Proceedings, 10th World Congress of Genetics Applied to Livestock Production

Improving uniformity of growth by mating and selection strategies in rainbow trout

A. Kause*, M. Janhunen*, H. Vehviläinen*, H. Koskinen†, and A. Nousiainen†
* MTT Agrifood Research Finland, † Finnish Game and Fisheries Research Institute

ABSTRACT: Minimal variation in fish growth increases profit of fish farming and improves fish welfare. Uniformity can be increased by reducing additive genetic and residual variation. We first present a mating strategy to create a production stock that has only 38% of the original genetic variance, and assuming heritability of 0.26 for body weight of rainbow trout, 84% of the original phenotypic variance. An experimental test confirmed that phenotypic variance can be indeed reduced to 80% of the variation in the original breeding programme. Secondly, genetic coefficient of variation for residual variation in body weight was notable (37%). Hence, one generation of sib selection for reduced residual variation is expected to reduce phenotypic variance to 87-89% of the original phenotypic variance. Both methods aid to produce more uniform populations for on-growing, while simultaneously maintaining genetic variation in the nucleus.
Keywords: additive genetic variance; heterogeneity of residual variance; relationships; rainbow trout

Introduction

Maintenance of genetic variation within a breeding programme is essential for long-term, sustainable genetic improvement of fish material. However, the maintenance of variation contradicts with other practical aims. A uniform fish school with minimum variation among individuals in body weight elevates fish welfare, and increases profit of aquaculture industry in particular due to decreased need for size grading (Gilmour et al. (2005)). Moreover, owners of a breeding programme may want to protect the improved genetic material of a nucleus population and are not willing to distribute the whole genetic base to external parties, hampering the establishment of new breeding programmes.

Hence, a question can be posed: How to resolve a challenge of maintaining genetic variance in the nucleus while simultaneously providing phenotypically and genetically more uniform fish material to multipliers and fish farmers?

Uniformity can be increased by reducing genetic and residual variation. Using rainbow trout (*Oncorhynchus mykiss*), we firstly quantify how much genetic variance can be reduced by a special KING mating design. This method uses a limited number of ancestors to generate highly related but non-inbred F2-generation production population for on-growing. Secondly, environmental variance of production traits is under some degree of genetic control, giving breeders an additional opportunity to improve uniformity permanently by selection. Here we calculate the expected genetic gain and selection accuracy for reducing residual variation by selection in rainbow trout. The calculations are based on a large-scale study on the genetics of environmental sensitivity in rainbow trout (Janhunen et al. (2012)).

Materials and Methods

Reducing additive genetic variance. An experiment was performed to test the KING mating design in which F2-generation production population is established from the breeding nucleus, first through full-sib mating within two unrelated high-EBV families to produce two groups of inbred F1-progeny, and then resolving the inbreeding in F2-generation through the mating of the unrelated F1-individuals (Janhunen et al. (2013)). The additive genetic relationships (a) between the F2 individuals is 0.625, and they have only four grand-parents. In case the F1 fish are not inbred, the F2 population has $a = 0.50$. The elevated relatedness reduces additive genetic variance (Hohenboken (1985)). Assuming a non-inbred F2 population, the additive genetic variance in the F2 offspring is: $\sigma^2_{A(OFF)} = \sigma^2_A(1-a)$ and phenotypic variance is $\sigma^2_{P(OFF)} = \sigma^2_P - (\sigma^2_P a h^2)$, where σ^2_A and σ^2_P are genetic and phenotypic variances and h^2 heritability in the parental generation. Moreover, one group of F1 generation fish can be hormonally sex-reversed to be phenotypic XX-males to be mated with normal XX-females, the cross producing all-female F2-fish.

The effect of the KING method on phenotypic variation was tested using rainbow trout. Three groups of fish were compared: KING F2-fish (34 families, E(a)=0.625); KING control F2-fish (13 families without inbreeding in F1 generation E(a)=0.50, made from the same grand parents as the KING families); and fish of the Finnish national breeding programme (SELEC, 22 random families). For KING and KING control, each family is a replicate for the method. KING and KING control fish were all-female populations, mimicking the Finnish commercial production. Body weight of a total of 1265 (KING), 495 (KING control) and 770 (SELEC) id tagged fish grown in a common raceway were recorded at age of 3 years. Variance of log-transformed weights was compared across the groups with a model: $y_{ijkl} = \mu + \text{group}_j + \text{gender}_k + \text{family(group)}_l + e_{ijkl}$, where y_{ijk} is log-weight of an individual i, group_j is fixed group effect (j=1-3), gender_k is fixed sex effect (male, female, unkown), family_l is random family effect nested wit-

hin KING and KING control groups, and e_{ijk} is residual. Genders did not differ in log variance. The family effect was not accounted for in SELEC to maintain between-family variance in this group. To compare the variance of the experimental groups, a full model with separate residual variances for each group was compared to a reduced model with one common variance for all groups (log-likelihood ratio test with two degrees of freedom).

