

Estimation of genetic parameters for growth trait of turbot using Bayesian and REML approaches

GUAN Jiantao^{1, 2}, WANG Weiji², HU Yulong², WANG Mosang^{2, 3}, TIAN Tao^{2, 3}, KONG Jie^{2*}

¹ Ocean University of China, Qingdao 266003, China

² Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, China

³ Shanghai Ocean University, Shanghai 201306, China

Received 21 May 2015; accepted 14 September 2015

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Abstract

Bayesian and restricted maximum likelihood (REML) approaches were used to estimate the genetic parameters in a cultured turbot *Scophthalmus maximus* stock. The data set consisted of harvest body weight from 2 462 progenies (17 months old) from 28 families that were produced through artificial insemination using 39 parent fish. An animal model was applied to partition each weight value into a fixed effect, an additive genetic effect, and a residual effect. The average body weight of each family, which was measured at 110 days post-hatching, was considered as a covariate. For Bayesian analysis, heritability and breeding values were estimated using both the posterior mean and mode from the joint posterior conditional distribution. The results revealed that for additive genetic variance, the posterior mean estimate ($\sigma_a^2=9\ 320$) was highest but with the smallest residual variance, REML estimates ($\sigma_a^2=8\ 088$) came second and the posterior mode estimate ($\sigma_a^2=7\ 849$) was lowest. The corresponding three heritability estimates followed the same trend as additive genetic variance and they were all high. The Pearson correlations between each pair of the three estimates of breeding values were all high, particularly that between the posterior mean and REML estimates (0.996 9). These results reveal that the differences between Bayesian and REML methods in terms of estimation of heritability and breeding values were small. This study provides another feasible method of genetic parameter estimation in selective breeding programs of turbot.

Key words: turbot, growth traits, heritability, breeding values, REML, Bayesian

Citation: Guan Jiantao, Wang Weiji, Hu Yulong, Wang Mosang, Tian Tao, Kong Jie. 2017. Estimation of genetic parameters for growth trait of turbot using Bayesian and REML approaches. Acta Oceanologica Sinica, 36(6): 47–51, doi: 10.1007/s13131-017-1034-y

1 Introduction

Turbot is a native marine fish in Europe and an important economic fish species in many areas because of its rapid growth, low-temperature resistance, and easy domestication (Lei and Liu, 1995). Since its introduction to China in 1992, the turbot farming industry has developed rapidly and it has become one of the most abundant marine species in the seas off the North China coast (Lei, 2002; Lei et al., 2003). However, inbreeding depression has emerged and growth rates have decreased because the stock originally came from limited sources (Lei et al., 2005). Therefore, maintaining sustainable development of the turbot farming industry and improving economic traits through genetic breeding is a promising solution.

Efficient genetic evaluation methods have long played an important role in aquatic animal genetic breeding. The restricted maximum likelihood (REML) algorithm was widely used in genetic evaluation for turbot and other flounder fishes (Fishback et al., 2002; Liu et al., 2011; Shikano, 2007; Zhang et al., 2008) since it was proposed by Patterson and Thompson (1971). Compared to the maximum likelihood (ML) method, REML overcomes the drawback of underestimation of the variance component, which occurs because it does not take into account the uncertainty in the mean (Hadfield, 2012). However, REML is also problematic

when the fixed and random effects are calculated using a variance estimator rather than the true variance. Nowadays, the Bayesian method is widely used in many fields. This method has gained popularity because it makes statistical inference through joint posterior conditional distribution completely based on phenotype data, and its flexibility in resolving a wide range of biological problems. In contrast to the REML method, one particular advantage of Bayesian inference methods is that the scale and location parameters are jointly inferred. The other advantage is that there is no need to find good initial values as required in restricted maximum likelihood (REML) techniques for which starting values might have an impact on the convergence (Ahlander and Sillanpää, 2013; Piepho et al., 2012). Additionally, the Bayesian method provides better estimation of heritability, especially when data does not fit a normal distribution (Jensen et al., 1994; Wang et al., 1994). Therefore, Walsh (2001) predicted that the next 20 years will likely be marked by a strong influx of Bayesian methods, which will replace its previously used counterparts. However, there is no report on the application of Bayesian methods in the genetic evaluation of turbot to date.

This study aims to estimate genetic parameters for harvest weight in a farmed population of turbot using both Bayesian and REML approaches. To overcome the computational difficulty in

Foundation item: The Taishan Scholar Program for Seed Industry under contract No. ZR2014CQ001; the National High Technology Research and Development Program of China under contract No. 2012AA10A408-7.

