992) and much higher than the trait measured to predict breast meat yield (0.64-0.69) in broiler (Gaya et al., 2006) or (0.47-0.75) in turkey (Case et al., 2012). When compared to Gjerde and Shaeffer (1989), Rye and Refstie (1995) and Neira et al. (2004) that measured morphological traits with calipers on slaughtered fish, ultrasounds constitutes a major advancement in fish breeding as the trait can be measured on live candidates.

4.3. Relative genetic gains

Whatever the numbers of sibs measured per family, FS selection create same range of genetic progress at the same selection pressure. Advantage of FS selection is its simplicity as no other measures than the processing yields have to be collected.

IS selection created less genetic progress than FS selection at the same selection pressure even if models are highly correlated with the yields to predict. This was associated with the two times lower heritability of the models. This is also associated with the better efficiency of FS selection when the family size is higher than 10.

However, when selection pressure applied to FS selection was decreased to more realistic and economic selection pressure [FS (40%, 10)] as reported by Gjerde et al. (2012), the relative efficiency of FS selection drop under the efficiency of IS selection kept at 10% selection pressure (IS, 10%). These highest selection responses benefits from the very high genetic correlation between the models and the yields to predict, these high genetic correlations having a more important impact in the estimation of the response than the nearly 50 % lowest heritability of the models than the yields to predict.

However, very low correlated responses may also be expected with IS selection when traits heritability is very limited or close to zero as for fillet yield in some experiments (Rutten et al., 2005; Powel et al., 2009; Nguyen et al., 2010; Gjerde et al., 2012; Van Sang et al., 2012).

The cost to measure traits in FS selection schemes (rearing costs of additional full-sibs, labour and financial loss of the carcasses) has to be balanced with the cost to measure the traits to be combined in the models for IS selection. Whatever the selection pressure applied by breeders, a technical limitation of IS selection on models is the time to collect the morphometric coordinates (here 1.5 month for nearly 2000 fish, without data treatment). *A posteriori* data collection from digitalized pictures, as done in this study, is applicable by breeding companies. The increase of selection pressure on models will imply to increase the number of fish measured. This should require the development of adapted 2D or 3D imaging software before field applications. Marty-Mahé et al. (2004) and Blonk et al. (2010) provided first basis of automation of picture and body size traits captures by digital image analyse in fish.

4.4. Uncertainty of selection on ratios

The genetic parameters estimated need to be taken with caution as they are composed of ratios or combinations of ratios. Theoretical bases of genetic parameters and selection on ratios is an unresolved subject (Sutherland, 1965) even if selection on condition coefficient K (that is a ratio) was efficient in fish (Ankorion et al., 1992). Pure mathematical combinations between the relative variations of the ratio compounds and body weight, their relative heritability and their high genetic correlations with body weight make results of such selection difficult to achieve. Several authors (Rutten et al., 2005; Nguyen et al., 2010; Gjerde et al., 2012) suggested preferring selection on body weight to increase the flesh quantity. But selection on body weight failed to improved fillet yield (Bonnet et al., 2002; Vandeputte et al., 2009; Nguyen et al., 2010). Combined selection on body weight and fillet yield (3 generations) also failed to increase fillet yield in tilapia (Gjerde et al., 2012), which is probably linked to the limited heritability of fillet yield (0.06 ± 0.04) reported in this study. However, the between strain variation of gutted yield in rainbow trout (Morkramer et al., 1985), the positive response to selection on body shape (Ankorion et al., 1992) or processing yields in the channel catfish (Bosworth and Wolters, 2009) provided first insights of potential interest of the selection on body shape, or fillet yield to improve fillet yield as suggested by other authors (Kause et al. 2007; Kocour et al., 2007; Haffray et al., 2007; Saillant et al., 2009; Navarro et al., 2009; Powell et al., 2009; Haffray et al., 2012b). The recent advances in using the residuals of allometric relationship between body compartments and body weight suggested (Haffray et al., 2012) or demonstrated (Egset et al., 2012) that selection on this residual, as used to select of feed efficiency in livestock, can be effective to modify equilibrium between body compartments independently of body weight.

