Predicted genetic gain for carcass yield in rainbow trout from indirect and genomic selection

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ABSTRACT

Carcass and fillet yields are traits of great economic importance in aquaculture species, including rainbow trout. Headless gutted carcass percentage (HC) is a convenient selection criterion to improve carcass yield given that it is highly genetically correlated with the latter and also with fillet yield. However, HC is a sib trait that cannot be recorded on selection candidates. Consequently, the within-family component of the genetic variance cannot be exploited with traditional pedigree-based BLUP selection. Two alternatives to exploit this component would be to select directly on an indicator trait genetically correlated with HC that can be recorded on live candidates or to apply genomic selection. The objective of this simulation study was to predict the phenotypic gains for HC in rainbow trout breeding programs when four alternative selection strategies are used: i) sib selection for HC, ii) indirect selection for a morphological indicator recorded in vivo; iii) genomic selection for HC; and iv) genomic selection for the indicator. Also, the four strategies were compared in a multitrait selection scenario where body weight was also included in the breeding objective. The different scenarios were compared at the same selection intensity and number of records (2000) for HC (on sibs) and IHC (on candidates). Two different heritabilities for HC (0.55 and 0.25) were considered. For the highest heritability, the phenotypic gain for HC was higher with sib than with indirect selection for both BLUP (1.03 versus 0.98) and genomic selection (1.22 versus 1.04). However, for the lowest heritability, the phenotypic gain for HC was lower with sib than with indirect selection for both BLUP (0.60 versus 0.64) and genomic selection (0.70 versus 0.71). In any case, the differences in phenotypic gains for HC between sib and indirect selection were not large. Therefore, given that sib selection implies extra costs associated with maintaining and genotyping sibs and indirect selection allows higher selection intensity for a given number of fish, indirect selection appears to be a more cost-effective option. The patterns found for single trait selection were maintained when the yield trait (HC or indicator) was selected simultaneously with body weight. We conclude that the optimum approach to improve carcass yield is a combination of genomic and indirect selection in both single and multitrait selection scenarios.

1. Introduction

One of the main breeding goal traits in aquaculture selection programs is growth rate, a trait that can be easily recorded and improved (Gjedrem et al., 2012). However, other economically important traits cannot be recorded on live animals and they are challenging to be incorporated in these programs. This is the case of carcass yield (i.e., the percentage of carcass weight out of wet body weight) and fillet yield (i. e., the percentage of fillet weight out of wet body weight), two economically very important traits, especially for species sold processed as gutted carcass or fillets (Kankainen et al., 2016; Fraslin et al., 2018;

Prchal et al., 2018).

Direct selection for fillet yield is not an easy task as fillet recording is laborious and is associated to large measurement errors, which lead to a relatively low heritability (Rutten et al., 2005; Powell et al., 2008; Haffray et al., 2012). Carcass yield is easier to record and several studies in rainbow trout have demonstrated that selection for this trait would result in a correlated response in fillet yield (Kause et al., 2007; Haffray et al., 2012; Vandeputte et al., 2019).

A more suitable selection criterion to improve carcass and fillet yield is headless gutted carcass percentage (HC). The heritability of HC is similar to that of carcass yield and higher than that of fillet yield, and the

genetic correlation between HC and fillet yield is higher than the correlation between carcass yield and fillet yield (Haffray et al., 2012, 2013; Vandeputte et al., 2017, 2019; Prchal et al., 2018). In particular, in rainbow trout, Haffray et al. (2012, 2013) showed that selection for HC could be more efficient than selection for fillet yield itself.

However, recording HC also requires sacrificing the fish, and thus, it is impossible to do it on selection candidates. For this kind of traits, selection is generally based on sibs' performance and consequently, only the between family component of the genetic variance can be exploited when applying traditional pedigree-based BLUP selection (Nielsen et al., 2009; Sonesson and Meuwissen, 2009). An alternative to improve HC would be to select for an indicator trait genetically correlated with HC that can be recorded on live fish (i.e., on the candidates themselves). In fact, HC predictors based on morphological records that permit non-lethal trait recording have been recently developed in different aquaculture species (Haffray et al., 2013; Vandeputte et al., 2017; Prchal et al., 2018, 2021).

Another alternative that allows exploiting the within-family component in the selection decisions would be to apply genomic selection (Meuwissen et al., 2001). Computer simulations (Nielsen et al., 2009, 2011; Sonesson and Meuwissen, 2009; Villanueva et al., 2011; Lillehammer et al., 2013; Sonesson and Ødegård, 2016) and analyses of empirical data of different aquaculture species (see reviews by Zenger et al., 2019, Houston et al., 2020 and D'Agaro et al., 2021) have shown important benefits of this approach in terms of genetic gain compared to traditional BLUP selection. These benefits are expected when selecting directly or indirectly for HC.

The objective of this study was to predict, through computer simulations, the potential of indirect and genomic selection to improve carcass yield in selective breeding programs for rainbow trout. Different selection strategies were evaluated both in a single trait setting, where selection was only for a yield trait and in a multi-trait setting, where body weight was also selected.