*Corresponding author, E-mail: kongjie@ysfri.ac.cn

the Bayesian method, the Markov Chain Monte Carlo (MCMC) method is usually used (Gilks et al., 1996; Kokate et al., 2011). Moreover, of the MCMC variants, Gibbs sampling has been widely applied in animal breeding (Gara et al., 2006; Kapell et al., 2011; Wang et al., 2011). Therefore, in this study, the Bayesian method based on Gibbs sampling will be compared to the REML method to explore its potential in the genetic evaluation of turbot.

2 Materials and methods

2.1 Experimental data

The base population was introduced from France and Denmark in 2005. The first generation was comprised of 51 families (11 maternal half-sib groups and 12 full-sib families), which were produced using 37 males and 31 females from the base population in 2005 in Haiyang City, Shandong Province, China. The brood fish used in the present study were selected from the first generation population. Among the brood fish, 12 female and 27 male parents were successively mated by artificial fertilization to form 28 families that consisted of 23 half-sib families (including 7 maternal half-sib groups and no paternal half-sib group) and 5 full-sib families in 2012. Fertilized eggs hatched in water at 14–16°C with the salinity of about 30. After hatching, all of the families were reared separately in fiberglass-reinforced plastic (FRP) tanks, and received the same management regime. The quantity of offspring of each family was standardized on the 60th day post-hatching. Approximately 500 individuals were left to be reared in each family. When the offspring reached 110 days age, Approximately 100 individuals from each family were selected as nucleus families and then labelled with visible implant elastomer (VIE). Twenty random individuals of each nucleus family were weighed. The nucleus families were mixed and split randomly into four equal subsets. The four subsets were reared in four 5 m×5 m×0.6 m (length×width×height) cement tanks. The four tanks were kept under the same management regime. When the offspring were 15 months old, 2 462 live individuals were weighed.

2.2 Statistical analysis

2.2.1 REML analysis

A single trait animal model was used as follows:

$$y_{ijt} = \mu + t_i + cb_j + a_{ijt} + e_{ijt}, \quad (1)$$

where y_{ijt} is the observation of each individual, μ is the mean, t_i is the fixed effect of tank i , b_j is the average weight of family j as a covariate, c is the regression coefficient for b_j , a_{ijt} is the additive genetic effect, and e_{ijt} is the residual effect. The additive genetic and residual effects are assumed to be both unrelated and normal, i.e., $a \sim N(0, A\sigma_a^2)$ and $e \sim N(0, I\sigma_e^2)$ where σ_a^2 and σ_e^2 are additive genetic and residual variance, respectively; A is the numerator relationship matrix and I is the identity matrix.

In the matrix notation, the model was as follows:

$$y = Xb + Zu + e, \quad (2)$$

where y is the vector of observations, X and Z are incidence matrices, and b , u , and e are vectors of fixed effect, random effect, and residual effect, respectively.

The mixed model equation proposed by Henderson (1975) was as follows:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\lambda \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}, \quad (3)$$

where X' and Z' are the transpositions of matrix X and Z , A^{-1} is the inversion of A , $\hat{b}$ and $\hat{a}$ are the estimations of fixed and random effects, respectively, and $\lambda = \sigma_e^2/\sigma_a^2$.

The mixed model equation was solved by the REML algorithm, which was completed in ASReml Version 3.0 (Gilmour et al., 2009).

2.2.2 Bayesian analysis

The REML model was also used in the Bayesian analysis. The Bayesian analysis was carried out in the R package MCMCglmm (Hadfield, 2010). A weak prior was set as follows: An inverse Wishart prior ($V=1$ and $nu=0.002$) was used for variance (V represents the variance at the limit and nu is the degree of belief parameter), and a normal prior $N(0, 10^{10})$ for fixed effect. The posterior marginal distribution of parameters was obtained through Gibbs sampling. The length of the Markov Chain (MC) was 2×10^6 rounds with a 7×10^5 rounds burn-in period and a 1 300 rounds thinning interval. The sum of sample was 1 000.

Gibbs chain convergence was checked with the Geweke test (Geweke, 1992), which is completed by the function `geweke.diag` in the R Coda library (R Core Team, 2013). The effective sample size (ESS) and the curve of posterior marginal density were also assessed to ensure the convergence. ESS is an estimate of the number of independent samples, and an ESS value close to the sum of the sample indicates that the MCMC samples are virtually uncorrelated (Riebler et al., 2008). In this study, the ESS was restricted to be greater than 900. The autocorrelation between successive stored iterations was limited to less than 0.1.