5. Conclusion and perspective

This study evaluated a procedure to identify internal and external measures combined in a linear regression model to predict phenotypic processing yields. This study provides a major advancement in fish breeding using real time ultrasound imagery to quickly and non-invasively measure a limited number of body thicknesses highly genetically associated with yields of economic interest.

Estimations of genetic progress to indirect selection on the models provided expectation of improvements due to the very high genetic correlations between prediction from the models developed and their yields to predict but also the higher potential selection pressure on live candidates than with sib family selection. The genetic parameters of these predicted yields are encouraging for application in fish breeding. However, potential mathematical bias

associated with estimations of heritabilities of ratios and their genetic correlation with other traits make it necessary to estimate realized heritability obtained after a selective breeding on these ratios or on the predicted yields.

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Figures

Figure 1: Landmarks (1a) (1 to 19) used to calculate: 1b) seven heights (Ht and H1 to H6) and the head perimeter (P); 1c) seven lengths (L1 to L7); 1d) and 1e) six surfaces (A1 to A6); 1e) two angles (β1 and β2) on large rainbow trout.

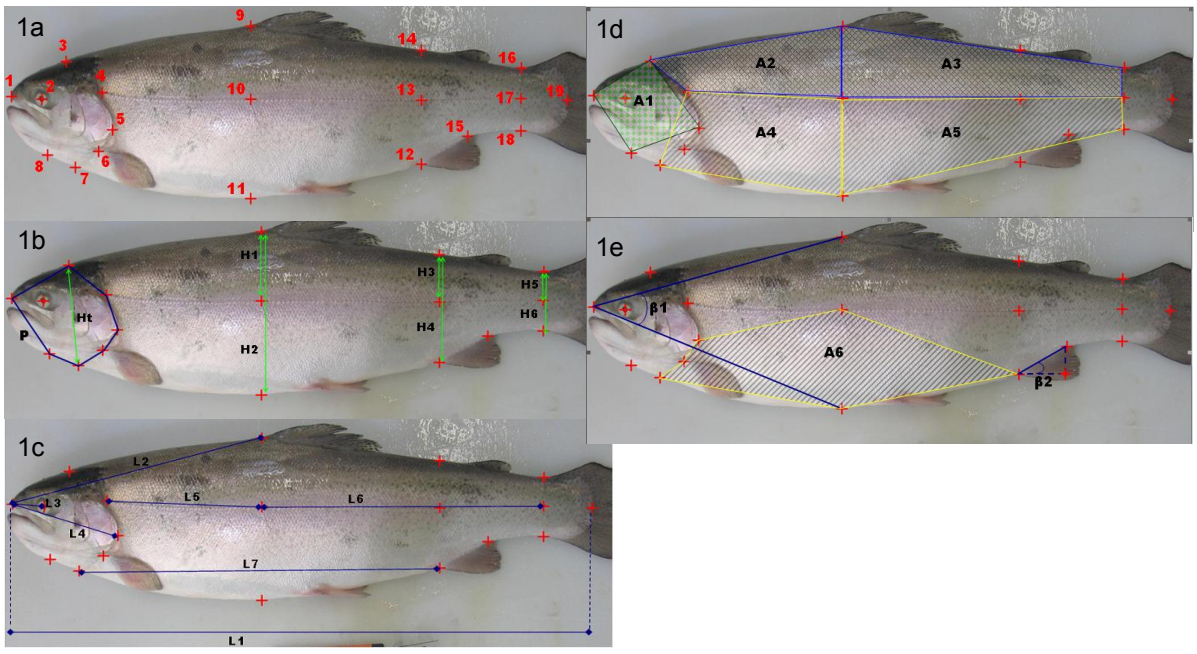


Figure 2: Position of the five Echo4, Echo5, Echo8, Echo11 and Echo23 ultrasound measures (± 0.01 mm) obtained with Hospimedi LC100 ultrasound machine equipped with linear 7.5 MHz probe.

