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Abstract :

Slaughter yields are traits of high interest especially for fish species sold in processed form like headless carcass or fillets, as well as with regard to increasing consumer preference for easy-to-prepare fish products. However, slaughter yields cannot be measured on live fish and thus their genetic improvement through mass selection is impossible. The usual alternatives are sib selection and/or indirect selection on correlated traits or morphological predictors of slaughter yields. In the present study, we assessed the possibility of using a combination of 3D digitized landmarks and ultrasound measurements in genetic improvement of slaughter yields in common carp. DNA – pedigreed market-size carp (n = 1553 fish) were produced from a partial factorial design of 20 dams and 40 sires. Morphological predictors were recorded in real-time using a 3D digitizer and ultrasound tomography, and combined by multiple linear regression to predict slaughter yields. The 3D model-predicted headless carcass and fillet yields explained 59% and 50%, respectively, of the total phenotypic variation in slaughter yields. Genetic parameters of model-predicted yields and of the best individual predictor (3D_P2 – ratio between abdominal fillet thickness – E8 and external 3D ventral height) were similar or slightly lower when compared to previous 2D-based predictors (Prchal et al., 2018a, 2018b, 2018c). This was also the case for the expected genetic gain using indirect selection on the same simple predictor for fillet yield improvement (0.48% fillet units for 3D vs. 0.52% for 2D). 3D model-predicted yields and especially simple predictors thus have a solid potential for genetic improvement of slaughter yields in common carp. While they are not better than 2D predictors, they are much more convenient and faster to collect in the field, as they do not imply post-processing of images. These practical aspects should be taken into account in the future carp breeding program.

Highlights

► We studied combination of 3D digitized landmarks and ultrasound measurements. ► 3D collection of morphological landmarks do not imply post processing of images. ► 3D models / predictors have a solid potential for genetic improvement of slaughter yields. ► Future carp breeding strategies have been suggested.

Keywords : fillet yields, 3D predictors, genetic parameters, indirect selection, breeding program

1. Introduction

Fish traits defined as ratio of inputs and outputs (such as feed efficiency), or ratio of edible high-valued biomass relative to total fish weight (such as fillet yield) are fundamental efficiency-related traits for aquaculture operations. They are of high economic value (Kankainen et al., 2016), yet tricky to measure and include in breeding programs (Haffray et al., 2013; Vandeputte et al., 2017; De Verdal et al., 2018; Fraslin et al., 2018).

Slaughter yields are traits of high interest especially for fish species sold in processed form like headless carcass or fillets (Kankainen et al., 2016), as well as with regard to increasing consumer preference for easy-to-prepare fish products (FAO, 2018). However, slaughter yields cannot be measured on live fish and consequently genetic improvement through mass selection on live breeding candidates is impossible. Similarly, the potential for marker-assisted selection (MAS) is significantly limited due to the polygenic structure of slaughter yields in fish species (Tsai et al., 2015; Gonzalez-Pena et al., 2016; Yoshida et al., 2019). Yet, genomic selection might be seen as future possibility for the genetic improvement of yields, as it allows a better precision on sib-recorded traits (Yoshida et al., 2019). However, genomic selection is still too costly and thus useful only for fish species with well-developed breeding programs e.g. Atlantic salmon (*Salmo salar*) or rainbow trout (*Oncorhynchus mykiss*) (Robledo et al., 2017) and for common carp (*Cyprinus carpio* or *Cyprinus rubrofuscus*) there is no available commercial SNP assay for such trait. Presently, edible part yields are commonly genetically improved by sib selection or by indirect selection via traits which are genetically correlated to slaughter yields (Kause et al., 2007; Gjedrem, 2010). Morphological predictors of slaughter yields based on non-destructive recording of external 2D landmarks and internal measures using ultrasound tomography could be an effective

option to select for improved yields, as they can be used on the candidates without need for (costly) sib or genomic information (Cibert et al., 1999; Bosworth et al., 2001; Rutten et al., 2004; Van Sang et al., 2009; Haffray et al., 2013; Vandeputte et al., 2017; Prchal et al., 2018a).

Common carp is an important fish species in world aquaculture, though its breeding programs are mainly focused on utilization of heterotic effect by crossbreeding (Vandeputte, 2003; Janssen et al., 2017). This is the case despite the evidence for high genetic potential in using additive effect by genetic selection (Vandeputte et al., 2004; Kocour et al., 2007; Vandeputte et al., 2008; Nielsen et al., 2010; Ninh et al., 2011; Ninh et al., 2013; Hu et al., 2017; Prchal et al., 2018b). In a previous study with common carp, we investigated phenotypic and genetic potential of slaughter yield predictors based on 2D image analysis and ultrasound measurements, and their use in carp breeding programs (Prchal et al., 2018a). We observed a high accuracy of predictors and a favourable genetic relationship to the real yields. However, digitization of 2D landmarks requires post processing of images and cannot measure variation in body width. So, this method is at the same time incomplete and time consuming, which is a major technical limitation for practical breeding programs. Alternatively, 3D collection of body landmarks could speed up digitization of potentially relevant morphological predictors and take into account the variability of carp body width. A variety of 3D imagery systems have been used in pigs (Tillett et al., 2004), chickens (Mortensen et al., 2016) and cattle (Cappai et al., 2019; Le Cozler et al., 2019). Moreover, 3D digitizers like the MicroScribe (Solution Technologies Inc, Oella, MD, USA) are often used for research related to direct 3D morphological digitization of animal skeletons (Drake, 2011; Owen et al., 2014; Hanot et al., 2017). However, their potential for real time digitization of slaughter yield predictors directly on live fish has never been studied.

In the present study, a 3D digitizer was used to collect landmarks on the fish body, instead of 2D digitizing from post-processing images. Thus, we aimed to i) determine the best morphological predictors of slaughter yields using combination of 3D landmarks and ultrasound imagery, ii) estimate genetic parameters of slaughter yield predictors and their association to the real yields, and iii) predict and compare expected genetic gain in response to selection for slaughter yield predictors based on 2D and 3D measurements and their practical implication in the carp breeding program.

2. Material and Methods

2.1 Ethics statement

The methodological protocol of the current study was approved by the expert committee of the Institutional Animal Care and Use Committee (IACUC) of the University of South Bohemia (USB), Faculty of Fisheries and Protection of Waters (FFPW) in Vodňany according to the law on the protection of animals against cruelty (Act no. 246/1992 Coll., ref. number 16OZ19179/2016-172 14). At market size the fish were humanely euthanized by trained person for subsequent processing and slaughter yield evaluation.