2.2.3 Genetic parameters

Heritability was calculated by the following notation:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2). \quad (4)$$

For the Bayesian method, estimates of posterior mean and mode for variance components, heritability, and breeding values were computed. Additionally, 95% high posterior density intervals (HPD intervals) were calculated for each parameter of interest.

For the REML method, estimated heritability was tested by a two-tailed t-test ($\alpha=0.05$). For the Bayesian method, estimated heritability was tested for its significance using 95% HPD intervals. For both methods, Pearson correlations between each pair of the three estimators of breeding values were calculated.

All calculations were completed in R (R Core Team, 2013).

3 Results

3.1 Variance component

The two plots on the left of Fig. 1 show a time series of values from the posterior distribution of variance components, of which fluctuation tended to be stable. The autocorrelations between successive samples for the variance components were in the range of 0.01–0.02. Through the Geweke test, the Z values (1.260 for additive variance and –1.048 for residual variance) were both < 1.96 ($\alpha=0.05$). All of these results demonstrate that convergence was reached. For the Bayesian method, descriptive analysis of posterior mean and mode of variance components can be seen in Table 1. The posterior mean, mode of additive genetic variance

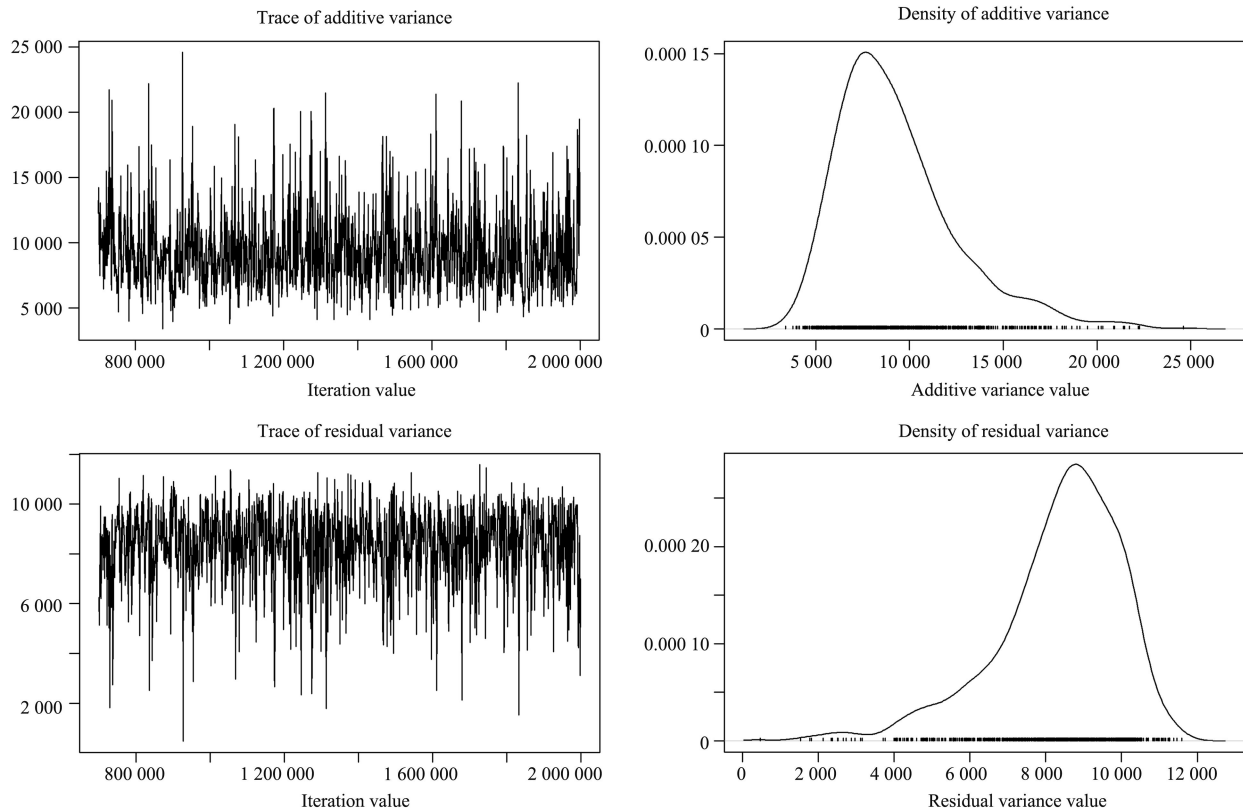


Fig. 1. The trace and posterior density function of additive and residual variance components from the Bayesian method. The X-axis and Y-axis of left two plots represent iteration and variance value, respectively. The X-axis and Y-axis of right two plots represent variance value and possibility, respectively.