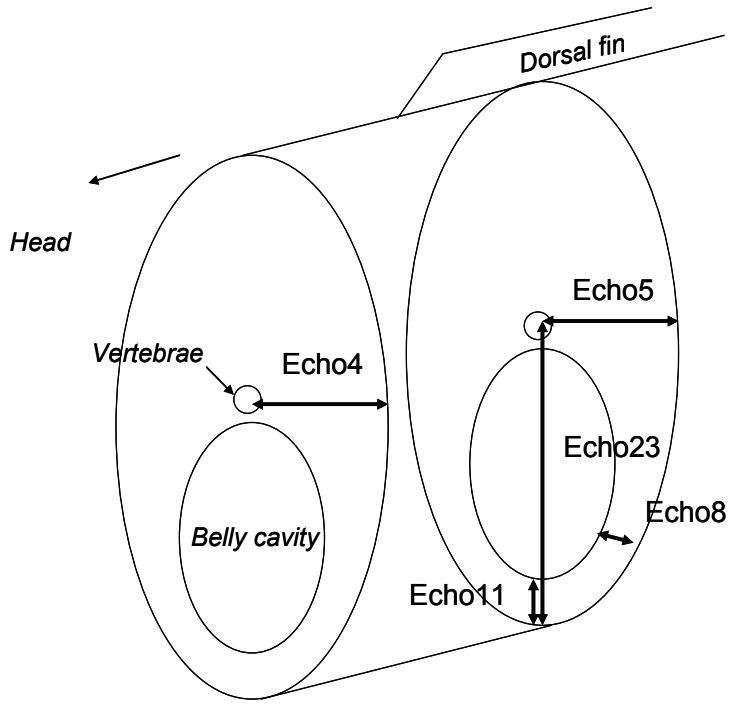


Figure 3: Graphical visualization of shapes differences with the discriminant vectors for *Carc%*, *Head%* and *HGCarc%* using APS software (Penin 2007): 2a) highest *Carc%* is represented in red and the lowest in blue; 2b) Highest *Head%* is represented in red and the lowest in blue; 2c) Highest *HGCarc%* is represented in red and the lowest in blue.

