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Accuracy of BLUP breeding values in a factorial mating design with mixed families and marker-based parentage assignment in rainbow trout *Oncorhynchus mykiss*

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Abstract :

Marker-based parentage assignment provides the opportunity to investigate factors of efficiency for mixed-family designs and factorial mating. In such designs, family size is both uncontrolled and small, which may be thought to limit the accuracy of estimated breeding values (EBVs). The objective of this work was to estimate the accuracy of EBVs of growth and quality traits in a large factorial mating design and in commercial breeding conditions.

An expected six hundred full-sib families of rainbow trout *Oncorhynchus mykiss* (2042 fish in total) were produced by ten factorial matings of six dams with ten sires. Fish were phenotyped for body weight, carcass yield, fillet yield, fillet fat content and fillet colour, and family information was recovered using microsatellite markers.

The accuracy of EBVs was estimated using or removing individual performance to mimic combined family selection (with individual phenotype) or sib selection (without individual phenotype).

The traits investigated had medium to high heritability (0.17–0.58). High to very high accuracy (0.630–0.817) was estimated for combined family selection. The accuracy of sib selection (not using individual phenotype) was 18–22% lower (0.542–0.638), but remained in the upper range reported for such traits.

This level of accuracy was higher than those reported in conventional breeding programs using separate family rearing. This was true even for families with a very low number of full-sibs. Individual EBV accuracy was more closely linked to the total number of full- and half-sibs of each fish than to its number of full-sibs. We hypothesize that this was due to the factorial mating, which led to a high number of the genetic ties between sibs.

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These results highlight the possibility of introducing precise estimated breeding values for quality traits into combined or sib selection in breeding programs when using mixed families from factorial designs and marker-based parentage assignment in aquaculture species.

Highlights

► This work reports for the first time accuracies of EBV in a mixed family breeding design assisted by DNA-parentage assignment for growth and quality traits (0.6-0.8). ► Theses accuracies were higher than those reported in classical family-based breeding program and similar or higher than reported by simulation for genomic selection ► The factorial mating is proposed as the factor that allow such interesting advantage ► This result confirms the potential interest to use such design to initiate domestication and selective breeding program

Keywords : Aquaculture, Salmonids, DNA parentage assignment, Sib selection, EBV accuracy

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1. Introduction

Less than 10% of world aquaculture production benefits from genetically improved seed. When it does, this comes mostly from conventional family-based breeding programs (Gjedrem et al., 2012), using families reared separately until tagging and Best Linear Unbiased Prediction, or BLUP (Henderson, 1984). One of the major reasons for this limited development is the high cost of these programs, which require both initial investment in numerous family tanks (>100) and highly trained staff using very good traceability and rearing practices to limit both pedigree errors and initial tank effect. This is a serious obstacle for small and medium enterprises (SMEs) and for the initiation of selective breeding in new aquaculture species.

Alternative breeding schemes using marker-based parentage assignment and combining mass selection on traits measurable in candidates (such as growth) and sib selection on lethal traits (quality, disease resistance, etc.) have not been greatly studied so far (Vandeputte and Haffray, 2014). This kind of breeding scheme limits both tank effect and initial investment, as all families can be reared together in just one tank. The use of common garden rearing and molecular pedigrees also relieves constraints on family number, allowing the production of more families for a fixed number of parents (e.g., by the use of factorial mating designs). This increases the potential for between-family selection intensity at a given level of inbreeding (Dupont-Nivet et al., 2006; Sorensen et al., 2005).

The relative efficiency of breeding programs can be assessed by the accuracy ($r_{A\hat{A}}$) of the estimated breeding values (EBVs). This accuracy is the correlation between the true breeding value (TBV) and the EBV, and can be derived from mixed-model equations (Van Vleck, 1993).