2. Material and methods

The simulated selection program started from a base population with a family structure (i.e., composed by full- and half-sib families). Three correlated traits were simulated in all scenarios, including body weight (BW, in g), percentage of headless carcass (HC), and a morphological indicator of HC measured by ultrasound tomography (IHC). Specifically, the indicator simulated was the ratio of abdominal wall thickness (Echo8) to depth of the peritoneal cavity (Echo23) as described in Haffray et al. (2013) and Vandeputte et al. (2019). Genetic parameters assumed for the three traits were taken from the literature (Kause et al., 2007; Haffray et al., 2012, 2013) and are shown in Table 1. These parameters correspond to traits recorded at ~510 days post fertilization (Haffray et al., 2013). The estimate of the heritability for HC (h_{HC}^2) found in previous studies was 0.55, but an alternative value (0.25) was also simulated to investigate the scenario where HC and IHC have similar heritabilities. Phenotypic gains for HC obtained from four different selection strategies were compared. These strategies included i) sib selection for HC based on sibs' phenotypes; ii) indirect selection for IHC based on candidates' phenotypes; iii) genomic selection for HC based on sibs' phenotypes; and iv) genomic selection for IHC based on

candidates' phenotypes. The four strategies were compared at the same selection intensity. A total of 100 males and 200 females were selected and mated following a nested design to generate 200 full-sib families, and each mating produced 20 offspring (10 males and 10 females). The simulations were carried out with our own Fortran 90 codes.

2.1. Genome structure

The genome simulated was composed of 30 chromosomes and had a total size of 20 Morgans, mimicking the trout genome. A total of 3,600,000 evenly spaced biallelic loci were simulated throughout the genome (120,000 loci per chromosome), of which 600,000 (20,000 per chromosome) were considered to be potential SNP (single nucleotide polymorphism) markers to be used in genomic selection. SNP markers were also evenly spaced within each chromosome.

2.2. Generation of the base population

Firstly, a population in mutation-drift equilibrium was simulated by randomly generating 100 males and 100 females across 4000 discrete generations. At each generation, sires and dams were randomly sampled with replacement. Population size was kept constant across generations. The mutation rate per locus and generation was 2.5×10^{-4}. Mutations were randomly distributed across individuals, chromosomes, and loci, switching allele 0 to allele 1 and vice versa. Initial frequencies were 0.5 for all loci. When generating the gametes, the total number of crossovers was drawn from a Poisson distribution with mean equal to the genome length. Crossovers were randomly distributed without interference. At the end of this process, the expected heterozygosity of the population had already reached an asymptote (i.e., mutation-drift equilibrium). At this point, the population was expanded over one generation in order to have enough individuals to sample replicates. One male and one female were randomly sampled with replacement and mated to produce 1 offspring and this process was repeated until a total of 1000 individuals were generated. These 1000 individuals constituted the expanded population from which replicates for the different scenarios were generated.

In order to create a base population ($t = 0$) with a family structure, 100 males and 200 females were randomly sampled from the expanded population for each replicate. Each male was randomly mated with two females following a nested design and 20 offspring per mating were generated. Thus, $t = 0$ was composed of 4000 fish belonging to 200 full-sib families (and 100 half-sib families). At $t = 0$, loci with a minor allele frequency less than 0.1 were discarded as QTLs (loci affecting the traits) or SNPs (loci to be used in genomic selection). Across the genome, a total of 48,000 loci (an average of 1600 loci per chromosome) were then randomly sampled as SNP markers (i.e., a marker density of 2400 SNPs/ Morgan). Also, from the total number of loci that remained segregating (1,005,000 loci, including the 48,000 SNPs), a total of 1000 loci were randomly sampled as QTLs that simultaneously affected the three polygenic traits (BW, HC, and IHC). In order to simulate specific pairwise genetic correlations between traits, each QTL had different effects on the three traits (see the specific approach taken below, in section 2.3). At $t = 0$, the average linkage disequilibrium measured as r^2 (the squared correlation between pairs of loci; Hill and Robertson, 1968) between SNPs separated 50 kb and 100 kb was 0.308 and 0.282, respectively. These r^2 values are similar to those found in the literature for rainbow trout (D'Ambrosio et al., 2019).

2.3. Generation of breeding and phenotypic values

The true breeding value of individual j for trait k (TBV$_{kj}$; k = BW, HC, IHC) was obtained as the sum of the (additive) genetic values across QTLs. For QTL i, these values were a_{ik}, 0 and -a_{ik} for homozygotes 11, heterozygotes 10 and homozygotes 00, respectively. For QTL i affecting trait k, a_{i_k} was obtained in two steps (Fernández et al., 2021; García-Ballesteros et al., 2021). Firstly, a random number (a_{i_k}*) was sampled

Table 1

Heritabilities (on diagonal), and genetic (above diagonal) and phenotypic correlations (below diagonal) between the traits considered.