2.2 Production and rearing of experimental stock

The fish are the same as those used in Prchal et al. (2018a). In short, an experimental stock of Amur mirror carp was produced at the Genetic Fishery Centre of University of South Bohemia (USB) in České Budějovice, Faculty of Fisheries and Protection of Waters (FFPW) in Vodňany, Czech Republic. Twenty dams and forty sires were propagated and crossed in a partial factorial design with four series of 5 dams and 10 sires. Each parental fish was DNA sampled (fin tissue) for later parentage assignment of the offspring fish. At the swimming

stage, the experimental stock was created by pooling equal volumes of larvae. These larvae were released (150,000 larvae. ha^{-1}) to the prepared nursery ponds at the Klatovy fish farm and reared communally in ponds under a semi-intensive culture system typical for Central Europe. At one-year old, a random sample of 3000 fish from one pond (50% survival, mean weight ± SD = 15.8 ± 4.7 g) was anesthetized with 2-phenoxyethanol (0.5 ml per 1 l of water) and individually marked by PIT-Tags and DNA sampled for parentage assignment. The fish were harvested after the second growing period and the second overwintering. In October 2016 the stock (mean weight = 1910 g) was harvested and moved to a storage pond before final traits recording at fish slaughter house of USB FFPV in České Budějovice, Czech Republic. A total of 1622 individuals were humanely killed by a hit on the head and bled by cutting the gills according to the law on the protection of animals against cruelty (Act no. 246/1992).

2.3 Final data collection

Briefly, as previously reported (Orchal et al., 2018a), 1622 fish were phenotyped for total length (TL), standard length (SL), body length (BL), head length (HL), body height (BH) and body width (BWI) with an in-house electronic ruler (to nearest 0.1 mm), and body weight (BW) was recorded with an electronic scale (to nearest 0.1 g). To describe the shape of the body, the head and the lateral line, a total of 15 coordinates (Figure 1.) of morphological points were digitized in 3 dimension (X,Y,Z) using a 3D digitizer (MicroScribe G2LX) connected to a computer, to which raw data were exported and stored in real time with a home-made software. The 11 landmarks and 4 semi landmarks (point 7, 10, 11 and 13) were chosen to be both easy to collect based on anatomical features (nose, operculum, fin, anus, lateral line) and evenly distributed all along the body to describe the whole body shape.

Four muscular thicknesses from anterior (E4), intermediate (E5, E8) and posterior (E6) were collected using ultrasound imagery (Hospimedi LC1000, 7.5 MHz). For more details see Haffray et al. (2013) and Vandeputte et al. (2017) that preceded this study.

The total muscle fat content (% Fat) was recorded using a Fish Fatmeter FM 692 (Distell Ltd., UK), using calibration option 'CARP – 1'. Biometrical indicators were calculated as Fulton's condition factor: $FC = 10^5 * [BW (g) / SL^3 (mm)]$, relative body height: RelBH = BH / SL, and relative head length: RelHL = HL / SL. After biometric recordings, each fish was processed and the following body portions were weighed (to nearest 0.5 g): head, left fillet, viscera, gonad, left fillet skin, half carcass, left fillet ribs + trimmings, fins and scales. The weight of slaughter body parts and vertebral axis was created by combining the previous body portions: headless carcass weight [hl-CarssW = left fillet + left skin + left ribs and trimmings + half carcass], fillet weight with skin [FilletW = (left fillet + left fillet skin) * 2]. The slaughter yields expressed in % were calculated as: headless carcass yield % [% hl-Carss = (hl-CarssW / BW) *100], and fillet yield [% Fill = (left fillet + left skin) * 2 / BW * 100]. The natural logarithm was calculated for the weight of each slaughtered part and regressed on the logarithm of body weight to obtain growth-independent allometry residuals in order to provide genetic and phenotypic parameters giving reasonable estimates of predicted gains in slaughter yield (Gunsett, 1984, 1987; Vandeputte et al., 2014). Therefore, for % headless carcass and % fillet yield, the surrogate traits are defined as log-log residuals (Logr) and termed as Logr_hl-Carss and Logr_Fill, respectively. In addition, logarithm of weight of all body portions was regressed on the logarithm of body weight to visualize body allometry (See Supplementary Material in Prchal et al., 2018a).

2.4 3D morphology and prediction models of slaughter yields

The association of the variation in carp morphology to the variation in processing yields was analysed using the MorphoJ software (Klingenberg, 2011) as described previously in Prchal et al. (2018a) but using 3D landmarks coordinates instead of 2D. The wireframe visualization was performed on the side (X and Y) and dorsal (X and Z) view of the fish. The R Package 'geometry' was used to calculate areas and volumes from 3D coordinates raw data. A multiple linear regression using the reg.best function of the FactoMineR of R software package was performed using external morphology descriptors, ultrasound measurements and fat meter value as independent variables and the Logr_hl-Carss and Logr_Fill as dependent variables. List of predictors calculated and initially included in the multiple linear regression are shown in Supplementary Table S1.

The best prediction model identification corresponds to those with the highest R^2 and F-value. The models were used to calculate the predicted yield values for each fish that are termed as Mod_hl-Carss for headless carcass yield and Mod_Fill for fillet yield. Models were cross validated using the crossval function of the bootstrap package in R software (Efron and Tibshirani, 1993).

2.5 Parental allocation

The 60 parents and 2035 offspring were genotyped with 12 microsatellites loci at LABOGENA-DNA, the French laboratory for livestock genotyping (ISO 170025 accredited, Jouy-en-Josas, France). Parental allocation was performed using the AccurAssign software, applying a maximum-likelihood method (Boichard et al., 2014).

2.6 Estimation of genetic parameters

The data set was checked for potential outliers and the final genetic model was applied on 1553 individuals assigned to a single parental pair with a complete set of variables.

Heritability (h^2), phenotypic and genetic correlations (r_p, and r_g, respectively) were estimated in multivariate mixed models using the restricted maximum likelihood method in DMU statistical software (Madsen and Jensen, 2013). The univariate (for heritability) and multivariate analysis (for genetic correlations) were on the following animal model:

$$Y_{ijk} = \mu_i + sex_{ij} + anim_{ik} + e_{ijk}$$

Where Y_{ijkl} is the measured phenotypic value of each analyzed trait, μ_i is the overall mean for trait *i*, sex_{ij} is the fixed effect of sex (*j* = female, male, unidentified sex) for trait *i*, $anim_{ik}$ is the random genetic effect of an animal *k* with pedigree based on parentage assignment (*k* = 1, 2, …, 1553) for trait *i*, and e_{ijk} is the random residual. Heritability estimates were calculated as the ratio of additive genetic variance (V_A) divided by the total phenotypic variance (V_P), $h^2 = V_A / V_P$. The likelihood ratio test (LRT) was used for comparing the goodness of fit of two models (including vs. excluding the animal genetic effect). The heritability estimates were considered significant when the difference of additive genetic effect in -2Log-likelihood was higher than the threshold value for $p < 0.05$ of a χ^2 distribution with 1 degree of freedom (Pinheiro and Bates, 2000). Genetic correlations were considered significant if $|r_g| - |1.96 \times S.E.|$ was higher than zero.