In aquaculture, there are few reports on the accuracy of EBVs for production traits, with only two references available on conventional breeding schemes with initially separated families

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(Gonzalez-Pena et al., 2016; Kause et al., 2007) and one on a mixed families scheme (Blonk et al., 2010). One problem with the mixed-families design, using *a posteriori* parentage assignment, is that the number of sibs per family is variable and unpredictable. In addition, as factorial designs generate very high numbers of families, they can result in very low numbers of fish recorded from each family. Small and variable family sizes could be seen as unfavourable to the accuracy of breeding values.

The aim of the present work was to estimate the accuracy of EBVs for different traits (growth, carcass traits and fillet quality) in a factorial mating design in rainbow trout *Oncorhynchus mykiss* using *a posteriori* parentage assignment. Genetic parameters, EBVs and $r_{A\hat{A}}$ were estimated within a single generation using performances collected from a random sample of 2000 offspring. Both univariate and multivariate models were investigated as the literature mostly reports evaluations or simulations with univariate models, but breeding programs generally rely on multivariate models. The accuracy of sib selection was compared with combined family selection for each trait and with univariate or multivariate models using a leave-one-out (LOO) procedure, where the phenotype of any given individual was either used (combined selection) or not (sib selection).

These estimates of accuracy in a mixed-family design in aquaculture are expected to support the introduction of combined family or sib-based selection on quality traits in mass selection programs initially designed to improve growth.

2. Methods

2.1. Management and phenotyping of animals

The measured traits and rearing environments were indexed according to the ATOL (Animal Trait Ontology for Livestock) and EOL (Environment Ontology for Livestock) ontologies

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available on the ATOL (http://www.atol-ontology.com/index.php/en/les-ontologies-en/visualisation-en) website.

The offspring sample had already been used to estimate genetic parameters and design predictors for quality traits in previous studies (Haffray et al., 2012a; Haffray et al., 2013) and was established from a commercial line (Aqualande breeding company, Pissos, France). Six hundred all-female full-sib families from 60 dams and 100 sires were produced in one day (November 2004) through a partial factorial mating design with 10 independent blocks. Each block was the full factorial mating of 6 dams with 10 sex-reversed sires (neomales) and thus comprised 60 families. A piece of fin from each parent was kept in 95% ethanol for later marker-based parentage assignment. Eggs from maternal half-sib families were incubated separately by dam. At eyed stage, non-genetic maternal effects were managed by creating 12 new batches, each grouping spawns from 5 dams with similar mean egg size (Haffray et al., 2012b). Each batch was then expected to contain $5 \times 10 = 50$ distinct full-sib families. Each batch was reared separately until 147 days post fertilization (D147) when they had reached the same mean length (BL, ATOL: 0001658) of 9.7 ± 0.7 cm. At this age, and before any selection, 250 individuals per batch (n = 3000 in total) were sampled at random and pooled (i.e., from 600 expected families). At D198 (BW = 73.2 ± 17.6 g), individuals were individually tagged with RFID transponders (Biolog-ID, France) and a piece of fin was preserved in 95% ethanol. At D220, fish were transferred to the "Viviers de la Hountine" fish farm (Belin-Béliet, France).

Water temperature varied from 3 to 20°C during the year. Tanks and raceways were supplied with the "first" water just entering in the fish farm. Fish were vaccinated against *Yersinia ruckeri* at D220. They were grown under non limiting oxygen availability (>80% oxygen saturation, EOL:0000186) and fed to satiation using Neo Extra extruded commercial feed (Le Gouessant, Lamballe, France; 43% protein and 23% lipids) from 40 g to 300 g and Neo Ultra

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(41% protein and 26% lipids; 25 ppm astaxanthine) from 300 g to the final harvesting. Density (EOL: 0000043) increased with growth, but was kept to a maximum of 70 kg/m^3.

For final phenotyping, fish were divided at random into two equal subgroups and slaughtered on two different dates (D509 and D511) in order to reduce the waiting time between slaughtering and phenotyping. Each sub-group was fasted for 3 days, anaesthetised (CO_2), killed by bleeding in icy water at the Aqualande processing plant (Roquefort, France, 50 km from the fish farms) and transported in a refrigerated truck to the IFREMER experimental facility (Nantes, France) for processing and data collection.