Trait	BW	HC	IHC
BW	0.30	0.15	0.30
HC	0.20	0.55 or 0.25	0.90
IHC	0.40	0.55	0.25

BW: body weight; HC: headless carcass percentage; IHC: indicator of headless carcass percentage.

from the following multivariate normal distribution:

$$N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 1 & \rho_{a_{BW,HC}} & \rho_{a_{BW,IHC}} \\ & 1 & \rho_{a_{HC,IHC}} \\ Symm & & 1 \end{bmatrix}\right),$$

where $\rho_{a_{k,l}}$ is the genetic correlation between traits k and l (k = BW, HC, IHC; l = BW, HC, IHC; $k \neq l$). Secondly, a_{i_k} was obtained by multiplying $a_{i_k}*$ by the factor $\sqrt{\{\sigma^2_{a_k}/[2p_k(1-p_k)n_{QTL}]\}}$, where $\sigma_{a_k}^2$ is the assumed additive genetic variance for trait k at $t = 0$, p_k is the average frequency across QTLs for trait k at $t = 0$ and n_{QTL} is the number of QTLs (i.e., 1000). Note that in this way the expected additive variance summed over all QTLs equals $\sigma_{a_k}^2$, assuming that covariances between loci generated by linkage disequilibrium are negligible. The phenotypic value of individual j for trait k was obtained by adding an environmental effect to TBV$_{kj}$. This environmental effect was sampled from the following multivariate distribution:

$$N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma^2_{e_{BW}} & \rho_{e_{BW,HC}}\sqrt{\sigma^2_{e_{BW}}\sigma^2_{e_{HC}}} & \rho_{e_{BW,IHC}}\sqrt{\sigma^2_{e_{BW}}\sigma^2_{e_{IHC}}} \\ & \sigma^2_{e_{HC}} & \rho_{e_{HC,IHC}}\sqrt{\sigma^2_{e_{HC}}\sigma^2_{e_{IHC}}} \\ Symm & & \sigma^2_{e_{IHC}} \end{bmatrix}\right),$$

where $\sigma_{e_k}^2$ is the environmental variance for trait k and $\rho_{e_{k,l}}$ is the environmental correlation between traits k and l. The environmental variance for trait k was obtained as $\sigma_{p_k}^2 - \sigma_{a_k}^2$, where $\sigma_{p_k}^2$ is the phenotypic variance for trait k that was set to 1 for the three traits). The environmental correlation was obtained as $\rho_{e_{k,l}} = (\rho_{P_{k,l}} - h_k h_l \rho_{a_{k,l}})/e_k e_l$, where h_k, h_l are the square roots of the heritabilities for traits k and l, respectively, e_k is $1 - h_k^2$, e_l is $1 - h_l^2$ and $\rho_{P_{k,l}}$ is the phenotypic correlation between both traits (Falconer and Mackay, 1996).

2.4. Genetic evaluation methods

The evaluation methods considered for obtaining estimates of breeding values were standard BLUP and genomic evaluation. The univariate model assumed for BLUP and trait k was.

$$\mathbf{y}_k = \mathbf{1}\mu_k + \mathbf{Z}\mathbf{a}_k + \mathbf{e}_k,$$

where $\mathbf{y}_k$ is the vector of phenotypes, μ_k is the mean, $\mathbf{a}_k$ is the vector of random additive genetic effects, $\mathbf{e}_k$ is the vector of random residuals, $\mathbf{1}$ is a vector of ones and $\mathbf{Z}$ is the incidence matrix for genetic effects. The variance-covariance matrices of random effects were assumed to be $\mathbf{V}(\mathbf{a}_k) = \mathbf{A}\sigma_{a_k}^2$ and $\mathbf{V}(\mathbf{e}_k) = \mathbf{I}_r\sigma_{e_k}^2$, where $\mathbf{A}$ is the pedigree-based numerator relationship matrix and $\mathbf{I}_r$ is an identity matrix of order r (number of records). Both $\sigma_{a_k}^2$ and $\sigma_{e_k}^2$ were assumed to be known.

The genomic evaluations were performed using the GBLUP method (Nejati-Javaremi et al., 1997; Villanueva et al., 2005; Hayes et al., 2009). The assumed model was the same as in BLUP but here $\mathbf{A}$ was replaced with the genomic relationship matrix ($\mathbf{G}$) computed following VanRaden's method 1 (VanRaden, 2008). Thus, $\mathbf{V}(\mathbf{a}_k)$ was assumed to be $\mathbf{G}\sigma_{a_k}^2$.

The BLUPf90 software (Misztal et al., 2015) was used for carrying out both BLUP and GBLUP evaluations.

2.5. Trait recording and genotyping

Recording HC implies slaughtering the fish and, thus, it cannot be done on selection candidates. Thus, HC is what is known as a 'sib trait' that was assumed to be recorded only in half of the fish per family (i.e., 10 fish per family). The other 10 fish per family were considered to be the selection candidates. Traits BW and IHC are 'candidate traits' that can be recorded on the selection candidates. To maintain the same number of records available for all traits, IHC and BW were assumed to

be recorded on the 10 selection candidates per family. Thus, in the scenarios where selection was for a single trait (i.e., either for HC, IHC, or BW) the total number of fish recorded for all traits was 2000.

In the scenarios where selection was simultaneous for two traits (BW and HC or BW and IHC), the total number of records for BW was 4000 (2000 candidates and 2000 sibs). This is because when BW and HC are jointly selected, it is necessary to record BW to obtain the HC phenotype and thus, BW records are available not only for the candidates but also for their sibs. This is not the case in the scenarios where BW and IHC are jointly selected but in order to make scenarios comparable, the total number of records for BW was also 4000.

