



Optimising resources and management of genetic variation in fish-breeding schemes with multiple traits



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ABSTRACT

When setting up a breeding program for fish, an optimal breeding scheme is sought, and especially the number of families to use is a pivot parameter in this regard. This simulation study tests a range of probable number of families, with the use of two different methods for implementation of optimum contribution procedures in fish: one based on individual quotas and one with family quotas. Schemes are compared at the same prescribed rate of inbreeding. The breeding goal consisted of two correlated traits, one that could be measured on all selection candidates, the second only on full-sibs. The number of families ranged from 50 to 400, whereas the number of offspring per full-sib family was fixed at 50. Average genetic gain for generations 5 to 15 was used for comparing the schemes, and the rate of inbreeding per generation was restricted to 1%. The individual-based method gave the overall highest genetic gain, but the superiority for this method was most evident for the breeding schemes with a high number of families. The biggest difference between the two methods tested stems from the fact that the family-based method furnished a relatively larger proportion of the gain on the first trait; measurable only on the informants. For the individual-based method, this trait had negative or almost no gain when the genetic correlation was negative. The study also showed that although the total gain did not differ too much, the choice of method could highly influence the specific gain in each of the two traits. It is concluded that for the parameters and assumptions used in this study, the optimal number of families for both methods are likely to be around 200 to 300 if economic considerations are also included.

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1. Introduction

Many fish-breeding programs have been started over the last decades, and some of them have adopted the breeding structure from the Norwegian salmon breeding programs, which commenced in the 1970s. Typically, these programs consisted of 100 to 200 families (Gjøen and Bentsen, 1997). However, at least one of the more competitive salmon breeding programs has recently more than doubled their number of families by generating 400 to 800 families each generation. The opportunity for obtaining a greater number of records is valuable because the gain obtained in a scheme is proportional to the number of candidates that are available (Woolliams et al., 1999), and because it usually allows for greater selection intensity. Typically, the breeding goal consists of several traits, some which can be measured on the selection candidates themselves, e.g. weight and shape, whereas some can only be measured on dead fish, e.g. quality traits like fillet yield, colour or mortality in challenge tests. For these latter traits, only family breeding values will be available on the live candidates and all candidates from a given full-sib family will get the same breeding value in the

absence of information from other traits measured on the candidate. Therefore, increasing the number of full-sib families is important for increasing the range for these critical traits from which to select.

Nevertheless, the number of families is critical in determining the infrastructure needed if physical tagging systems are to be used as it determines the number of family tanks or compartments that are required. It also defines the total number of measurements that are needed because the number of tagged individuals per family is often treated as a relatively fixed entity; usually 50 to 70. If the number of informants from each full-sib family is to be kept constant, the increase in the number of sib tests required for the quality traits is also costly. Therefore, in addition to the extra infrastructure, there are significant recurrent costs arising from increasing the size of the breeding scheme. It is thus crucial to assess the effect of the number of families on the genetic gain in a breeding scheme, and eventually determine a suitable number that gives an acceptable cost–benefit ratio.

Typically, a conventional fish-breeding program using physical tags will rear full-sib families in separate tanks until the fish are large enough to be tagged. A fixed number of individuals from each family are then tagged and subsequently mixed. Due to the inclusion of the same sib-test information, candidates from the same family will tend to have more similar selection indices than would be expected simply from their genetic relationship. With unrestricted truncation selection, this

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promotes the co-selection of relatives, and greater rates of inbreeding, particularly when potentiated by the large families and the high reproductive capacity of fish species. Too high rates of inbreeding will inevitably lead to genetic erosion and inbreeding depression (Falconer and Mackay, 1996; Fessehaye et al., 2007; Gjerde et al., 1983; Robertson, 1954), so measures must be taken to limit this. A common method in fish breeding today is to set a limit on the number of individuals selected from each family, i.e. a quota per family that on average will give an acceptable level of inbreeding. But this is a very static criterion, and is not the best way to restrict inbreeding in a given generation.

In the last decades, several dynamic selection tools, which optimise the genetic contributions from selection candidates while simultaneously controlling inbreeding, have been developed (Grundy et al., 1998; Meuwissen, 1997; Wray and Goddard, 1994), and now these optimal contribution (OC) procedures are recommended in most live-stock breeding programs. These methods have not been used widely in aquaculture, although the OC method has been implemented in the Finnish breeding program for rainbow trout since 2002 (Kause et al., 2005). Some simulation studies have been carried out to look at the benefits of implementing OC in fish breeding (Holtmark et al., 2008; Sonesson, 2005). A common problem of these studies is that the practical limitations were not fully considered, and the results obtained may be misleading. However, Amer and Symonds (2000) developed practical applications of the OC algorithm that can be achieved by focusing on and optimising the contribution from families, as opposed to an approach pivoting around individuals. Skaarud et al. (2011) has investigated this approach further, and showed through simulations that OC can be implemented in fish-breeding designs in an economic and operational way, to give a greater genetic gain than the methods currently in use. However, none of the studies mentioned have investigated the use of optimised selection when more than one trait is included in the breeding goal. This issue might be particularly acute if it is anticipated that traits measured on the candidate (such as growth) may be negatively correlated genetically with traits measured in sib tests (such as disease resistance).