The genetic gain (ΔG) per generation were estimated using the breeder's equations from Falconer and McKay (1996) under a mass (MS), full-sib (FSS) and indirect (IS) selection responses for fillet yields. The theoretical genetic gain under mass selection (although it cannot be applied in practice) was calculated as $\Delta G_M = i\ h^2\ \sigma_P$, where *i* is the selection intensity and h^2 and σ_P are the heritability and phenotypic standard deviation of the trait under selection, respectively. The response to selection of FSS was estimated as $\Delta G_{FS} = \frac{i \times \sigma_P \times h^2 \times n \times r}{\sqrt{n(1+(n-1)\ t)}}$, where *n* is the number of sibs sampled per family (*n* = 10), *r* is the genetic correlation between sibs (*r* = 0.5 for full sibs) and *t* is the phenotypic intra class correlation (*t*

= rh^2). The estimated genetic gain for indirect selection criteria was calculated as $\Delta G_I = i$ x h_1 x h_2 x r_g x σ_{P2}, where ΔG_I is the estimated genetic gain on the target trait, h_1 and h_2 are the square roots of heritability of the indirect selection trait (on which selection is applied) and of the target trait, respectively, r_g is the genetic correlation estimated between the indirect trait and the target trait and σ_{P2} is the phenotypic standard deviation of the target trait. Finally, the real genetic gain was scaled back to the percent body weight units by multiplying ΔG by the real mean fillet yield in the present experimental stock (50%). The selection intensities were set up of 10% and 30%, with 10 sibs per family in FSS as the most practical intensities for potential common carp breeding program.

3. Results

3.1 Representation of families

The 1553 fish used in this study arise from 197 full-sib families. The number of progeny per sire varied from 14 to 79, the average was 39. The number of progeny per dam varied from 25 to 128, the average was 78.

3.2 Slaughter yields percentage

Percentage of headless carcass was 66% ± 2.19 and fillet yield was 50% ± 1.95. Such values were higher than usual values in common carp, most likely due to the specific experimental processing which was different from the commercial one but more valuable for studying the variation in the biological characteristics of the traits.

3.3 3D morphology and prediction equations of slaughter yields

A graphical visualization of body and ventral part morphology associated to low (blue line) and high (red line) yield for Logr_hl-Carss and Logr_Fill is shown in Fig. 2. The greatest

differences were observed on the abdominal part of the fish and on the head. Fish with higher yields present a lower ventral area, mainly under the dorsal fin, and also have a smaller head area.

The most informative morphological predictors ($3D\_P_{1-7}$) included into two prediction equations (3DMod_hl-Carss and 3DMod_Fill), and their R^2 and Fisher test values (F) are listed in Table 1. The selected 3D morphological landmarks (1-15) of carp body are shown on Figure 1.

Logr_hl-Carss was best predicted with a model combining five simple predictors ($3D\_P_2$, $3D\_P_3$, $3D\_P_4$, $3D\_P_5$, $3D\_P_6$). $3D\_P_2$ = the ratio of abdominal fillet thickness (E8) to height between the lateral line and the aligned ventral point 7-8; $3D\_P_3$ = 3D area between 2-3-7-10-11-6 divided by 3D area 3-4-5-8-9-10-7; $3D\_P_4$ = volume between 2-3-7-10-11-6 divided by volume 3-4-5-8-9-10-7, $3D\_P_5$ = width at point 7 divided by width at point 4 and $3D\_P_6$ = width at point 10 divided by width at point 4. 3DMod_hl-Carss explains 59.2% (R^2CV = 58.8%) of total phenotypic variation in Logr_hl-Carss.

Logr_Fill was best predicted by a model combining four predictors. Two of them were the same as for Logr_hl-Carss (**$3D\_P_2$, $3D\_P_6$**) and the different ones were **$3D\_P_1$** = 3D head area divided by total area (except the 14-15-12-13) and **$3D\_P_7$** = volume between 6-11-10-7 divided by volume 7-10-9-8. 3DMod_Fill explains 49.6% (R^2CV = 49.3%) of total phenotypic variation of Logr_Fill.

3.4 Heritability estimates and genetic correlations

Heritability estimates of the single predictors ($3D\_P_1$ – $3D\_P_7$), Logr slaughter yields (Logr_hl-Carss and Logr_Fill) and model-predicted slaughter yields (3DMod_hl-Carss and 3DMod_Fill) are given in Table 2. All heritabilities were significantly different from zero and achieved moderate to high values in the range of 0.29 – 0.66. Heritability estimates and

genetic correlations of yield-related phenotypes (BW, % Fat, FC, RelBH, RelHL) are detailed in Prchal et al. 2018a.

The genetic correlations between individual predictors, Logr and 3DMod slaughter yields are listed in Table 2. 3D_P_1 was highly negatively correlated to 3D_P_6 (r_g = -0.70). 3D_P_3 and 3D_P_4 were highly correlated to each other (0.98) as well as to 3D_P_7 (r_g = 0.87, 0.85, respectively). Besides, 3D_P_3 and 3D_P_4 were also negatively genetically associated to 3D_P_5 and 3D_P_6. Moreover, 3D_P_5 and 3D_P_6 were in moderately high genetic relationship (r_g = 0.73). Only 3D_P_1, 3D_P_2 and 3D_P_6 achieved favourable genetic relationship with Logr slaughter yields (r_g = |0.44 – 0.80|). Likewise, 3D model-predicted slaughter yields showed high genetic associations to the real yields to be predicted (r_g = 0.84 – 0.88). Besides, residual weights to be predicted (Logr) as well as model-predicted (3DMod) slaughter yields were highly correlated to each other (r_g = 0.84 – 0.97).