2.2. Data collection and parentage assignment

The fish were phenotyped for body weight (BW in g, ATOL: 0000351), gutted carcass yield (Car%, ATOL: 0000548), fillet yield (Fil%, ATOL: 0002305) as previously reported (Haffray et al., 2012a), as well as fillet fat content (Fat%; ATOL: 0001663) and redness (a*; ATOL: 0001017). Fat% was indirectly estimated by microwave absorption (Distell Fish Fat Meter) as the mean of the Fat Meter measurements at the anterior and the posterior dorsal positions above the lateral line of the left side of the fish (Douirin et al., 1998). Redness of the fillet was measured according to the international CIE L*a*b* colour space model (CIE, 1976) using a Minolta CR200 Chroma Meter to obtain the mean value of the a* component at three dorsal positions on the left fillet (anterior, medium or posterior). Malformed fish (ATOL: 0002265) were identified by visual observation of the vertebral axis after filleting. The very few fish found to have malformations of the vertebral axis (0.07 %) were discarded from further analysis.

Fish were assigned to their parents by a private laboratory for livestock genotyping (Labogena, ISO 17025 accredited, Jouy en Josas, France) using thirteen microsatellites. Only fish unambiguously assigned by exclusion to both their parents with a maximum of two

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authorized mismatches were kept for statistical analysis. As previously reported (Haffray et al., 2012b), parthenogenetic autotriploids (n = 29) were discarded from the statistical analysis.

2.3. Genetic parameters

The weight of the carcass and fillets, as well as muscle fat% and a* are phenotypically linked to body weight. As commercial body weight was not expected to increase following selection (i.e., slaughter weight is fixed by the market), these traits were regressed on BW and the residual of the regression was used as the phenotype. For carcass weight and fillet weight, phenotypes at a fixed mean body weight were used as a proxy for the ratio (carcass yield Carc% and fillet yield Fil%, respectively) as suggested by Koch et al. (1963) to avoid spurious genetic correlations between the ratio and its denominator, in this case body weight.

Day of slaughter (2 levels), number of days after slaughtering (3 levels) and filleting operator (2 levels) were significant fixed effects (PROC MIXED, SAS; $p<0.01$) for Fil% and the first two of these effects were significant for fillet a* colour.

Significance of maternal effect was tested (Chi-2 test) by comparing log-likelihoods (-2LL) of models with or without maternal effect (Haffray et al., 2012b), and was never significant.

Heritabilities (h^2) and EBVs were estimated with REMLF90 (Misztal et al., 2002) with an animal model and fixed effects when significant (see above). Data were normalized with the following formula, $x_{new} = [x - \mu] / \sigma$, where x is the phenotypic performance measured, μ is its mean and σ is its phenotypic standard deviation; so that all transformed traits had zero mean and unity variance. Univariate models (to enable comparison with previously published results) and multivariate models were applied to estimate accuracy. Multivariate models included all of the following traits: BW, Carc%, Fil%, Fat% and a*.

2.4. Accuracy of EBVs

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The accuracy of EBVs ($r_{A\hat{A}}$) was calculated as the square root of the $r^2_{A\hat{A}}$ determination coefficient (or CD) equal to *1 – [var (û – u) / var u]*, where *û* is the trait EBV, *u* the true but unknown BV and *var u* the estimated genetic variance of the trait. For each individual, *var (û – u),* also called prediction error variance (PEV), was calculated as the square of the standard error (SE) of each EBV with the above-mentioned univariate or multivariate models. These accuracies corresponded to a combined family-based breeding program with performance also measured on candidates. In order to evaluate the accuracy of sib selection (with no performance measured on the candidates), the EBVs of each individual were also alternatively estimated without using their own performance in the model, in a leave-one-out (LOO) cross-validation procedure (Arlot and Celisse, 2010) in the multivariate model including all traits. The difference in mean accuracy with or without the use of own performance was tested with a Student's t-test ($p< 0.001$) for each trait.