Therefore, the aim of this simulation study was to investigate the effect on the genetic gain of increasing the number of families in a breeding program with selection on two correlated traits and when rates of gain were constrained. This was explored in the situation in which the first trait was measurable on all selection candidates and the second only on full-sibs, and when genetic correlations between the two traits were either positive or negative. Two different methods of implementing OC were used; one based on optimising contributions for individuals, the other for families. The need for using contributions of families may arise when the desired individual contributions are hard to achieve. For example, the individual may not reach sexual maturity within practical time limits for establishing the next generation of families, or there may be mortalities between the time when contributions are calculated and the actual matings. The results were used to understand to what degree the extra gain achieved by increasing the number of families suffers from diminishing returns when inbreeding rate is constrained, as the results of Woolliams and Bijma (2000) demonstrate that such a relationship exists.

2. Methods

2.1. Generating simulated populations

Populations with discrete generations under artificial selection were modelled by stochastic simulation. Breeding values and phenotypes for two correlated traits were simulated. Each generation consisted of n_{fam} families, and each family had n_o offspring available for selection and n_{inf} full-sib informants. These *informants* refer to the individuals in whom the second trait is measured. These individuals need to be killed or slaughtered to provide information on the second trait, and thus cannot

be breeding candidates themselves. An equal number of males and females were generated in all families.

Genotypes, g_i , of unrelated base population animals (generation 0) were sampled from the distribution $\begin{bmatrix} G_1 \\ G_2 \end{bmatrix} = L \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix}$,

where $L = \begin{bmatrix} \sigma_{A1} & 0 \\ \frac{\rho}{\sigma_{A1}} & \sqrt{\sigma_{A2}^2 - \frac{\rho^2}{\sigma_{A1}^2}} \end{bmatrix}$ is a lower triangle matrix from the

Cholesky decomposition of the variance/covariance matrix for the two traits, and ε_i are independent samples from a standard normal distribution. Genotypes in the following generation were then obtained by

$$\begin{bmatrix} G_1 \\ G_2 \end{bmatrix} = \frac{1}{2} \begin{bmatrix} G_{1s} \\ G_{2s} \end{bmatrix} + \frac{1}{2} \begin{bmatrix} G_{1d} \\ G_{2d} \end{bmatrix} + \frac{1}{2} \sqrt{1-F_s} L \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix} + \frac{1}{2} \sqrt{1-F_d} L \begin{bmatrix} \varepsilon_3 \\ \varepsilon_4 \end{bmatrix}$$

G_S , G_D and F_S , F_D are genotypes and inbreeding coefficients of the sire and dam, respectively. The environmental covariance between the traits was assumed to be zero, because they are measured on different individuals, and phenotypic values were generated so that both traits had a phenotypic variance of 1 in the base generation, i.e.

$$\begin{bmatrix} P_1 \\ P_2 \end{bmatrix} = \begin{bmatrix} G_1 \\ G_2 \end{bmatrix} + \begin{bmatrix} E_1 \\ E_2 \end{bmatrix}, \text{ where } E_i \sim N(0, 1 - \sigma_{Ai}^2).$$

2.2. Evaluation

BLUP estimated breeding values (EBVs) were calculated for trait A based on observations on both the selection candidates and the informants, and for trait B, where information was only available from the informants. Because true economic weights are sometimes difficult to obtain, an index, I , was constructed using a method typically used in many fish-breeding programs. The EBVs for each trait were thus first standardized by $EBV'_i = (EBV_i - \bar{EBV}) / \sigma_{EBV}$, and then equal weight in the index was put on each trait:

$$I_i = \frac{1}{2} EBV'_{Ai} + \frac{1}{2} EBV'_{Bi}. \quad (1)$$

This index was used, together with the genetic relationship matrix, as input for the optimum contribution (OC) procedure of Meuwissen (1997) to maximise the genetic gain whereas constraining ΔF per generation to a pre-defined level, here set to 1%. OC provides output in the form of a vector \mathbf{c} containing individual gametic contributions to the next generation. \mathbf{c} is obtained by maximising $c'EBV$ subject to restrictions. The first is the desired rate of inbreeding ΔF , which is obtained by constraining the weighted average coancestry of the selection candidates in generation t , $\frac{1}{2} c'Ac \leq 1 - (1 - \Delta F)^t$. The other restrictions are that the contributions of each sex should sum to $\frac{1}{2}$, i.e. $c'1_m = c'1_f = 1/2$, where 1_m is a vector with 1 for males and 0 for females and 1_f is a vector with 0 for males and 1 for females; and that contributions should be non-negative ($c_i \geq 0$). The resulting equations are then solved numerically to obtain \mathbf{c} . In addition to the two two-trait schemes, a one-trait scheme was run, using $I = EBV_A$, to show the effect of including trait B in the breeding goal.

Achieved selection intensity was estimated for both traits, $j = A, B$ to investigate and explain the differences in observed genetic gain. It was calculated for each generation as $i_j = \frac{R_j}{r_{EBV,G_j} \sigma_{A_j}}$. Where R_j is the true genetic gain, r_{EBV,G_j} is the accuracy, i.e. the correlation between estimated and true breeding values, and $\sigma_{A_j}^2$ is the true genetic variation in the population at the time of selection.

2.3. Selection and mating

Two different methods for implementation of OC were studied, one based on the family mean EBV_{It} , whereas the other emphasized each candidate's EBV_{It} .

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