The genetic correlations of yield-related phenotypes to the most informative simple predictors and 3D model-predicted yields are presented in Table 3. The predictors 3D_P_1 and 3D_P_6 were in absolute values in the same genetic pattern to all yield-related phenotypes. Thus, these predictors were genetically related to lower BW and FC (low correlation), RelBH (medium correlation) and RelHL (strong correlation). Oppositely, selecting for such predictors might lead to a slightly higher muscle fat (r_g = |0.31 – 0.37|). 3D_P_2 was not significantly correlated to BW, FC and RelBH but was also positively genetically associated to % Fat and negatively but at the edge of significance with RelHL. Regarding model-predicted yields, genetic correlations were similar to 3D_P_1 and 3D _P_6 predictors but generally stronger for 3DMod_Fill especially in relation to BW, FC (insignificant for 3DMod_hl-Carss) and RelHL (r_g = -0.47 vs. -0.67, respectively).

3.5 Expected genetic gain

Expected genetic gains (Table 4.) were calculated for fillet yield and compared among mass (MS), full-sib (FSS) and indirect selection (IS) scheme using 3D model (3DMod_Fill) and 3D single predictors ($3D\_P_1$ – $3D\_P_7$).Genetic gain calculated for hypothetical mass selection (MS) was 0.70% (10% selection intensity) and 0.46% (30% selection intensity) per generation. Genetic gain for full-sib selection (FSS) with 10 sibs selected per family (10% and 30% selection pressure) was slightly lower (0.61% and 0.40%) than for MS. Estimated genetic gain achieved by indirect selection on the 3D model-predicted fillet yields (3DMod_Fill) was 0.65% and 0.43% for 10% and 30% selection intensity, respectively. Genetic gains of the most effective 3D predictors ($3D\_P_1$, $3D\_P_2$ and $3D\_P_6$) ranged from 0.27% to 0.47%. Other predictors showed much lower values (0.01% – 0.19%). Relative genetic changes of yield-related traits were calculated for fillet yield improvement using IS scheme (Supplementary Table S2).

4. Discussion

In the present study, we showed i) favourable phenotypic prediction accuracy of real slaughter yields, ii) moderate to high heritability estimates of simple 3D predictors and 3D model-predicted yields; iii) strong genetic correlations of 3D predictors / models with the real slaughter yields suggesting that the indirect selection could be strong enough to be used in genetic improvement of slaughter yields. Moreover, iv) potential genetic gain based on indirect selection of the 3D model (3DMod_Fil) was similar to that achieved by previously developed 2D model (2DMod_Fil) (Prchal et al., 2018a), however, best individual 3D predictor – 3D_P2 (E8/ 3D height in the ventral part) achieved less favorable genetic parameters than the same predictor in 2D – 2D_P2 (E8/ 2D height) (Prchal et al., 2018a). Still, 3D models / predictors have a solid potential for genetic improvement of slaughter yields in common carp as they are much faster evaluated on live breeding candidates, so that

breeding program would be simple, efficient and sustainable, compared to previously used methods of external and internal measures (Cibert et al., 1999; Bosworth et al., 2001; Rutten et al., 2004; Van Sang et al., 2009; Haffray et al., 2013; Vandeputte et al., 2017; Prchal et al., 2018a).

The 3D model-predicted yields explained 59% of the phenotypic variation in the real headless carcass yield, and 50% in real fillet yield. Accuracy to predict headless carcass yield using 3D was slightly lower than the accuracy in a previous study (63%) that used 2D and ultrasound measurements (Prchal et al., 2018a). Yet, prediction accuracy of 3D and ultrasound values for fillet yield prediction was equal to 2D and ultrasound recording in common carp (Prchal et al. 2018a) but higher than in rainbow trout (Haffray et al., 2013) and European sea bass (Vandeputte et al., 2017). So, model-predicted yields using 2D or 3D showed almost similar phenotypic prediction accuracy of real slaughter yields in common carp, explaining 49% – 63% of phenotypic variation. Nevertheless, in common carp headless carcass yield was only predicted using three simple 2D predictors (Prchal et al., 2018a) but the best models of headless carcass yield used six predictors in rainbow trout (Haffray et al., 2013), nine predictors in European sea bass (Vandeputte et al., 2017) and five predictors in present study. It might have been caused by different digitization procedure between 2D and 3D, as the previous 2D study in carp involved additional landmarks in the caudal part (Prchal et al., 2018a). So, comparison between 2D and 3D predictions might be affected by the number of landmarks digitized (15 in 3D vs. 20 in 2D) as more landmarks may lead to more precise measurements (especially areas) but on the other hand require more time for acquisition. Yet, the time required for post processing of morphological 2D landmarks and the lack of information on body width are the main limitations of 2D prediction. Moreover, Logr_Fill could be predicted only with 4 predictors using 3D instead of 5 2D predictors in Prchal et al. (2018a) and 6 predictors in Vandeputte et al. (2017), suggesting a simplified

model of fillet yield using 3D digitization. 3D model-predicted yields have generally a strong prediction accuracy similar to 2D models, but 3D predictions are more practical for using in the field on a large sample of fish, due to the possibility to acquire data in real time. On the other hand, the initial cost of 3D digitizer is higher than collection of 2D images by camera (10,000 € vs 1,000 €). However, when taking into account time required for post processing by one skilful person (almost one month), the return on this investment and practical use of such device is fast and clear. Briefly, during own recording it takes about 1.5 min. of skilful person to get 3D coordinates and no further post-processing is required. To have 2D picture it takes about 1 min. (correct positioning of fish to take an informative picture, checking the result) and further 1 min. to process the image later. So, 2D is about 30 s slower than 3D. However, the most important is that 3D coordinates we have immediately and can select the fish directly during one manipulation, meanwhile when using 2D we need to manipulate with all fish again later to select proper candidates. It represents further time and more stress for fish (two manipulations, longer short-term storage of fish in tanks). So, being able to select the fish during one manipulation is a crucial task. However, both 2D and 3D model-predicted yields rely on precise coefficients for linear combination of predictors. So, directly evaluating the potential of simple predictors is therefore potentially much simpler for practical indirect selection.

Heritability estimates of 3D model-predicted yields were high (0.46 for hl-Carss and 0.56 for fillet) and slightly lower than the estimates predicted using 2D digitization (0.48, 0.63, respectively; Prchal et al., 2018a). Yet, the heritability estimates for 3D traits were higher when compared to other fish species (Van Sang et al., 2012; Haffray et al., 2013; Vandeputte et al., 2017). Predicted yields of both 2D and 3D models were strongly genetically correlated to the real yields (0.84 – 0.88), showing their strong potential for indirect selection to improve edible part yields. It is also necessary to know the genetic correlations between the

selected yield traits with other traits such as growth, body composition and fish welfare traits, as these traits may be changed indirectly by selection on yield traits. Some examples can be clearly seen in the previous studies that focused on improvement of yield that would indirectly lead to degradation of the flesh quality in cattle (Feitosa et al., 2017) and in common carp (Prchal et al., 2018c), pulmonary disease in broiler chicken (Hocking, 2010; Muir et al., 2014) or loss of flavour in tomatoes (Tieman et al., 2017).