In summary, the total number of records was 2000 for HC (sibs) and IHC (candidates), but the total number of records for BW was 2000 (candidates) in scenarios where selection was only for this trait and 4000 (2000 candidates and 2000 sibs) in scenarios where selection was jointly for BW and a yield trait (HC or IHC).

When performing genomic evaluations, fish were considered to be genotyped for the 48,000 SNPs (on average 1600 SNPs per chromosome). Thus, as indicated above, the marker density was 2400 SNPs/Morgan.

2.6. Selection scenarios

Selection was performed for a single generation, in which the 100 males and 200 females with the highest estimated breeding values were selected and randomly mated. Nested mating designs, where each male was randomly mated with two females, were applied. In all scenarios simulated the number of selection candidates per family was 10 (2000 in total) which implies proportions selected of 10% and 20% for males and females, respectively. Thus, the different scenarios were compared at the same selection intensity.

Different BLUP (scenarios B$_X$) or GBLUP (scenarios G$_X$) selection scenarios were considered:

i) Selection for a single trait including direct selection for BW (B$_W$ and G$_W$), sib selection for HC (B$_H$ and G$_H$), or indirect selection for IHC (B$_I$ and G$_I$). Scenarios B$_H$ and G$_H$ (sib selection for HC) were also run with an increased number of sibs tested per family (20, 40, 60, 80, and 100).
ii) Simultaneous selection for both BW and HC (B$_{W+H}$ and G$_{W+H}$).
iii) Simultaneous selection for both BW and IHC (B$_{W+I}$ and G$_{W+I}$).

In scenarios ii) and iii), the final estimated breeding value of an individual i was the sum of the estimated breeding values for each trait (BW and HC or IHC) multiplied by the corresponding relative weight given to each trait. The relative weight for BW was set at 1, and different weights were investigated for the yield trait (HC or IHC) (0.25, 0.50, 0.75, and 1).

Scenarios were compared in terms of the accuracy of evaluation (measured as the correlation between true and estimated breeding values) and phenotypic gain in trait units after one generation of selection. We assumed initial phenotypic means of 1639 g for BW, 76.6% for HC, and 72.4 units for IH,C and phenotypic variances of 351 for BW, 2.25 for HC, and 1.30 for IHC (Kause et al., 2007; Haffray et al., 2012, 2013).

Each scenario was replicated 50 times and the results presented are averages over replicates.

3. Results

3.1. Selection for HC or IHC

With BLUP selection and $h_{HC}^2 = 0.55$ (Table 2), the highest response in HC was achieved with sib selection for this trait (1.03 with scenario B$_H$ versus 0.98 with scenario B$_I$). However, for a lower heritability of HC ($h_{HC}^2 = 0.25$, Table 3) and also with BLUP selection, the highest increase

Table 2

Increase in the phenotypic means of body weight (BW), headless carcass percentage (HC) and the indicator of headless carcass percentage (IHC) after one generation of selection when giving different relative weights to the three traits and when using two different evaluation methods (BLUP, scenarios B_X, or GBLUP, scenarios G_X), for a heritability of HC of 0.55. [a, b]

Scenarios[c]	Selection for	Weights			BLUP			GBLUP		
		BW	HC	IHC	BW	HC	IHC	BW	HC	IHC
B_W and G_W	BW	1	0	0	187.50	0.17	0.17	204.21	0.19	0.18
B_H and G_H	HC	0	1	0	25.17	1.03	0.48	36.47	1.22	0.57
B_I and G_I	IHC	0	0	1	54.37	0.98	0.56	61.53	1.04	0.59
B_{W+H}_1 and G_{W+H}_1	BW and HC	1	0.25	0	189.72	0.46	0.30	207.65	0.56	0.36
B_{W+H}_2 and G_{W+H}_2	BW and HC	1	0.50	0	173.87	0.66	0.38	189.94	0.78	0.45
B_{W+H}_3 and G_{W+H}_3	BW and HC	1	0.75	0	154.28	0.78	0.43	166.01	0.93	0.50
B_{W+H}_4 and G_{W+H}_4	BW and HC	1	1	0	137.73	0.85	0.45	143.70	1.03	0.54
B_{W+L}_1 and G_{W+L}_1	BW and IHC	1	0	0.25	188.84	0.38	0.28	210.69	0.40	0.30
B_{W+L}_2 and G_{W+L}_2	BW and IHC	1	0	0.50	180.03	0.50	0.35	199.47	0.54	0.38
B_{W+L}_3 and G_{W+L}_3	BW and IHC	1	0	0.75	169.74	0.59	0.39	187.71	0.63	0.43
B_{W+L}_4 and G_{W+L}_4	BW and IHC	1	0	1	158.21	0.70	0.44	176.22	0.74	0.49

[a] The initial phenotypic means for BW, HC, and IHC were 1639 g, 76.6%, and 72.4 units, respectively.
[b] Standard errors were equal to 0.1 for BW scenarios, 0.03 for HC scenarios, and 0.01 for IHC scenarios.
[c] Numbers 1 to 4 simply enumerate the scenarios with different weights for each trait to facilitate referring to them in the text.