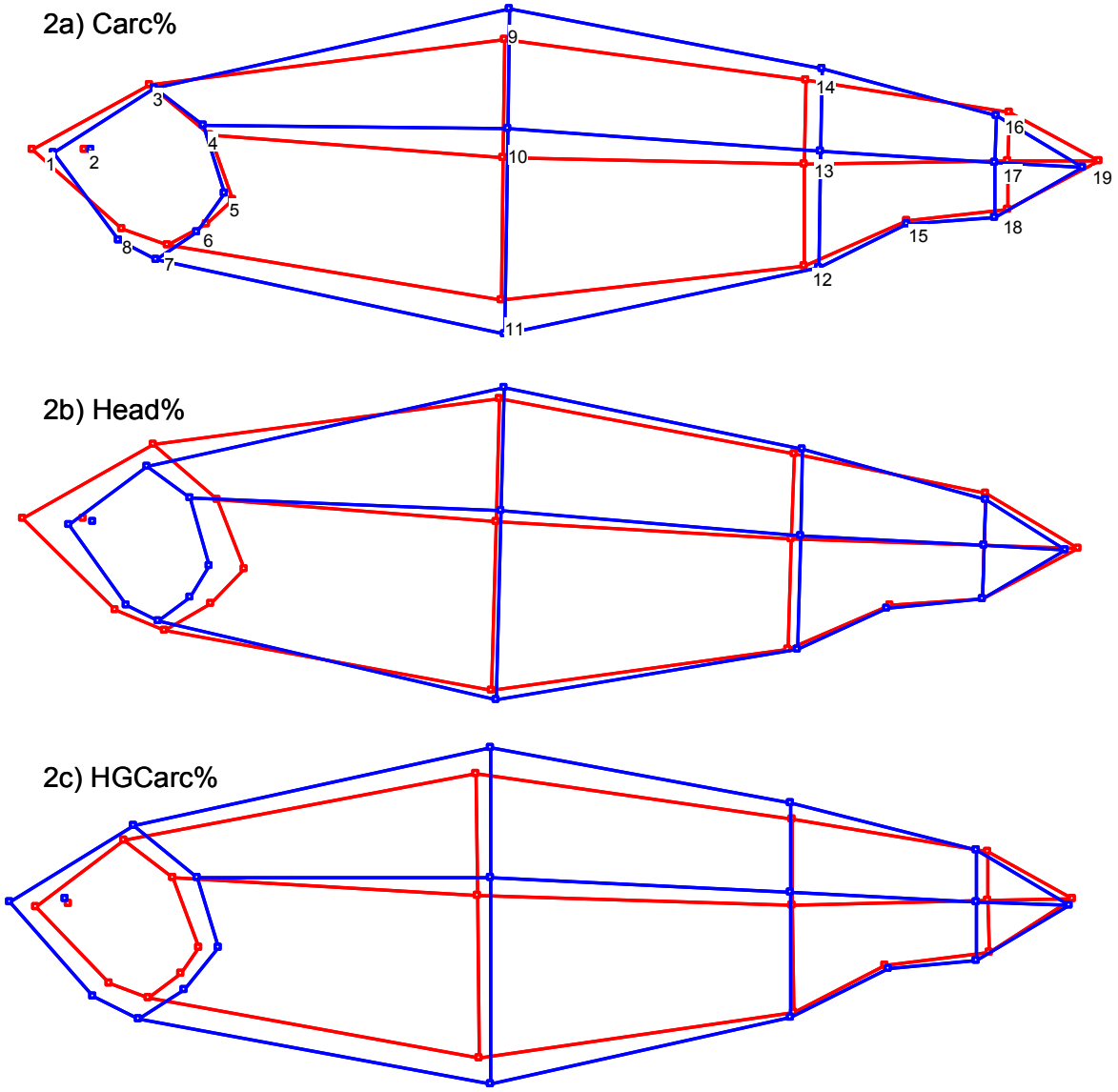


Figure 4a, b, c and d: Heritability of: a) body lengths (L1 to L7; b) body heights (Ht and H1 to H6); c) ultrasound measures (Echo4 to Echo23) and d) surface (A1 to A6) and angles (β1 and β2). Error bars: standard errors.