In this study, we observed that selecting for 3D model-predicted yields would indirectly lead to several undesirable impacts similarly as in case of 2D-based predictors (Prchal et al., 2018a). Thus, such selection would more likely increase muscle fat, slightly decrease body weight and cause fast change to an oblong like body shape with a limited head size. A similar negative effect was also observed in other studies as a genetic consequence of the selection for improved slaughter yields (Kause et al., 2007; Nguyen et al., 2010; Haffray et al., 2012; Janhunen et al., 2017; Fraslin et al., 2018). However, such changes could lead to negative fitness effects in a long-term breeding program (Fraslin et al., 2018). Therefore, these undesirable genetic relationships must be accounted for when breeding goal would be focused on increased slaughter yields.

Yields predicted by multitrait models are constructed from several simple individual predictors and the collection of all of them requires time and precision of measurements. Our results showed that recording of suitable individual predictors seems to be efficient for a simplified breeding program. Seven individual predictors from which the yield predictors were estimated achieved moderate to high heritability (0.29 – 0.66). Three of them (3D_P_1, P_2, P_6) could be eventually used in a breeding program due to their high heritabilities (h^2 = 0.44 – 0.66) and significant genetic correlations with the Logr yields (r_g = |0.44 – 0.80|). In addition, 3D_P_1 and 3D_P_2 are the same morphological predictors as the previous 2D predictors 2D_P_1 and 2D_P_2 differing only in a way of digitization (Prchal et al., 2018a).

The best simple predictor seems to be 3D_P_2 (ratio between abdominal fillet thickness – E8 and external ventral height measured between points 7-8 in 3D), similar to 2D predictor P_2 in Prchal et al. (2018a) and ratio of E8 to E23 (depth of the peritoneal cavity) in rainbow trout (Haffray et al., 2013). 3D_P_2 is a highly heritable predictor, has genetic association to edible part yields showing its strong potential to be used in a breeding program as "*quick-to measure*" indirect selection criterion for improvement of yields in common carp. In addition, selection for that predictor would not lead to such significant decrease on head size and general body shape as in case of selection on 3D model predicted yields. On the other hand, both yield models and simple predictors are positively genetically correlated to muscle fat. Hence, a selection program focused on improvement of slaughter yields should check muscle lipid level and eventual change of feeding strategy would be necessary to keep high flesh quality with respect to beneficial fatty acids (Prchal et al., 2018c). 3D_P_1 as well as 2D_P_1 are defined as a ratio between head area to total body area with a negative genetic correlation to the real yields. Nevertheless, 3D_P_1 has a higher heritability than 2D_P_1 (h^2 = 0.50 vs. 0.34 in 2D) and is also more correlated to Lo$_g$ yields (r_g = -0.54 – -0.59 vs. -0.52 – -0.57 in 2D). 3D_P_6 (width at point 10 divided by width at point 4) was a new simple predictor with very high heritability (0.66) and favourable genetic relationship to the slaughter yields (0.44 – 0.58). However, selection based on these simple predictors could indirectly lead to several unwanted changes similarly like in case of selection on 2D/3D yield models already discussed above. Therefore, the use of predictors in a selection index including shape and fat content would be a suitable breeding scenario to avoid a negative impact of indirect selection for fillet yield on other traits of interest.

The calculations of expected genetic gains showed that 3D model-predicted yields or simple predictors are interesting candidates for a selection program. The highest genetic gain in fillet yield was observed by hypothetical mass selection (MS) on real fillet yield (0.70% for

10% selection intensity). Such selection method is typically used as benchmark value to compare with other selection schemes, though it is not possible in the breeding program. Slightly lower genetic gain was observed using sib selection (FSS) on real fillet yield, a typical approach applied for traits requiring destructive recording (slaughter yields, meat quality) or disease resistance (Gjedrem, 2010). However, costs for FSS are higher and in our case cover also parentage assignment and processing costs of sib groups. Thus, our work confirm that indirect selection may be an interesting alternative to establish a lower cost and sustainable breeding program. Indeed, indirect selection on 3D model-predicted fillet yields showed even better genetic progress than FSS. This result was also in accordance with previous 2D fillet model yields (Prchal el., 2018a) that showed the same expected response to selection. However, main limitations of using model predicted yields in a breeding program have been already discussed above. Expected genetic gains of simple predictors were generally lower than from 2D or 3D fillet yield models but still significant enough to be included in a selection program. 3D_P_1 achieved a better gain than the same predictor in 2D (0.41% vs. 0.33%). Alternatively, new 3D_P_6 predictor was better for genetic progress than 3D_P_1 but these predictors are genetically related to unfavourable consequences that might be considered as reasonable biological limits in a long-term breeding program. The best genetic progress using a simple predictor would be obtained by 3D_P_2 (0.48%), similarly to our previous 2D experiment where the gain was even higher (0.52%) (Prchal et al., 2018a). Moreover, this predictor is more favourably genetically connected to other phenotypes and easy and especially quick to record in the field and thus a very practical simple trait for indirect selection of slaughter yields in common carp.

5. Conclusions

The accuracy of the phenotypic prediction of slaughter yields by 3D models is high and almost similar to 2D prediction models. Likewise, expected genetic progress to be obtained by selection on model-predicted yields and on the best individual predictor ($3D\_P_2$) were similar or only slightly lower when compared to the 2D-based models and the best 2D simple predictor (Prchal et al., 2018). In conclusion, model-predicted yields and especially simple 3D predictors have a solid potential for genetic improvement of slaughter yields in common carp. While such predictors are not better than 2D predictors, they are much more convenient and faster to collect in the field, as they do not imply post-processing of images. These practical aspects should be taken into account in the future carp breeding program and we expect to verify the applicability of such predictors in a practical selection response experiment.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MP, DG, and MK established and reared the experimental stock. MP and MK PIT tagged and sampled the DNA from finclips. PH and MV provided the methodology and equipment. MP, JB, MV, AV, JZ, DG, AB, VK, and MK shared on final trait recordings. AK introduced MP to the quantitative genetic analysis. JB carried out 3D digitization and the phenotypic prediction of slaughter yields. LG performed the DNA extractions and parentage assignment. MP estimated the genetic parameters. All authors contributed to drafting the manuscript and approved the final version.

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Tables

Table 1: Multiple linear regression models to predict Logr headless carcass and Logr fillet yields in common carp including predictors characteristics, regression statistics R^2, F - Fisher test value and prediction equations.