Table 3

Increase in the phenotypic means of body weight (BW), headless carcass percentage (HC) and the indicator of headless carcass percentage (IHC) after one generation of selection when giving different relative weights to the three traits and when using two different evaluation methods (BLUP, scenarios B_X, or GBLUP, scenarios G_X), for a heritability of HC of 0.25.[a, b]

Scenarios[c]	Selection for	Weights			BLUP			GBLUP		
		BW	HC	IHC	BW	HC	IHC	BW	HC	IHC
B_W and G_W	BW	1	0	0	186.80	0.12	0.17	201.12	0.14	0.19
B_H and G_H	HC	0	1	0	24.89	0.60	0.41	29.52	0.70	0.48
B_I and G_I	IHC	0	0	1	54.88	0.64	0.54	58.25	0.71	0.59
B_{W+H}_1 and G_{W+H}_1	BW and HC	1	0.25	0	194.77	0.22	0.24	213.83	0.26	0.28
B_{W+H}_2 and G_{W+H}_2	BW and HC	1	0.50	0	186.61	0.31	0.30	205.25	0.36	0.34
B_{W+H}_3 and G_{W+H}_3	BW and HC	1	0.75	0	177.69	0.37	0.33	194.59	0.43	0.39
B_{W+H}_4 and G_{W+H}_4	BW and HC	1	1	0	165.37	0.43	0.36	182.43	0.49	0.41
B_{W+L}_1 and G_{W+L}_1	BW and IHC	1	0	0.25	192.93	0.25	0.28	209.04	0.28	0.30
B_{W+L}_2 and G_{W+L}_2	BW and IHC	1	0	0.50	183.75	0.35	0.35	202.61	0.37	0.37
B_{W+L}_3 and G_{W+L}_3	BW and IHC	1	0	0.75	174.32	0.41	0.40	189.05	0.44	0.42
B_{W+L}_4 and G_{W+L}_4	BW and IHC	1	0	1	163.99	0.46	0.43	176.25	0.50	0.47

[a] The initial phenotypic means of BW, HC, and IHC were 1639 g, 76.6%, and 72.4 units, respectively.
[b] Standard errors were equal to 0.1 for BW scenarios, 0.02 for HC scenarios, and 0.01 for IHC scenarios.
[c] Numbers 1 to 4 simply enumerate the scenarios with different weights for each trait to facilitate referring to them in the text.

in HC was achieved with indirect selection (0.60 with scenario B_H versus 0.64 with scenario B_I).

The highest increase in the phenotypic mean of HC was obtained with genomic selection (Tables 2 and 3) both with sib (scenario G_H) and indirect (scenario G_I) selection. As with BLUP, the highest phenotypic response in HC was achieved with sib selection for the highest h_{HC}^2 and with indirect selection for the lowest h_{HC}^2 with genomic selection. The benefit (in terms of phenotypic means for HC) from genomic selection (compared with BLUP) in sib selection scenarios (scenarios G_H versus scenarios B_H) was 18% for $h_{HC}^2 = 0.55$ and 17% for $h_{HC}^2 = 0.25$. In indirect selection scenarios (scenarios G_I versus scenarios B_I), the benefit from genomic selection was lower (6% for $h_{HC}^2 = 0.55$ and 11% for $h_{HC}^2 = 0.25$). Note that this extra gain or benefit (in %) was computed as $100(\overline{\Delta P_{B_I}} - \overline{\Delta P_{B_H}})/\overline{\Delta P_{B_H}}$, where $\overline{\Delta P_{B_I}}$ and $\overline{\Delta P_{B_H}}$ are the increases in the phenotypic mean of HC in scenarios B_I and B_H, respectively.

The accuracy of evaluation for the different traits and scenarios is given in Tables S1 and S2 of supplementary material. In general, when the accuracy for IHC (scenarios B_I and G_I) was higher (lower) than the accuracy for HC (scenarios B_H and G_H), indirect selection led to higher (lower) phenotypic means for HC. For instance, for $h_{HC}^2 = 0.25$, with both BLUP and GBLUP the accuracy for IHC was higher than the

accuracy for HC and indirect selection led to a phenotypic mean of HC than over sib selection (Table 3). Also, for $h_{HC}^2 = 0.55$, with GBLUP the highest accuracy was for HC and this was reflected in the higher phenotypic mean of HC with sib selection (Table 2). However, with BLUP the accuracy for IHC (scenario B_I) was higher than the accuracy for HC (scenario B_H) but the increase in the phenotypic mean of HC was higher with sib selection than with indirect selection.