3. Results

Basic statistics for all traits measured at slaughter are given in Table 1.

DNA parentage assignment success was 99.5%. All parents were represented in the progeny. The observed number of full-sib families was 559 (93.1% of the expected 600). The average full-sib family size was 3.5 ± 2.2 and varied from 0 to 13. Paternal (or maternal) half-sib family size varied from 8 to 45 (from 12 to 61).

Heritability at processing for the traits previously published (BW, Carc%, Fil%) for this experiment (Haffray et al., 2012a) and new traits (Fat% and a*) is given in Table 2. The traits with the highest h^2 were Fat% (0.55 ± 0.04) and Carc% (0.49 ± 0.04).

The mean accuracy of EBVs is given for combined family selection (using all data, including individual phenotype) or for sib selection (using LOO cross-validation – leaving out the individual phenotype) in Table 2. Accuracy was high for combined family selection and

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significantly higher (t-test; $p < 0.001$) with multivariate models (0.724–0.803) than with univariate models (0.583–0.717), while both were significantly higher than the accuracy of sib-based selection with multivariate models (0.587–0.627).

Non-genetic maternal effects were not significant (Haffray et al., 2012b), heritability was intermediate, and common environmental effects (c^2) were supposed to be close to zero (all animals being reared in a common garden). Thus, the number of relatives of each individual was expected to determine $r_{A\hat{A}}$ (Van Vleck, 1993). Figure 1 shows the effect of the number of full-sibs or the number of full-sibs and half-sibs on the accuracy of EBV for Carc%, as an example. When considering only the number of full-sibs of an individual (Figure 1a), there was a significant logarithmic regression between accuracy and the number of full-sibs (r^2 = 0.52). However, some families with very few full-sibs (1 or 2) had accuracies similar (0.64) to others with many more full-sibs (>10). When also considering the number of half-sibs per family (Fig. 1b), the logarithmic regression was much improved (r^2 = 0.73), with a total number of full and half-sibs for each candidate varying between 22 and 89 in the same dataset. Similar trends were observed for all the other traits.

4. Discussion

We estimated genetic parameters and breeding accuracies for individual and sib evaluated traits (growth and quality traits) in a mixed-family factorial mating design. Intermediate to high accuracy of EBVs was estimated even with a low number of full-sibs per family (3.3 on average) for combined family selection and sib-based selection.

Heritability estimates for BW, Fil% and Carc% (already published in Haffray et al., 2012a) and for new traits (Fat% and a*) were in the upper range of previous estimates already reported in rainbow trout (Kause et al., 2007).

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Intermediate to high accuracy of EBVs was estimated for all traits in combined family selection with a multivariate model when the traits were measured on all individuals (0.630-0.817). These accuracy estimates were all above 0.5, the maximum when using half-sibs in a univariate model, and some estimates were higher than 0.71, the maximum when using full-sibs in a univariate model (Falconer and Mackay, 1996; Van Vleck, 1993). Logically, the lowest accuracy estimates were associated with the traits with the lowest heritability (Fil% and a*) and the highest with the traits with the highest heritability (Car% and Fat%). These accuracy estimates were higher than those simulated in *Solea solea* (Blonk et al., 2010) for body weight (0.558), with a much higher mean number of progenies per sire (n = 67.8) and per dam (n = 78.8). They were also higher than those simulated in Atlantic salmon (0.558–0.58) for a trait of intermediate theoretical heritability (0.40) based on 200 to 400 offspring per family for 200 independent full-sib families (Nielsen et al., 2011). They were still higher than those reported in a real breeding program for body weight (0.58) in Atlantic salmon (Tsai et al., 2015) with 712 individuals from 61 families, or those estimated in rainbow trout for fillet or gutted yield (0.54) based on 575 families phenotyped over two generations and a mean number of 4.65 individuals per family (Kause et al., 2007). Finally, these accuracy estimates were also much higher than those recently reported in rainbow trout for similar traits, such as the residual of fillet weight to body weight (0.25) or fillet yield (0.13) with five fish per family for 98 to 102 families produced over three generations (Gonzalez-Pena et al., 2016).