Headless carcass yield 3D model	Predictor characteristics
$3D\_P_2$	Ratio between E8 and 3D height between points 7-8
$3D\_P_3$	3D area between 2-3-7-10-11-6 divided by area 3-4-5-8-9-10-7
$3D\_P_4$	Volume between 2-3-7-10-11-6 divided by volume 3-4-5-8-9-10-7
$3D\_P_5$	Width at point 7 divided by width at point 4
$3D\_P_6$	Width at point 10 divided by width at point 4
Regression statistics: $R^2 = 0.59$, F = 449.7	
$3DMod\_hl\text{-}Carss = -0.18 + 5.88\ 3D\_P_2 + 0.21\ 3D\_P_3 - 0.13\ 3D\_P_4 - 0.02\ 3D\_P_5 + 0.09\ 3D\_P_6$	
Fillet yield 3D model	**Predictor characteristics**
$3D\_P_1$	3D head area divided by total area (except the 14-15-12-13)
$3D\_P_2$	Ratio between E8 and 3D height between points 7-8
$3D\_P_6$	Width at point 10 divided by width at point 4
$3D\_P_7$	Volume between 6-11-10-7 divided by volume 7-10-9-8
Regression statistics: $R^2 = 0.49$, F = 381.9	
$3DMod\_Fill = -0.10 - 0.46\ 3D\_P_1 + 5.88\ 3D\_P_2 + 0.11\ 3D\_P_6 + 0.02\ 3D\_P_7$	

Table 2: Heritability (± standard error) estimates (diagonal) in bold, phenotypic (below the diagonal) and genetic correlations ± standard error (above the diagonal) in common carp for simple predictors ($3D\_P_1$ – $3D\_P_7$), log-log residuals (Logr) of slaughter yields and 3D models (Mod) to predict slaughter yields.

	$3D\_P_1$	**$3D\_P_2$**	**$3D\_P_3$**	**$3D\_P_4$**	**$3D\_P_5$**	**$3D\_P_6$**	**$3D\_P_7$**	**Logr_hl-Carss**	**Logr_Fill**	**3DMod_hl-Carss**	**3DMod_Fil**
$3D\_P_1$	**0.50 ± 0.08**	-0.25 ± 0.15	0.27 ± 0.15	0.38 ± 0.14	-0.46 ± 0.12	-0.70 ± 0.08	0.17 ± 0.16	-0.54 ± 0.11	-0.59 ± 0.10	-0.47 ± 0.12	-0.72 ± 0.08
$3D\_P_2$	-0.07	**0.44 ± 0.08**	-0.02 ± 0.16	-0.09 ± 0.16	-0.25 ± 0.15	0.18 ± 0.15	0.12 ± 0.16	0.80 ± 0.06	0.73 ± 0.08	0.93 ± 0.02	0.80 ± 0.06
$3D\_P_3$	0.15	0.25	**0.39 ± 0.07**	0.98 ± 0.01	-0.39 ± 0.14	-0.41 ± 0.13	0.8[illegible] ± 0.[illegible]	-0.10 ± 0.16	-0.19 ± 0.16	-0.07 ± 0.16	-0.22 ± 0.15
$3D\_P_4$	0.17	0.21	0.95	**0.42 ± 0.08**	-0.44 ± 0.13	-0.51 ± 0.12	0.85 ± 0.05	-0.20 ± 0.16	-0.29 ± 0.15	-0.17 ± 0.16	-0.33 ± 0.15
$3D\_P_5$	-0.41	-0.06	-0.17	-0.22	**0.48 ± 0.09**	0.73 ± 0.08	-0.37 ± 0.14	-0.01 ± 0.16	0.17 ± 0.15	-0.01 ± 0.16	0.23 ± 0.15
$3D\_P_6$	-0.49	0.15	-0.16	-0.19	0.56	**0.66 ± 0.09**	-0.25 ± 0.15	0.44 ± 0.12	0.58 ± 0.10	0.49 ± 0.12	0.69 ± 0.08
$3D\_P_7$	0.09	0.30	0.63	0.70	-0.19	0.02	**0.29 ± 0.06**	0.05 ± 0.16	-0.03 ± 0.16	0.12 ± 0.16	-0.01 ± 0.16
Logr_hl-Carss	-0.23	0.65	0.21	0.14	0.05	-0.23	0.22	**0.46 ± 0.08**	0.97 ± 0.01	0.86 ± 0.04	0.85 ± 0.05
Logr_Fill	-0.38	0.54	0.04	0.01	0.19	-0.38	0.17	0.77	**0.50 ± 0.08**	0.84 ± 0.05	0.88 ± 0.04
3DMod_hl-Carss	-0.18	0.94	0.[illegible]0	0.20	0.05	-0.18	0.30	0.70	0.60	**0.46 ± 0.08**	0.94 ± 0.02
3DMod_Fil	-0.53	0.83	0.12	0.08	0.26	0.53	0.26	0.66	0.67	0.90	**0.56 ± 0.09**

Table 3: Genetic correlations ± standard error between most informative simple predictors, 3D model-predicted yields and yield-related traits

	3D_P_1	**3D_P_2**	**3D_P_6**	**3DMod_hl-Carss**	**3DMod_Fil**
r_g **BW**	0.36 ± 0.13	-0.10 ± 0.15	-0.32 ± 0.13	-0.21 ± 0.14	-0.30 ± 0.14
r_g **FC**	0.47 ± 0.11	-0.05 ± 0.14	-0.36 ± 0.12	-0.18 ± 0.13	-0.30 ± 0.13
r_g **% Fat**	-0.37 ± 0.13	0.37 ± 0.13	0.31 ± 0.13	0.43 ± 0.13	0.49 ± 0.11
r_g **RelBH**	0.50 ± 0.11	-0.13 ± 0.13	-0.51 ± 0.10	-0.31 ± 0.13	-0.43 ± 0.11
r_g **RelHL**	0.86 ± 0.04	-0.27 ± 0.13	-0.61 ± 0.08	-0.47 ± 0.11	-0.67 ± 0.08

Table 4: Genetic gains (in percent body weight units) per generation with two selection intensities (% selected – 10%, 30%) using mass (MS), full sib (FSS), and indirect (IS) selection for fillet yield improvement.