Table 1. Descriptive statistics of variance components and heritability from the Bayesian method

	Min	Posterior mode	Posterior mean	Max	HPD interval (95%)
Additive variance	3 391	7 849	9 320	24 604	(4 430, 16 505)
Residual variance	469.8	8 765	8 342	11 590	(4 729, 10 991)
Heritability	0.23	0.45	0.53	0.98	(0.31, 0.80)

Note: Min, Max and HPD interval represent minimum, maximum, high posterior density interval, and estimated breeding values, respectively.

and residual variance were 9 320, 7 849, 8 342, and 8 765, respectively. They were all in the range of 95% HPD intervals. Additive genetic and residual variances estimated by the REML method were 8 088 and 8 925, respectively.

3.2 Genetic parameters

Heritability estimates from the Bayesian method are shown in Table 1. The trace and posterior density function of heritability estimated through Bayesian analysis are shown in Fig. 2. The posterior mean and mode of heritability were 0.53 and 0.45 with a 95% credible interval of 0.31–0.80. Heritability from the REML method was 0.48 with a standard error of 0.11.

The minimum, mean, maximum, and standard deviations of estimated breeding values from the REML and Bayesian methods can be seen in Table 2. The mean and max posterior mean estimates (11.72 and 1 072.76) were larger than those from both REML and the posterior mode estimate with a larger standard deviation (65.64). The Pearson correlations between each pair of the three estimators of breeding values are shown in Table 3.

4 Discussion

As an important quantitative trait in aquaculture, growth plays an critical role in harvest body weight, farming cycles and

costs. Many researchers have studied harvest body weight in different aquatic species, for example, Atlantic salmon (*Salmon salar*), Pacific oysters (*Crassostrea gigas*), hybrid striped bass (*Morone chrysops* ♀ × *Morone saxatilis* ♂), and rainbow trout (*Oncorhynchus mykiss*) (Quinton et al., 2005; Evans and Langdon, 2006; Wang et al., 2006; Sae-Lim et al., 2013). For heritability of harvest weight in turbot, there are various reports depending on different experimental populations and models. Gjerde (1997) reported heritability estimates from 0.45–0.70 based on dam and sire variance components, and the large standard errors could be a result of the maternal and common full-sib effects. Ma et al. (2009) demonstrated that heritability in turbot at 15 months of age ranged from 0.34–0.88 based on different models using the REML method. However, there are few reports on harvest body weight and none on the estimation of genetic parameters using Bayesian methods in turbot.

Variance components and heritability estimates of posterior mean and mode were both in their corresponding HPD intervals. Compared with REML estimates, Bayesian estimates for the additive variance component from the posterior mean was higher but residual variance was lower (Table 1). This result was in accordance with Waldmann and Ericsson (2006) and Alijani et al. (2012). For the posterior mode, Bayesian additive and residual