Reducing residual variance. Genetic variation of residual variation in body weight of rainbow trout was estimated using a bivariate animal model applied to a multigenerational data of 45,900 individuals from the Finnish national breeding programme (Janhunen et al. (2012)). The data originated from eight year classes. Each year class consisted of 94-270 full-sib families established from matings of 37-90 sires with 92-270 dams. Each sire had at least 35 offspring (n = 457 sires).

The first trait analyzed was body weight for which a linear mixed 'mean model' was fitted: $y_{ijk} = \mu + year_j + tank_k + A_i + e_{ijk}$, where y_{ijk} is body weight of an individual i, μ is the overall population mean, $year_j$ is the fixed effect of birth year (j=8 years), $tank_k$ is the random interaction effect of birth year and common tank environment shared by full-sibs before tagging (k = 1- family tank × year number), A_i is the random genetic animal effect with a pedigree (i = 1 - number of animals), and e_{ijk} is the residual error term with separate error variance for each sire family.

The second trait was residual variation (microenvironmental sensitivity) which was quantified by the log-transformed squared residual values ($\ln(e^2)$) taken from the analysis of the first trait. The 'variance model' was: $\ln(e^2_{ijk}) = \mu + year_j + A_{resi} + e_{resij}$, where A_{resi} is the genetic effect of animal i for $\ln(e^2)$ and e_{resij} is the random residual effect. The bivariate model results are the average of 30 rounds of iterations in which the $\ln(e^2)$ of the variance model was updated each time.

The expected genetic gain in response to mass and sib selection for reduced residual variation was calculated following Mulder et al. (2007). Selection accuracy of body weight and $\ln(e^2)$ was calculated for progeny and fullsib testing schemes with number of tested animals ranging between 10 and 100. For body weight, the genetic parameters of weight used in the routine breeding value evaluation were used (Kause et al. (2005)). For $\ln(e^2)$, the genetic parameters from the bivariate mean-variance model were used (Janhunen et al. (2012)).

Results and Discussion

Reducing additive genetic variance. In the KING mating design, when only one inbred F1 sire and one inbred F1 dam are used as parents, the additive genetic relationship of the F2 offspring is 0.625 and hence the remaining additive genetic variance in the F2 offspring generation is 37.5% of the original additive genetic variance. When using outbred unrelated KING control parents, 50% of the original additive genetic variance remains in the F2 offspring generation (a=0.5). Thus, it is possible to maintain genetic variance within a nucleus population, but simultaneously deliver stocks with limited genetic variance for on-growing. This restricts the use of F2 progeny to establish new breeding programmes, thereby protecting the genetic material of the nucleus. Because a single female may produce thousands of offspring in trout and other fish species, two large groups of F1 sibs can be produced that are mated to produce hundreds of thousands of F2 production fish that are all highly related. However, the protection of intellectual property by KING is not complete. Considerable amount of genetic variance still remains in the KING F2 progeny because Mendelian sampling term still harbors ample genetic variance. Moreover, competitors can potentially acquire several batches of KING fish that are unrelated and thus differ in their genetic background.

The KING method is expected to reduce only additive genetic variance, and hence the higher the heritability, the higher the reduction in phenotypic variance. Assuming heritability estimate of 0.26 for body weight of rainbow trout (Kause et al. (2005)), the remaining proportion of phenotypic variance in weight is expected to be 83.8% (1-(1×0.625×0.26)) when KING and 87% when KING control design is employed. With a heritability of 0.5, the remaining phenotypic variance is 68.8% and 75%, respectively. In fish, most of the economically important production, quality and health traits display low-to-moderate heritabilities (h^2 = 0.10-0.40), with only few traits such as skin spottiness having very high heritabilities (Kause et al. (2003)). Accordingly, KING is expected to reduce phenotypic variation moderately (<20%) in traits typically selected in fish breeding programmes.

The KING method was tested with rainbow trout. The mean body weight did not differ significantly between the experimental groups (F=0.61, df_1 = 2, df_2 = 68.6, P = 0.55; Figure 1a). In contrast, the phenotypic log-variance in body weight of KING and KING control fish were, respectively, 80% and 83% of the variance of the whole breeding programme, the difference being statistically significant (G^2 = 12.7, df = 2, P = 0.002; Figure 1b). These values are in line with the expectations of 84-87% reduction, validating the benefit of the KING method. The reduced variation in growth may have positive impact on health traits and survival of fish, and on the profitability of aquaculture operations.

Reducing residual variance. The animal model analysis revealed the presence of genetic heterogeneity in residual variation of body weight in rainbow trout. The coefficient of genetic variation for residual variation was notable (37%), suggesting substantial potential for selection

response (Table 1; Janhunen et al. (2012)). With a range of realistic selection intensities, one generation of mass or sib selection for reduced residual variation is expected to reduce residual variance to 77-90% of the original residual variance (Table 2). Hence, the phenotypic variance after selection is 87-95% of the phenotypic variance before selection.