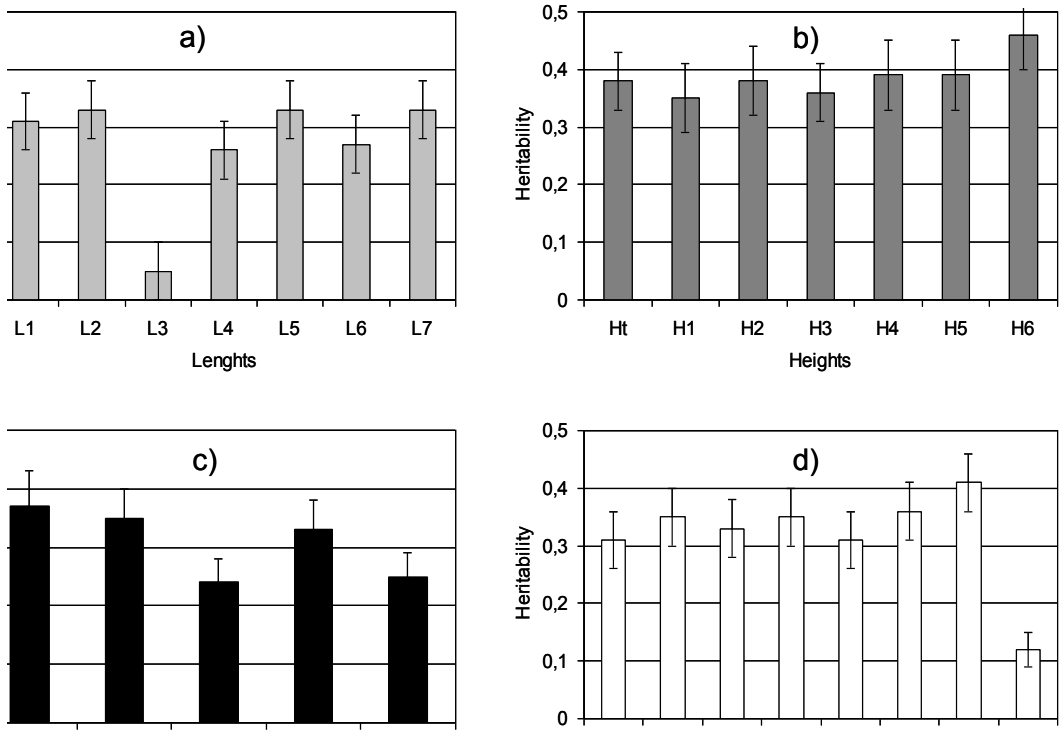
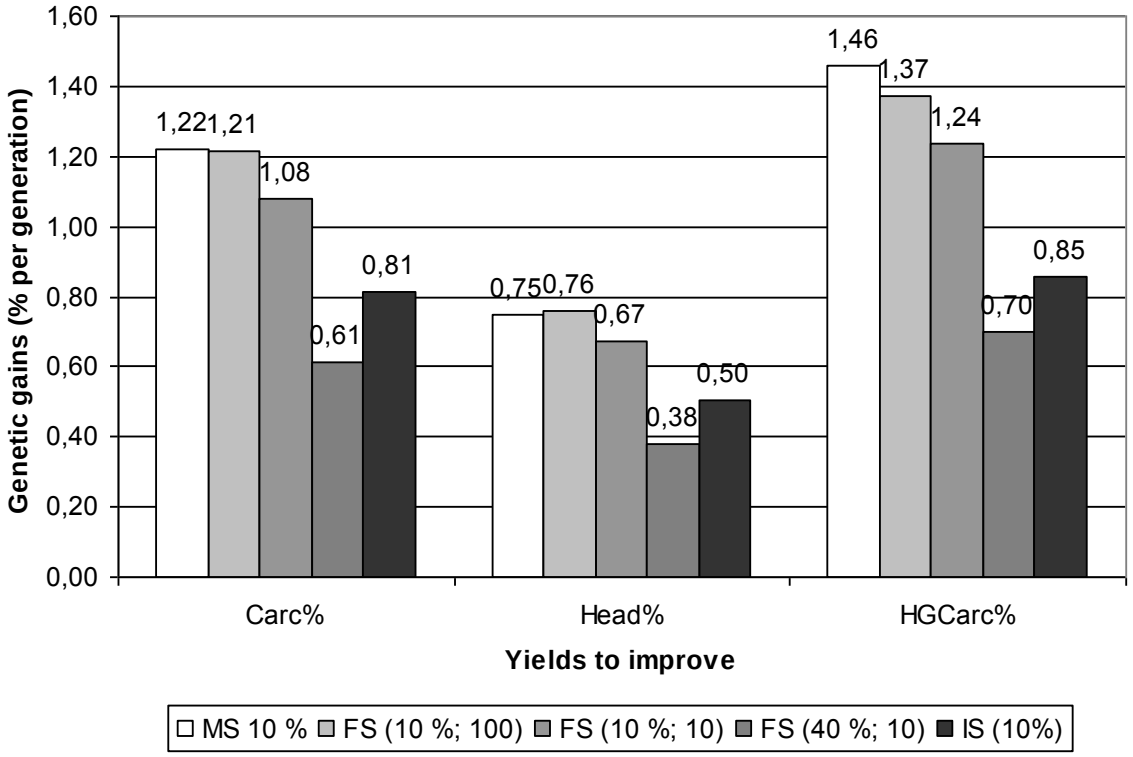