Trait selected	Type of selection	Genetic gain (10%)	Genetic gain (30%)
Logr_Fill	MS	0.70	0.46
Logr_Fill	FSS	0.61	0.40
3DMod_Fill	IS	0.65	0.43
3D_P_1	IS	0.41	0.27
3D_P_2	IS	0.48	0.32
3D_P_3	IS	0.12	0.08
3D_P_4	IS	0.19	0.12
3D_P_5	IS	0.09	0.06
3D_P_6	IS	0.47	0.31
3D_P_7	IS	0.02	0.01
2DMod_Fill	IS	0.66	0.43
2D_P_1*	IS	0.33	0.22
2D_P_2*	IS	0.52	0.34

* cited from Prchal et al., (2018a)

Figure Captions

Figure 1: 3D landmarks place on each carp.

1: head extremity; **2:** end of the head beginning of the fillet on the back; **3:** intersection between opercula and lateral line; **4:** opercula at the maximum length from the landmark 1; **5**: end of the head beginning of the fillet on the ventral part; **6:** beginning of the dorsal fin; **7:** intersection between the lateral line and the vertical of landmark 6; **8:** intersection of the ventral part and the vertical of point 7; **9:** beginning of the anal fin; **10:** intersection between lateral line and vertical of point 9 towards the carp back; **11:** vertical of point 10 on the back; **12:** end of anal fin; **13:** intersection of lateral line and vertical of 12; **14:** vertical of point 13 on the carp back; **25:** end of the caudal fin at the fork.

Figure 2: A graphical visualization of body and ventral part morphology associated to low (blue line) and high (red line) yield for Logr_hl-Carss (A, B) and Logr_Fill (C, D)