When only sib selection was considered (i.e., individual phenotype not used), accuracies decreased to intermediate levels (0.587–0.627). They were in the same range as those simulated with univariate models in Atlantic salmon (0.56–0.58) in the only publication on sib-selection available that provides such estimates for sib selection (Lillehammer et al., 2013).

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Such intermediate to high breeding accuracy may be surprising considering our very low mean sib number per full-sib family (3.5-4), which was expected to lead to low accuracies. In mixed-family breeding programs using factorial designs, the number of full-sibs and half-sibs per candidate, not only the number of full-sibs, must be considered when discussing $r_{A\hat{A}}$ estimates. This hypothesis is in agreement with the positive effect of factorial mating structure on genetic gain proposed for genomic selection of sib-evaluated traits (Nirea et al., 2014). However, the number of full- and half-sibs was not sufficient to explain the residual variability of accuracy for a given number of sibs in Fig. 1b. This therefore implies variation in the number of cousins and half-cousins due to some parents being more or less related across and within factorial blocks. Finally, the combined use of a factorial mating design and BLUP estimations may thus compensate the very low number of full-sibs per family by also using additional information provided by the numerous genetic connections between factorials in the population.

Nevertheless, our results were obtained in a salmonid species with well-controlled reproduction and in which it is easy to produce factorial mating designs. Transfer to other situations (e.g., with natural spawning) or selection strategies, including genomics selection, would require further investigation to take into account the variations in biological or technical factors.

5. Conclusions and perspectives for application

This study is the first of its kind estimating genetic parameters, EBVs and $r_{A\hat{A}}$ of growth, processing traits and fillet quality in a mixed-family rearing design. The accuracy of EBVs was high, at least equivalent with those simulated in conventional (using separate families) breeding programs, and superior to those estimated from conventional breeding program data. This provides new insights for starting selection programs combining mass selection for

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growth and sib-based selection on quality traits. The results were obtained from a particular dataset and generalisation to other species or situations should be made with care.

The relative simplicity of this procedure and the high $r_{A\hat{A}}$ support the development of combined mass and sib-based selection programs without investment in specialized family rearing units, at least for species with limited market size or at an early stage in domestication. Preliminary results or simulations also highlighted the practical feasibility of using similar designs to integrate disease resistance from non-selected sibs (Chapuis et al., 2010; Norris et al., 2008).

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

PH managed the project, estimated the heritabilities and $r_{A\hat{A}}$ and wrote the manuscript, FE estimated accuracy of EBVs and set up the LOO procedure, JB managed the data collection on a* colour and Fat%, HC supervised the estimation of genetic parameters and of EBV accuracy, MDN and MV supervised the genetic data treatment and the writing of the manuscript. All authors contributed to designing the study, interpreting the results, revising the manuscript and read and approved the final manuscript.

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Table 1: Phenotypic performance at slaughter.

Trait	Mean ± SD	CV%	N
Body weight in g (BW)	1639± 351	21.4	1962
Carcass yield in % (Carc%)	87.7 ± 1.4	1.6	1948
Fillet yield in % (Fil%)	66.8 ± 2.0	3.0	1925
Fat %	8.9 ± 1.1	12.4	1876
Red saturation (a*)	9.1 ± 1.0	11.0	1910

Mean, standard deviation (SD), coefficient of variation (CV%) and number of fish (N) considered in the genetic analysis.