Figure 5: Theoretical genetic gain (%) per generation on carcass yield (Carc%), head yield (Head%) and headed and gutted carcass yield (*HGCarc%)* according to five strategies of selection: 10 % selection pressure when selection is done on the trait by theoretical mass selection (MS(10%)), when the trait is family selected with 100 or 10 full sibs measured per family (FS(10 %, 100) or FS(10 %, 10)), when indirect selection on morphological models is applied on live candidates (IS, 10%)), or with 40 % selection pressure with 10 full sibs per family (FS (40 %, 10)).



Tables

Table 1: Mean ± standard deviation, maximum, minimum and number of rainbow trout *Oncorhynchus mykiss* measured (N) in for body weight (BW), body length (BL), condition coefficient (K), carcass yield (*Carc%*), head yield (*Head%),* headless gutted carcass yield (*HGCarac%*).

Trait	Mean ± SD	Minimum	Maximum	N
BW (g)	1639.2 ± 350.9	424.5	2801.5	1962
BL (cm)	48.1 ± 3.0	36.2	55.2	1958
K (100 * g/cm^3)	1.46 ± 0.11	1.08	1.93	1935
Carc%	87.7 ± 1.4	82.3	93.4	1948
Head%	11.1 ± 0.9	8.3	14.9	1925
HGCarc%	76.6 ± 1.5	71.0	81.4	1913

Table 2: Multiple linear regression models to predicted carcass yield (*ModCarc%*), head yield (*ModHead%)* and headed and gutted carcass yield (*ModHGCarc%*) in rainbow trout with R^2,F Fisher test value, RMSEP and prediction equation.

Variables selected		Descriptions
		Carc%
X1	(H4-H3)/(H2-H1)	Ratio between ventral heights
X2	Echo8/Echo23	Ratio between belly ultrasound measures
X3	A6/(A1+A2+A3+A4+A5)	Ratio between belly surface and the total body surface
		Regression characteristics: R^2: 0,40 F: 400,7 RMSEP=1.07

ModCarc% = 88,6607 + 7,5733.X1 + 32,8458.X2 - 26.1840.X3

		Head %
X4	(A1/E5)/BW	Ratio between head surface and body thickness measured by ultrasound reported to the total body weight
X5	Ht/(L5+L6)	Ratio between head height and lateral line length
X6	K	Fulton coefficient
X7	A1/BW	Ration between head surface and body weight
		Regression characteristics : R^2: 0,50 F: 440,6 RMSEP=0.64

ModHead% = 9,21682 - 0,30296.X4 + 19,90169.X5 - 2,17887.X6 + 1,97149.X7

		HGCarc%
X2	Echo8/Echo23	Ratio between belly ultrasound measures
X1	(H4-H3)/(H2-H1)	Ratio between ventral heights
X3	A6/(A1+A2+A3+A4+A5)	Ratio between belly surface and the total body surface
X4	(A1/E5)/BW	Ratio between head surface and body thickness measured by ultrasound reported to the total body weight
X5	Ht/(L5+L6)	Ratio between head height and lateral line length
X7	A1/BW	Ration between head surface and body weight
		Regression characteristics: R^2: 0,38 F: 179 RMSEP=1.18

ModHGCarc% = 84,47835 + 30,57464.X2 + 4,38170.X1 - 26,00902.X3 + 0,47883.X4 - 17,75211.X5 - 3,01471.X7

Table 3: Heritability of selected traits included in the three different models to predict carcass yield (*Carc%*), head yield (*Head%*) and headed and gutted carcass yield (*HGCarac%*) and their genetic correlations with body weight (BW), body length (BL) and the yields to predict: carcass yield (*Carc%*), head yield (*Head%*) and headed and gutted carcass yield (*HGCarc%)*

