Effect of assortative mating on genetic gain and inbreeding in aquaculture selective breeding programs

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ABSTRACT

In this simulation study, the effect of the mating scheme on genetic gain and inbreeding has been explored for aquaculture selection programs where tank effects and large family sizes are common. Different selection methods were investigated (individual, family, sib, combined and within-family selection). Our results suggest that under family and sib selection, genetic gain was increased with assortative mating in comparison to random mating. The advantage of assortative mating increased when common environmental effects were present. Contrarily, a decrease in genetic gain was observed with disassortative mating, except for the case of within-family selection. The advantage of assortative mating over random mating was due to the increase in the between-family component of the additive genetic variance that was exacerbated with the presence of common environmental effects. Under family and sib selection, the join effect of assortative mating and common environmental effects produced an increase in genetic gain of around 80 and 40% at early generations, and around 10 and 60% at later generations, respectively. Inbreeding was low under family selection for all mating schemes but much higher under sib selection when assortative mating was performed. In fact, the inbreeding coefficient after 10 generations of selection was 300% higher when assortative matings were performed under sib selection, compared to random matings. This was due to the fact that under sib selection, matings were based on family means, leading to an increased frequency of within-family matings. To our knowledge, this is the first study that investigates the effect of the mating scheme on genetic gain and inbreeding in an aquaculture context where family sizes are large and tank effects are present, and shows that assortative mating can substantially enhance the response to selection, particularly when family selection methods are applied.

Statement of relevance: Our article complies with the Policy Statement for submission of manuscripts to the Genetics Section, as it provides insight into the issue of breeding programs. Here, we have connected previous work in the field to address new questions, focusing on how the mating scheme may affect both genetic gain and inbreeding in aquaculture selection programs, where family sizes are typically large and tank effects are usually present.

In fish species, it is possible to consider different mating schemes because fecundity is high and because in vitro fertilization is often possible. A particular problem in aquaculture breeding programs is the impossibility of tagging physically newborn individuals. Given this, a common practice in aquaculture is to rear families in separate tanks until the fish are large enough to be individually tagged. This introduces an environmental effect common to the members of the same family (tank effect) which can lead to a reduction of the response to selection that needs to be considered.

We studied here the efficiency of different selection methods in terms of genetic gain and inbreeding and investigated the effect of the mating scheme to optimize breeding programs in aquaculture when tank effects are present. We have shown that assortative mating can substantially enhance the response to selection, particularly when family selection methods are applied and tank effects are present. To our knowledge, the effect of the mating scheme in an aquaculture context has never been addressed before. Our results suggest that assortative mating in the presence of common environmental variance may be considered in selection programs in aquaculture. Our conclusions will help breeders make optimal mating choices.

1. Introduction

The potential for high genetic gains through selective breeding are well documented for aquatic species, particularly due to the possibility

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of applying high selection pressures as a consequence of their high reproductive capacity (see Gjedrem and Baranski, 2009 for a review). Applying high selection pressures, however, can lead to high increases in inbreeding and, consequently, to reductions in fitness (i.e., inbreeding depression), genetic variance and long-term genetic progress.

The levels of genetic gain and inbreeding achieved in a selection program are highly dependent on the selection decisions taken. Traditionally, the most relevant selection methods for aquatic species have been individual and family selection (Gjedrem and Baranski, 2009). Individual selection is based on individual phenotypic values and gives the same weight to both between-family and within-family components. This method is easy to apply and has been for many years the most commonly used method of selection in aquaculture, particularly for improving growth (Neira et al., 2006; Gjedrem, 2012). With family selection, individuals are selected based on their family mean, i.e. all weight is given to the family component.

Although the genetic gain achieved depends mostly on selection decisions, the mating design may also affect the selection response. Theoretical studies (Falconer and Mackay, 1996; Lynch and Walsh, 1998) have demonstrated that, in the absence of selection, assortative matings (i.e., matings between individuals of similar phenotype) can increase the additive genetic variance of a quantitative trait. In particular, under the infinitesimal model assortative matings increase the between-family variance although does not affect the within-family variance provided the number of loci controlling the trait is not small (Falconer and Mackay 1996). Breese (1956) and James and McBride (1958) were the first to suggest that assortative matings could be used to increase the response to selection and this increase has been demonstrated empirically in a number of studies (e.g. experiments with *Drosophila*, by McBride and Robertson, 1963).