Figures

Figure 1

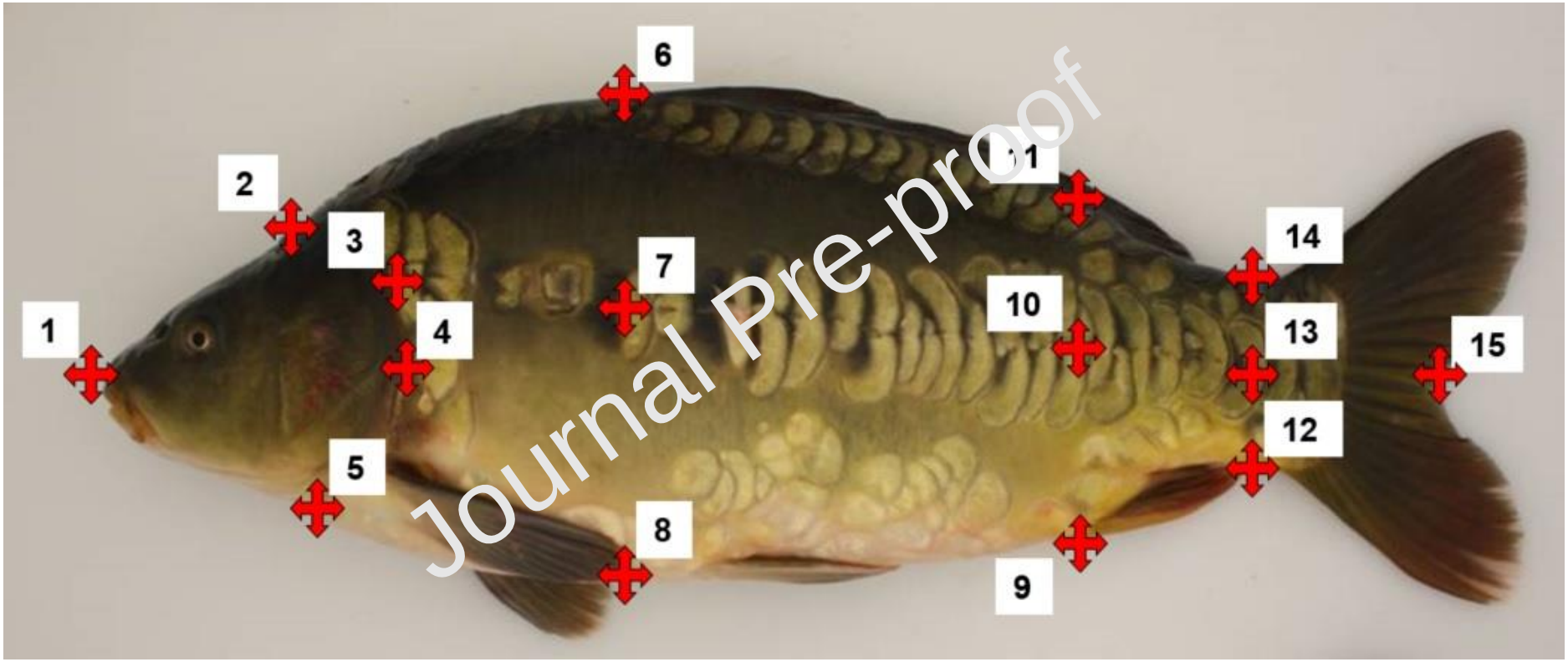


Figure 2A

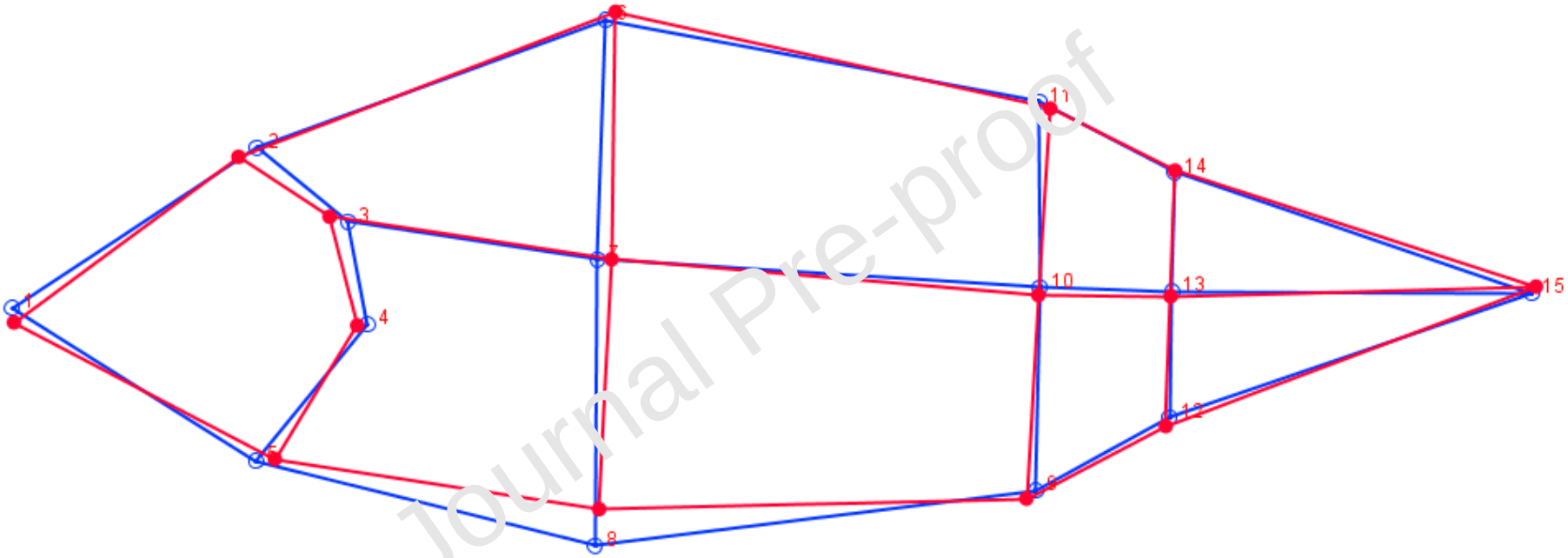


Figure 2B

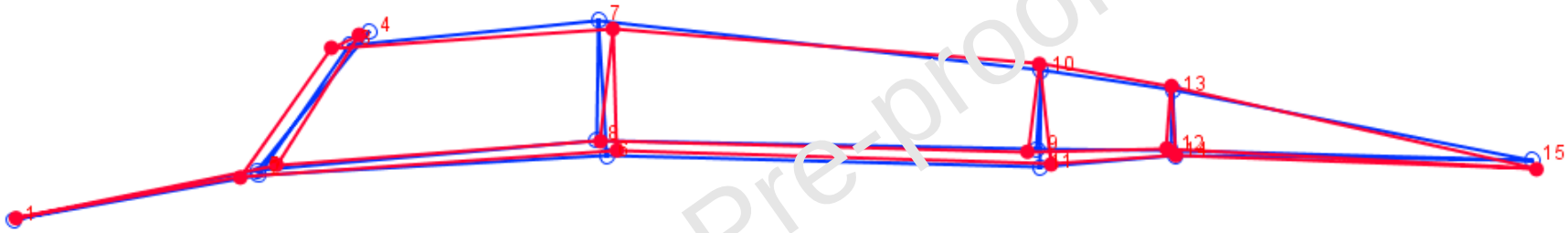


Figure 2C

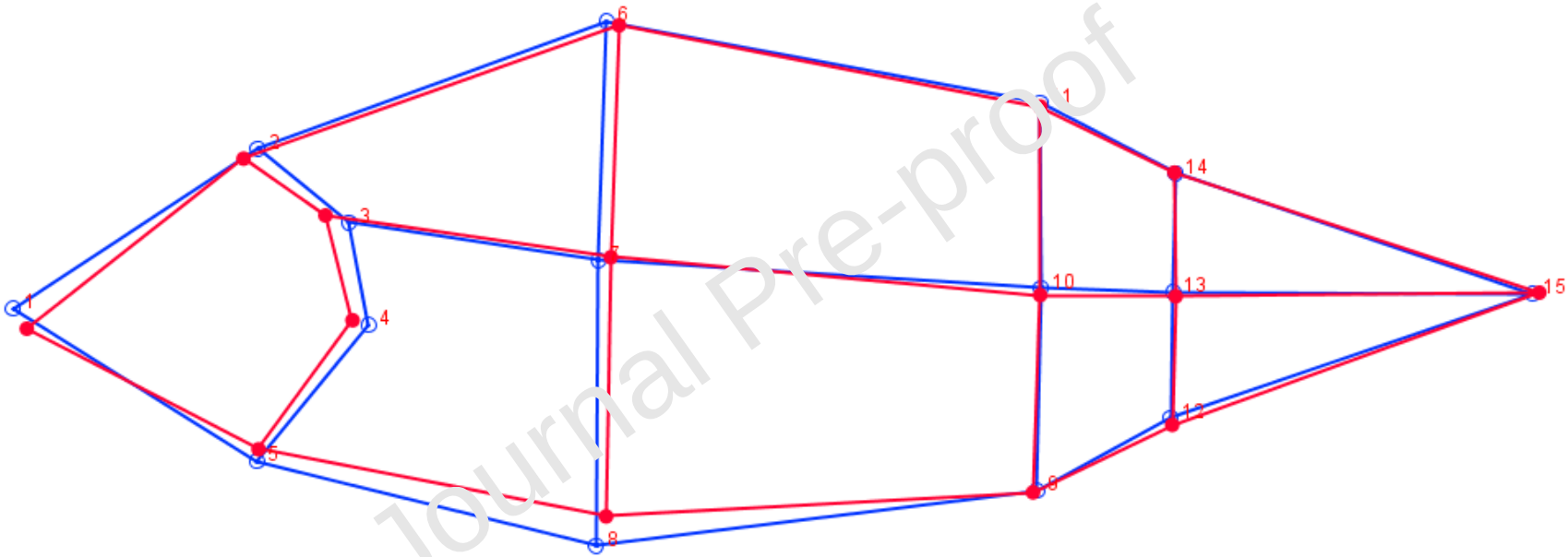
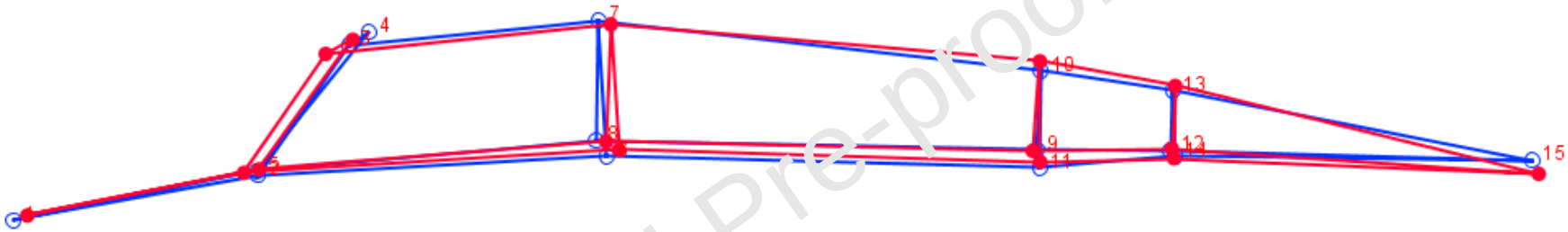


Figure 2D



Highlights

- We studied combination of 3D digitized landmarks and ultrasound measurements
- 3D collection of morphological landmarks do not imply post processing of images
- Genetic parameters of 3D model/simple predictors were solid
- Future carp breeding strategies have been suggested