Table 4 shows the accuracy and the phenotypic mean of HC scenarios B_H and G_H (sib selection scenarios) when the number of sibs tested per family is increased from 10 to up to 100. For $h_{HC}^2 = 0.25$, the accuracy and phenotypic means increased more rapidly with increasing numbers of sibs compared to $h_{HC}^2 = 0.55$. The highest increase in the accuracy was obtained when doubling the number of sibs recorded from 10 to 20 for both h_{HC}^2 and both evaluation method. However, these high increases in accuracy did not translate into high increases in the HC mean. For $h_{HC}^2 = 0.55$, the increase in accuracy was 6% (8%) with BLUP (GBLUP) but the increase in the HC mean was only 0.05% (0.1%) with BLUP (GBLUP). For $h_{HC}^2 = 0.25$, the increase in the accuracy was 13% with both BLUP and GBLUP and this translated into an increase in the HC mean of less than 0.1%. With BLUP, there were no further increases in the accuracy and phenotypic mean when increasing the number of sibs beyond 20 and 40 for $h_{HC}^2 = 0.55$ and $h_{HC}^2 = 0.25$, respectively.

Table 4

Accuracy of evaluation and phenotypic mean of headless carcass percentage (HC) from sib selection for this trait for different number of sibs tested per family (n_{sibs}), evaluation methods (BLUP and GBLUP), and heritabilities for HC (h_{HC}^2).[a]

		Accuracy		Phenotypic mean	
	n_{sibs}	BLUP	GBLUP	BLUP	GBLUP
$h_{HC}^2 = 0.55$	10	0.63	0.76	77.63	77.82
	20	0.67	0.82	77.68	77.92
	40	0.68	0.87	77.69	78.01
	60	0.69	0.90	77.70	78.06
	80	0.70	0.91	77.73	78.08
	100	0.70	0.92	77.73	78.08
$h_{HC}^2 = 0.25$	10	0.55	0.63	77.20	77.30
	20	0.62	0.71	77.27	77.39
	40	0.65	0.78	77.33	77.46
	60	0.67	0.82	77.36	77.50
	80	0.68	0.84	77.36	77.52
	100	0.68	0.86	77.36	77.54

[a] Standard errors were equal to 0.02 for accuracies and 0.03 for phenotypic gains.

However, with GBLUP, the accuracy continued increasing beyond 40, particularly for $h_{HC}^2 = 0.25$.

Note that for $h_{HC}^2 = 0.25$, sib selection requires at least 4000 sib records (and a total of 6000 fish to be managed) to achieve a phenotypic mean for HC higher than that obtained with indirect selection using 2000 records (only 2000 fish to be managed) (see also Table 3).

3.2. Simultaneous selection for BW and a yield trait (HC or IHC)

As expected, the increase in the phenotypic mean of HC was lower when BW was also selected, particularly when the weight given to the latter was relatively high (Tables 2 and 3).

The patterns described in the previous section when BLUP single trait selection was applied (scenarios B_H and B_I) were also observed when BW was also selected (scenarios B_{W+H} and B_{W+I}). Thus, the highest gain in HC was obtained from sib selection (B_{W+H}) for $h_{HC}^2 = 0.55$ (Table 2) and from indirect selection (B_{W+I}) for $h_{HC}^2 = 0.25$ (Table 3), for the whole range of relative weights considered. For $h_{HC}^2 = 0.55$, the difference between sib and indirect selection in terms of gain in HC was higher when BW was also selected (see gains in scenarios B_{W+H} and B_{W+I} for the whole range of relative weights in Table 2).

The benefit of genomic selection, in terms of extra gains in HC, described above for single trait selection scenarios was also observed when BW was also selected. Genomic selection led to increased gains in HC with both sib (scenarios G_{W+H}) and indirect (scenarios G_{W+I}) selection for any combination of relative weights. The highest response in HC was achieved again with genomic sib selection (G_{W+H}) for $h_{HC}^2 = 0.55$ and with indirect genomic selection (G_{W+I}) for $h_{HC}^2 = 0.25$. The benefit from genomic selection (compared with BLUP) was higher in sib selection scenarios (up to 22% for $h_{HC}^2 = 0.55$ and 18% for $h_{HC}^2 = 0.25$) than in indirect selection scenarios (up to 8% for $h_{HC}^2 = 0.55$ and 9% for $h_{HC}^2 = 0.25$).

As expected, when selecting simultaneously for BW and a yield trait, genomic selection led not only to benefits in HC but also in BW. The extra gains in BW from genomic selection were up to 9% (10%) for $h_{HC}^2 = 0.55$ ($h_{HC}^2 = 0.25$) with sib selection and up to 12% (10%) for $h_{HC}^2 = 0.55$ ($h_{HC}^2 = 0.25$) with indirect selection when compared to the equivalent BLUP scenarios. The scenarios leading to higher increases in the phenotypic mean of BW were those leading to lower increases in the phenotypic mean of HC. Thus, a higher increase in BW was obtained from indirect genomic selection (scenario G_{W+I}) for $h_{HC}^2 = 0.55$ and from genomic sib selection (scenario G_{W+H}) for $h_{HC}^2 = 0.25$.

4. Discussion

This study has investigated the potential of indirect and genomic

selection to increase carcass yield in rainbow trout. This is a very important trait due to its relationship with production efficiency as more edible meat (increased profitability) and less waste (decreased environmental impact) for a given amount of resources (such as facilities, feed, labor, and energy) are produced. However, it is difficult to improve. A wide range of selection strategies differing in the traits selected (the carcass yield itself or an indicator trait) and the evaluation method (BLUP or GBLUP) have been compared at the same selection intensity. Similar patterns in the efficiency of the different strategies were found when selection was applied for the yield trait (HC or IHC) and when this trait was simultaneously selected with growth (BW).