	X1	X2	X3	X4	X5	X6	X7
Trait	(H4-H3)/ (H2-H1)	Echo8/Echo23	A6/ (A1+A2+A3+A4+A5)	(A1/E5)/BW	Ht/ (L5+L6)	K	A1/BW
Heritability	0.23 ± 0.04	0.24 ± 0.04	0.25 ± 0.04	0.31 ± 0.05	0.33 ± 0.05	0.54 ± 0.06	0.26 ± 0.05
rg BW	-0.26 ± 0.11	-0.14 ± 0.13	0.29 ± 0.12	-0.86 ± 0.03	0.21 ± 0.12	0.71 ± 0.06	-0.70 ± 0.07
rg BL	-0.13 ± 0.13	-0.13 ± 0.13	0.11 ± 0.13	-0.72 ± 0.06	0.02 ± 0.12	0.34 ± 0.10	-0.55 ± 0.09
rg *Carc%*	0.63 ± 0.08	0.85 ± 0.05	-0.75 ± 0.06	0.22 ± 0.11	0.01 ± 0.11	-0.13 ± 0.09	0.30 ± 0.11
rg *Head%*	0.37 ± 0.11	0.12 ± 0.13	-0.18 ± 0.12	0.80 ± 0.05	0.48 ± 0.09	-0.47 ± 0.08	0.85 ± 0.04
rg *HGCarc%*	0.40 ± 0.11	0.72 ± 0.07	-0.59 ± 0.09	-0.23 ± 0.11	-0.27 ± 0.11	0.13 ± 0.10	-0.21 ± 0.12

Table 4: Heritability (± standard error) estimates (diagonal), phenotypic correlations (below the diagonal) and genetic correlations ± standard error (above the diagonal) in rainbow trout *Oncorhynchus mykiss* for body weight (BW), body length (BL), condition coefficient (K), carcass yield (Carc%), head yield (Head%), headless gutted carcass yield (*HGCarc%*) already published (Haffray et al., 2012b) and models of prediction of carcass yield (*Mod Carc%*), head yield (*ModHead%*), headless gutted carcass yield (*Mod HGCarc%*).

	P	L	K	*Carc%*	*Head%*	*HGCarc%*	*ModCarc%*	*ModHead%*	*ModHGCarc%*
P	**0.37 ± 0.05**	0.91 ± 0.02	0.71 ± 0.06	-0.13 ± 0.11	-0.51 ± 0.10	0.15 ± 0.11	-0.26 ± 0.12	-0.68 ± 0.07	0.32 ± 0.11
L	0.93	**0.29 ± 0.05**	0.34 ± 0.10	-0.04 ± 0.11	-0.39 ± 0.09	0.16 ± 0.10	-0.13 ± 0.12	-0.49 ± 0.10	0.33 ± 0.11
K	0.62	0.29	**0.54 ± 0.06**	-0.13 ± 0.09	-0.47 ± 0.08	0.13 ± 0.10	-0.29 ± 0.11	-0.64 ± 0.07	0.19 ± 0.12
Carc%	-0.16	-0.08	-0.24	**0.49 ± 0.06**	0.13 ± 0.11	0.83 ± 0.03	0.88 ± 0.04	0.26 ± 0.11	0.51 ± 0.10
Head%	-0.61	-0.51	-0.5	0.22	**0.47 ± 0.06**	-0.45 ± 0.09	0.22 ± 0.11	0.90 ± 0.03	-0.69 ± 0.07
HGCarc%	0.22	0.23	0.07	0.8	-0.39	**0.55 ± 0.06**	0.70 ± 0.07	-0.28 ± 0.11	0.87 ± 0.05
ModCarc%	-0.22	-0.14	-0.27	0.64	0.23	0.46	**0.28 ± 0.05**	0.42 ± 0.11	0.45 ± 0.11
ModHead%	-0.63	-0.49	-0.58	0.22	0.68	-0.18	0.35	**0.26 ± 0.05**	-0.59 ± 0.09
ModHGCarc%	0.39	0.38	0.19	0.3	-0.46	0.56	0.44	-0.66	**0.25 ± 0.05**