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Table 2: Heritability and accuracy of EBVs for combined family selection or sib-based selection with multivariate or univariate models

Trait	Heritability	Combined family selection with univariate model	Combined family selection with multivariate model	Sib selection with multivariate model
Body weight (BW)	0.37 (0.04)	0.717 ± 0.009	0.730 ± 0.015	0.598 ± 0.068
Carcass yield (Carc%)	0.49 (0.06)	0.626 ± 0.015	0.776 ± 0.017	0.618 ± 0.069
Fillet yield (Fil%)	0.31 (0.05)	0.583 ± 0.020	0.724 ± 0.016	0.587 ± 0.067
Fat content of the fillet (Fat%)	0.55 (0.06)	0.632 ± 0.015	0.803 ± 0.037	0.627 ± 0.070
Red colour saturation of the fillet (a*)	0.30 (0.05)	0.587 ± 0.020	0.736 ± 0.015	0.592 ± 0.067

Heritability and mean accuracy (± standard deviation) of EBV estimated for combined family selection with a univariate or multivariate model or sib-based selection with a multivariate model for growth (BW), processing traits (Carc% and Fil%) or fillet quality traits (Fat% and a*)

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Figure 1:

Effect of the number of full-sibs or the sum of full-sibs and half-sibs on EBV accuracy of the candidates of the CAND group for Carc% using sib information from the REF group.

Legend of Figure 1: Familial EBV accuracy as a function of the number of 1a) sib number per family; 1b) full- and half-sib number per family.

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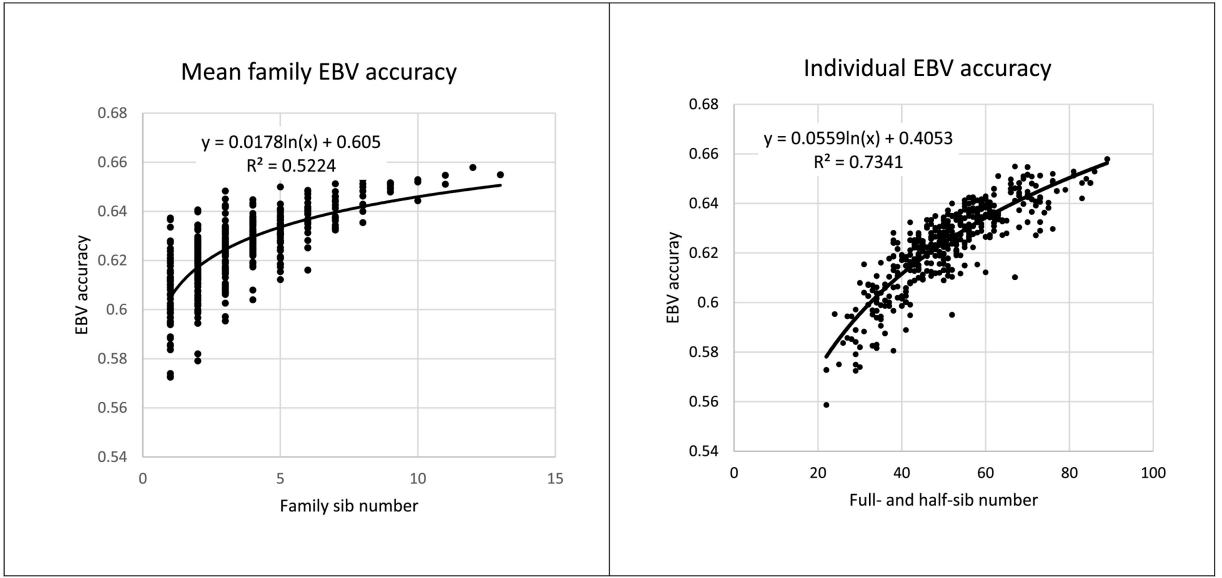
Mean family EBV accuracy
y = 0.0178ln(x) + 0.605
R² = 0.5224
EBV accuracy
Family sib number
0.68
0.66
0.64
0.62
0.6
0.58
0.56
0.54
0
5
10
15
Individual EBV accuracy
y = 0.0559ln(x) + 0.4053
R² = 0.7341
EBV accuray
Full- and half-sib number
0.68
0.66
0.64
0.62
0.6
0.58
0.56
0.54
0
20
40
60
80
100

Figure 1