In general, when the accuracy of evaluation for the indicator trait was higher (lower) than the accuracy for HC, indirect selection led to higher (lower) phenotypic means for HC than sib selection. However, for $h_{HC}^2 = 0.55$ higher gains in HC were obtained in the scenarios applying BLUP sib selection than in those applying indirect selection despite the fact that the accuracy of the evaluation for IHC was higher than that for HC. This is because, although the accuracy of the evaluation was lower with sib selection (records on sibs rather than on candidates), the genetic variance for HC was much higher than that for IHC. Previous studies that focused on mass selection where fish are selected solely in accordance to phenotypic values of sibs or candidates also found higher gains in HC with sib selection (Haffray et al., 2013; Vandeputte et al., 2017; Prchal et al., 2018).

Even with a h_{HC}^2 more than twice the heritability of IHC, the differences in phenotypic gains for HC between sib and indirect selection scenarios were not large (77.63% for B_H versus 77.58% for B_I and 77.82% for G_H versus 77.64% for G_I). These differences increased in favor of sib selection as we increased the number of sibs tested (up to 20 in the case of BLUP and up to 60 in the case of GBLUP). However, sib selection implies costly lethal recording and extra costs associated with maintaining and genotyping a higher number of fish (sibs). Also, for a given number of fish kept in the program, indirect selection permits a higher intensity of selection as more candidates can be raised, leading to higher responses. Extra simulations were run for indirect selection (and $h_{HC}^2 = 0.55$) with an increased selection intensity (4000 candidates instead of 2000 candidates and 2000 sibs which implies proportions selected of 5% for males and 10% for females instead of 10% and 20%), and the results (not shown) indicated that indirect selection led to a higher gain in HC than sib selection for both BLUP and GBLUP. In these extra scenarios, gains from BLUP indirect selection and from genomic sib selection were very similar. Taking into account these considerations, it is very likely that indirect selection would be a more profitable option than sib selection with either BLUP or GBLUP.

The benefit of indirect selection (when compared with sib selection) was higher in a more hypothetical scenario with a lower heritability for HC ($h_{HC}^2 = 0.25$). In this scenario, a higher gain in HC was obtained from indirect selection in both BLUP and GBLUP scenarios. Decreasing h_{HC}^2 to be at the same level as the heritability of the indicator trait increased the efficiency of indirect selection, especially for BLUP selection. In this case, for sib selection to give the same gain as indirect selection, we would need to increase the number of tested sibs to 20 per family.

With indirect selection, the benefit of genomic selection (i.e, GBLUP versus BLUP indirect selection) assuming 2000 candidates, was 6% and 11% for $h_{HC}^2 = 0.55$ and $h_{HC}^2 = 0.25$, respectively. Although GBLUP implies extra (genotyping) costs, the benefits for the on-growing farmers are expected to be high due to the high biomass of farmed fish. Small improvements in carcass and fillet yields can result in large profits when farming millions of kilos of fish (Kankainen et al., 2016). Currently, genomic selection is normal practice in the salmon breeding industry, and it can be expected that the same will occur in the near future in other aquaculture species. Industry leaders typically apply the most effective tools and, in the long-term, companies that use the best tools prevail. In recent years, the number of medium- and high-density SNP arrays available for aquaculture species has increased. This together with the

reduction of genotyping costs associated with the new advances in next-generation sequencing, make genomic evaluations more affordable (Joshi et al., 2018; Robledo et al., 2018). Recent research has demonstrated the potential of applying genomic selection in rainbow trout as the prediction accuracies from genomic evaluations are substantially higher than those from pedigree-based BLUP evaluations for reproductive traits (D'Ambrosio et al., 2020) and disease resistance (Vallejo et al., 2017; Silva et al., 2019; Vallejo et al., 2019; Yoshida et al., 2019a; Vallejo et al., 2020; Vallejo et al., 2021). The accuracy of genomic selection could be increased further by including information on allele effects of SNPs affecting the selected traits into the genetic evaluations (e.g., Zhang et al., 2016; Griot et al., 2021). In fact, this application has been investigated to improve yield traits in rainbow trout (Gonzalez-Pena et al., 2016; Salem et al., 2018) and Nile tilapia (Yoshida et al., 2019b).

Interestingly, the accuracy with GBLUP sib selection continued to increase when the number of tested fish per family increased above 60 while the accuracy with BLUP did not increase further when increasing the number above 40. This is because GBLUP captures the genetic variation existing within families, and the benefits from this evaluation method are greater when family sizes are large. These results are in concordance with those found by Dagnachew and Meuwissen (2019) that showed that the accuracy of evaluation was still increasing when 90 sibs per family were tested for a trait with a very low heritability ($h^2 = 0.05$). This means that the structure of traditional pedigree-based breeding programs may need to be changed when genomic selection is implemented.