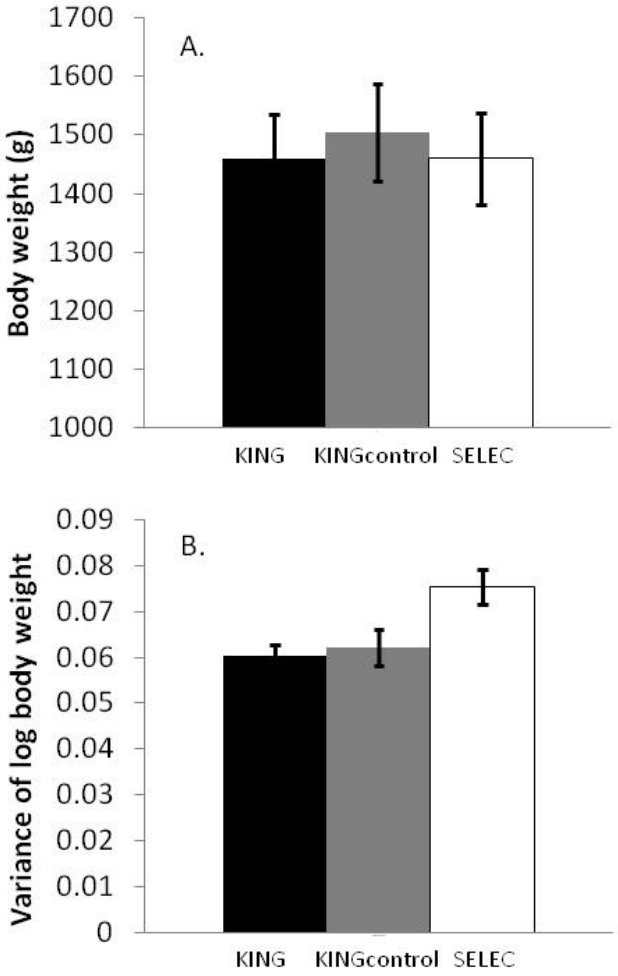

Figure 1. Average body weight (A), variance of log body weight (B), and their SEs for the three experimental groups of rainbow trout compared.

Table 1. Estimates of genetic parameters[1] for body weight and log squared residuals

Trait	Body weight	Log squared residuals
σ_P^2	59652	-
σ_A^2	20 888	1.81 E+8
σ_C^2	3 089	-
h^2 (SE)	0.35 (0.05)	0.02 (0.006)
CV_G	14.2	37.6

[1] σ_P^2 - phenotypic variance; σ_A^2 - genetic variance; σ_C^2 - environmental variance common to fullsibs; h^2 - heritability; CV_G - coefficient of genetic variation.

Table 2. Proportion of residual variance remaining after one generation of selection for reduced residual variation in mass selection or full-sib testing schemes with 25 tested sibs

Proportion of selected animals	Phenotype	25 full sibs
0.10	0.90	0.77
0.15	0.91	0.80
0.20	0.92	0.82

Table 3. Accuracy of selection for body weight and log squared residuals in progeny and sib testing schemes

	Body weight		Log squared residuals	
Nro of progeny or full sibs	Progeny testing	Sib testing	Progeny testing	Sib testing
10	0.64	0.50	0.24	0.23
25	0.80	0.55	0.36	0.34
50	0.88	0.58	0.48	0.44
100	0.94	0.59	0.61	0.52

Heritability of residual variation (0.02) was much lower than for body weight (0.35) (Table 1). Heritability strongly influences the level of selection accuracy. Consequently, selection accuracy for residual variation remained much lower compared to mean body weight (Table 3). For instance, a realistic breeding programme has around 25 full sibs, which results in accuracy of 0.55 for body weight but 0.32 for residual variation. The challenge is that in fish breeding, fish of the offspring generation are typically used as breeding candidates, which have lower selection accuracy than the parents. It would be useful to find highly heritable traits that both correlate with environmental sensitivity and could be accurately recorded from the offspring. The use of such correlated trait in a multitrait breeding value evaluation would increase selection accuracy, allowing more effective selection. The genetic correlation between body weight and log squared residuals is low (r_A=-0.16±0.04) (Janhunen et al. (2012)), the body weight records providing only modest additional correlated information to increase accuracy value for log squared residuals.

Conclusion

The KING mating design can be used to increase uniformity of fish material via a major reduction in genetic variance. This method also partially protects the genetic material of a nucleus, when fish material is distributed outside the breeding organization. Selection, in turn, can be used to reduce residual variation. Both of these methods can be used to produce more uniform fish populations for on-growing, while still simultaneously maintaining genetic variation in the nucleus population.

Literature Cited

Gilmour, K. M., DiBattista, J. D., and Thomas, J. B. (2005). Integr Comp Biol 45:263-273

Hohenboken, W. D. (1985). J. Anim. Sci. 60:101-110

Janhunen, M., Kause, A., Mäntysaari, E. A. et al. (2013). Aquacult. Res. 44:1847-1859

Janhunen, M., Kause A., Vehviläinen, H. et al. (2012) *PLoS ONE* 7:e38766

Kause, A., Ritola, O., Paananen, T. et al. (2003). J. Fish Biol. 62:610-622

Kause, A., Ritola, O., Paananen T. et al. (2005). Aquaculture 247:177-187

Mulder, H. A., Bijma, P., and Hill W. G. (2007). Genetics 175:1895-1910