A particular problem in aquaculture breeding programs is the impossibility of tagging physically newborn individuals. Given this, a common practice in aquaculture is to rear families in separate tanks until the fish are large enough to be individually tagged. This introduces an environmental effect common to the members of the same family (usually known as the tank effect) which can lead to a reduction of the response to selection (Gjedrem and Baranski, 2009).

The effect of assortative matings on genetic gain and inbreeding has not been investigated in the aquaculture context, where most species display external fertilization (and therefore matings can be directed), family sizes are large and tank effects are usually present. The objective of this study was therefore to examine, through computer simulations, this effect under different selection methods applied in aquaculture breeding programs.

2. Methods

2.1. Simulation of the population

One hundred founder individuals (50 sires and 50 dams) were generated. The genome was composed of ten chromosomes of one Morgan each. The trait under selection was assumed to be controlled by 100 biallelic additive QTLs per chromosome. QTLs were evenly distributed across the chromosomes. Linkage and Hardy-Weinberg equilibrium were assumed. The genotypic values for each QTL were a, 0 and $-a$ for individuals with genotype AA, Aa and aa, respectively. Alleles were chosen at random with probability $p = 0.5$. Phenotypic variance was set to one so that the additive genetic variance was equal to the heritability. Two heritabilities ($h^2 = 0.1$ and 0.4) were simulated. The a value was calculated such that $2p(1 - p)a^2 = h^2 / 1000$. The between and within components of the additive genetic variance were calculated through standard ANOVA on the additive genetic values.

Generation 0 ($t = 0$) consisted of unselected individuals with family structure and was obtained from mating at random the founder individuals. It was composed by 50 families of 100 full-sibs (half of each sex) for all scenarios but sib selection, where (50) families were composed by 200 full-sibs (half of each sex), as explained below. The population was subjected to artificial selection during ten discrete generations. At $t \geq 0$, the genotype for each individual was obtained by sampling at random one gamete from each parent. The probability of recombination between adjacent QTLs was 0.01, according to the length of each chromosome. Common environmental (tank) effect was sampled from a normal $N(0, c^2)$, where c^2 is the proportion of phenotypic variance due to common environmental effects. Two values for c^2 (0.0 and 0.4) were considered. Phenotypic values were obtained by adding a normally distributed individual environmental effect with mean zero and variance V_E to the sum of genetic value and common environmental effect.

The percentage of individuals selected at each generation was 2% in all scenarios; i.e. 100 individuals (50 males and 50 females) were always used as breeders to produce the next generation that was composed by 50 families, as indicated above. One hundred replicates were run for all scenarios and the results presented are averages over replicates.

2.2. Selection methods

Different selection methods were investigated including:

(i) *Random selection.* The 50 males and 50 females were selected at random from the 50 families.
(ii) *Individual selection.* The 50 males and 50 females with the highest phenotypic values were selected.
(iii) *Family selection.* First, a number of families (1 or 25) with the highest average phenotypic value were selected. Then, 50 or 2 individuals of each sex were selected at random from these selected families.
(iv) *Sib selection.* This is a particular case of family selection that is widely used in aquaculture for improving traits that cannot be measured on live individuals (e.g. disease resistance or fillet quality traits), and consists of selecting candidates based on phenotypic records obtained on their sibs. Under sib selection, the number of offspring simulated per family was 200. One hundred of them were measured for the quantitative trait and the remaining 100 sibs were the selection candidates. As with family selection, 1 or 25 families with the highest average phenotypic value were first selected. Then, 50 or 2 individuals of each sex were selected at random from these selected families.
(v) *Combined selection.* The weights given to the family mean and the within-family deviations were optimized for maximizing the accuracy of the index (Falconer and Mackay 1996). Then, the 50 males and 50 females with the highest index values were selected.

For completeness, we also investigated an additional selection scenario:

(vi) *Within-family selection.* One male and one female (those with the highest phenotypic values) within each of the 50 families were selected.

2.3. Mating schemes

Three alternative mating schemes were evaluated: RM (random mating of selected parents), AM (assortative matings) and DM (disassortative matings or matings between individuals of dissimilar phenotypes). In individual, family and within-family selection AM and DM were based on individual phenotypic values while in sib selection they were based on the family means (in practice, individual phenotypes would be unavailable). In combined selection schemes, AM and DM were based on index values.