The SNP density used in GBLUP scenarios in this study was similar to that found in the SNP arrays already developed for rainbow trout (Palti et al., 2015; Salem et al., 2018), and increasing the marker density further is not expected to improve the accuracy of genomic selection. Solberg et al. (2008) showed that the accuracy remained responsive to increasing marker density at least up to $8N_e$/Morgan, where N_e is the effective population size. Our N_e (estimated as $4 N_m N_f /(N_m + N_f)$, where N_m and N_f are the number of breeding males and females, respectively; Falconer and Mackay, 1996) was 267 and thus the accuracy would increase up to a density of about 2136 SNPs/Morgan, a value lower than the density used here (2400 SNPs/Morgan). Recently, Kriaridou et al. (2020) have investigated the value of low- and medium-density SNP arrays to accurately predict breeding values in populations of a variety of aquaculture species (Atlantic salmon, common carp, gilthead sea bream, and Pacific oyster). Despite the differences in genome size, family number, population size, and target trait across the datasets, they found that in general 1000 - 2000 SNPs would be enough to achieve accuracies close to the maximum and explained the consistency across species by their large family sizes (long haplotypes are shared between many individuals in the reference and test population). In particular, recent studies in rainbow trout have shown the benefit of genomic selection when compared to BLUP selection even when using low-density SNP panels and a small training population which facilitates the implementation of genomic selection by reducing the cost of genotyping (Vallejo et al., 2017; Vallejo et al., 2018; Vallejo et al., 2021). This is due to the high LD found in breeding populations of this species (Vallejo et al., 2017; Vallejo et al., 2018).

The growing interest in aquaculture breeding programs to improve traits related to production efficiency that are difficult to quantify and measure (e.g., fillet and carcass yield, fillet and visceral lipid deposition, feed intake or feed conversion ratio), has led to a large amount of research to find appropriate indicator traits (Rutten et al., 2004; Van Sang et al., 2009; Haffray et al., 2012, 2013; Janhunen et al., 2017; Vandeputte et al., 2017, 2019; Knap and Kause, 2018; Prchal et al., 2018, 2020, 2021). These indicators need to be easy to measure and non-lethal so that they can be recorded on candidates thus allowing to exploit the within-family variability. Most indicators for fillet yield developed so far are based on one or a combination of several morphological measurements (Rutten et al., 2004; Van Sang et al., 2009; Haffray et al.,

2012, 2013; Vandeputte et al., 2017, 2019; Prchal et al., 2020, 2021). Here, we have simulated one of these indicators (the ratio of abdominal wall thickness to depth of the peritoneal cavity or E8/E23) that was developed for HC (Haffray et al., 2013; Prchal et al., 2018; Vandeputte et al., 2019) and showed that indirect selection based on it would be a very valuable approach to improve carcass yield, particularly when combined with genomic selection. Although the best scenario would be to record the indicators close to market size (i.e., at harvest), Prchal et al. (2021) have shown recently in common carp that the genetic correlation between the E8/E23 recorded on two-year old fish and at market size is high. Thus, another advantage of applying indirect selection through the indicator could be the possibility of obtaining phenotypes at an earlier age which would facilitate fish manipulation (Prchal et al., 2021).

All selective breeding programs in aquaculture include growth traits in their breeding objectives (Gjedrem et al., 2012). These traits (e.g., body weight and daily gain) are relevant to increase production and reduce the duration of the rearing cycle but have generally a modest direct impact on production efficiency. This is because growth traits have a lower impact on the ratio input/output than yield traits or feed efficiency (Rutten et al., 2004; Kause et al., 2007; Vandeputte et al., 2017; Knap and Kause, 2018; Prchal et al., 2018). Thus, breeding goals should also include other traits such as HC to increase the profitability of the aquaculture industry. Our results show that when the yield trait is simultaneously selected with BW, the selection approach leading to the highest response in HC is the same as when single trait selection (for the yield trait or even only for BW) is performed.

Given the values of the genetic correlations (higher between BW and IHC than between BW and HC), the reduction in the response in BW when selecting also the yield trait was lower when this trait was IHC (scenarios B$_{W+I}$ and G$_{W+I}$) than when it was HC (scenarios B$_{W+H}$ and G$_{W+H}$) which reinforces the value of indirect selection. When combining indirect with genomic selection there was an extra response in BW (about 10% extra gain when compared to BLUP indirect selection, for $h_{HC}^2 = 0.55$). It should be noted that, if GBLUP is going to be used for evaluating the yield trait, once the fish are genotyped, other traits including BW can be evaluated using GBLUP at the same genotyping expense. This will increase the benefit-cost ratio of indirect genomic selection.

5. Conclusions

This study has shown that the most profitable option to improve yield traits is a combination of genomic and indirect selection. In other words, indirect genomic selection for the indicator of HC is an interesting cost-benefit option to increase carcass yield. This was the case not only when selection was for a single yield trait but also when a growth trait was simultaneously selected with the yield trait, for a wide range of relative weights given to both traits.

Code availability statement

The Fortran F90 codes are available from the corresponding author on reasonable request.

CRediT authorship contribution statement

Silvia García-Ballesteros: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Visualization. **Jesús Fernández:** Conceptualization, Software, Investigation, Writing – review & editing, Visualization, Supervision. **Antti Kause:** Conceptualization, Investigation, Writing – review & editing. **Beatriz Villanueva:** Conceptualization, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2022.738119.

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