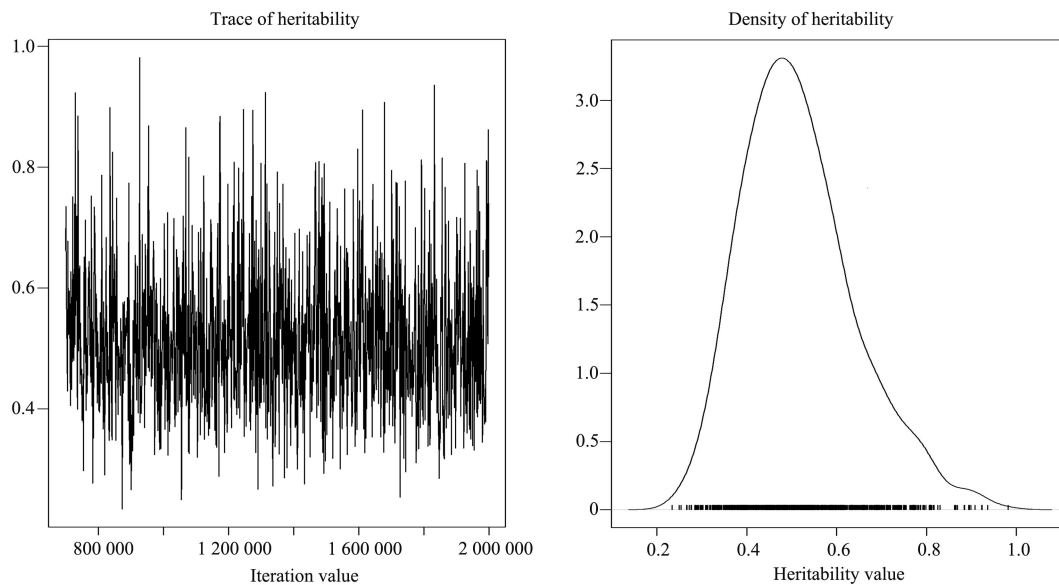


Fig. 2. The trace and density function of heritability from the Bayesian method. The X-axis and Y-axis of left plot represent iterations and heritability value, respectively. The X-axis and Y-axis of right two plots represent heritability value and possibility, respectively.

Table 2. Descriptive statistics of estimated breeding values (EBV) from the REML and Bayesian methods (posterior mean and mode)

EBV	Min	Mean	Max	SD
REML	-136.60	11.46	937.30	56.83
Posterior mean	-142.27	11.72	1 072.76	65.64
Posterior mode	-167.19	11.52	813.38	64.62

Note: Min, Max, and SD denote minimum, maximum, and standard deviation, respectively.

Table 3. Correlations between the estimated breeding values from both the REML and Bayesian methods (posterior mean and posterior mode)

Correlation	EBV* from REML	Posterior mode of EBV	Posterior mean of EBV
EBV from REML	1	0.963 7	0.996 9
Posterior mode of EBV	0.963 7	1	0.962 1
Posterior mean of EBV	0.996 9	0.962 1	1

Note: * estimated breeding values.

variances were both lower than the REML estimates. Additionally, the posterior mode of the additive variance was much lower than the posterior mean estimate (Table 1). In a simulation study, van Tassel et al. (1995) reported that the posterior mean of the genetic variance component and the REML estimates were quite similar, particularly for traits with high heritability, and the posterior mode of the genetic variance component was always the lowest. In this study, three estimators for the additive variance component followed a similar trend to the above (Table 1).

For heritability, REML estimates were intermediate between the posterior mean and mode estimates. However, they all demonstrated that the heritability of harvest weight for turbot is high (Table 1), based on the following classification: low (0.05–0.15), medium (0.20–0.40), high (0.45–0.60), and very high (>0.65) (Cardellino and Rovira, 1987). The estimated heritability agreed with the estimates reported by Gjerde (1997) and Ma et al. (2009). A simulated study by Waldmann and Ericsson (2006) found that the REML heritability estimate was more accurate but lower than Bayesian estimates regardless of whether heritability was low or high, and the posterior mean estimate was the highest. However, the differences in heritability estimates were small in this simulated study, this is similar to our results in which the three heritability estimates were close. Alijani et al. (2012) and de Villemereuil et al. (2013) also proved that REML

and Bayesian methods work equally well when heritability is high and population size is large. For a large population size, a priori information tends to be overwhelmed by the likelihood function in the establishment of the posterior distribution. In this case, parameter estimates are close to those obtained by methods based on likelihood functions (Alijani et al., 2012; Lin and Berger, 2001). For estimated breeding values, all of the correlations between each combination of the three estimators were high, especially for that between breeding values from the posterior mean and REML, which was close to 1 (Table 3). Schenkel et al. (2002) found that posterior mean of estimated breeding values has nearly equal MSE (mean square error) with breeding values from REML. Therefore, in terms of estimation of breeding values, the Bayesian and REML methods performed identically.

Concerning computation time, REML analysis was much quicker than Bayesian in this and other studies (de Magnabosco et al., 2000). However, the Bayesian method is considered more appropriate in threshold models for binary traits (Sorensen et al., 1995). Therefore, studies on the application of the Bayesian method for binary traits should be further developed in selective turbot breeding programs.

In conclusion, for the heritability and additive variance components, Bayesian posterior mean estimates were higher and the posterior mode was lower than REML estimates. However, the

differences between the Bayesian and REML methods were small in a large population. The heritability estimates of harvest body weight from both methods were high. Our results suggest that the Bayesian method based on Gibbs sampling is feasible in the estimation of genetic parameters for turbot.

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