*Acta Oceanol. Sin.*, 2016, Vol. 35, No. 6, P. 42–49
DOI: 10.1007/s13131-016-0875-0
http://www.hyxb.org.cn
E-mail: hyxbe@263.net

# Influence of parental sample sizes on the estimating genetic parameters in cultured clam *Meretrix meretrix* based on factorial mating designs

LIANG Bingbing[1, 2], YUE Xin[1, 3], WANG Hongxia[1, 3]*, LIU Baozhong[1, 3]

[1] Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

[2] University of Chinese Academy of Sciences, Beijing 100049, China

[3] Laboratory for Marine Biology and Biotechnology, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266200, China

Received 31 March 2015; accepted 14 September 2015

**Abstract**

The precise and accurate knowledge of genetic parameters is a prerequisite for making efficient selection strategies in breeding programs. A number of estimators of heritability about important economic traits in many marine mollusks are available in the literature, however very few research have evaluated about the accuracy of genetic parameters estimated with different family structures. Thus, in the present study, the effect of parent sample size for estimating the precision of genetic parameters of four growth traits in clam *M. meretrix* by factorial designs were analyzed through restricted maximum likelihood (REML) and Bayesian. The results showed that the average estimated heritabilities of growth traits obtained from REML were 0.23–0.32 for 9 and 16 full-sib families and 0.19–0.22 for 25 full-sib families. When using Bayesian inference, the average estimated heritabilities were 0.11–0.12 for 9 and 16 full-sib families and 0.13–0.16 for 25 full-sib families. Compared with REML, Bayesian got lower heritabilities, but still remained at a medium level. When the number of parents increased from 6 to 10, the estimated heritabilities were more closed to 0.20 in REML and 0.12 in Bayesian inference. Genetic correlations among traits were positive and high and had no significant difference between different sizes of designs. The accuracies of estimated breeding values from the 9 and 16 families were less precise than those from 25 families. Our results provide a basic genetic evaluation for growth traits and should be useful for the design and operation of a practical selective breeding program in the clam *M. meretrix*.

**Key words:** *Meretrix meretrix*, parental sample sizes, genetic parameter, factorial design, restricted maximum likelihood, Bayesian inference

**Citation:** Liang Bingbing, Yue Xin, Wang Hongxia, Liu Baozhong. 2016. Influence of parental sample sizes on the estimating genetic parameters in cultured clam *Meretrix meretrix* based on factorial mating designs. Acta Oceanologica Sinica, 35(6): 42–49, doi: 10.1007/s13131-016-0875-0

## 1 Introduction

The clam *Meretrix meretrix*, which is widely distributed in the shallow seas of South and Southeast Asia, is an important commercial shellfish species in China (Liu et al., 2006). The successful artificial breeding of *M. meretrix* has promoted the development of an aquaculture industry in this species. However, a lack of high-quality seed has become a limitation to its production. Therefore, the establishment of a suitable selection program is needed to guide genetic breeding.

A sustainable genetic improvement program is largely dependent on the effective use of additive genetic variance and the accuracy of estimates of heritability. However, the accuracy of genetic parameter estimates is affected by the mating design, the number and size of families and the method of analysis (Falconer and Mackay, 1996). Typically, three different mating designs are used in genetic parameter estimation: factorial design, nested mating design and single pair design. The nested mating design is the most commonly used mating design in the genetic parameter estimation of bivalves (Mallet et al., 1986; Nguyen et al., 2011; Strömgren and Nielsen, 1989; Toro et al., 2004; Yan et al., 2014). However, many studies have shown that the factorial design has better performance in breeding programs than either the nested mating design or single pair design, as it can increase the accuracy of genetic parameter estimation (Blanc, 2003), produce a higher genetic response and lower inbreeding depression for the traits of interest (Dupont-Nivet et al., 2006; Engström et al., 1996). In addition, Busack and Knudsen (2007) also hypothesized that the factorial design could increase the effective number of breeders in fish hatchery operations.

The accurate estimation of the variance component by statistical methods is a fundamental component of the development of accurate estimates of genetic parameters and is an active area of

---

Foundation item: The National High Technology Research and Development Program (863 program) of China under contract No. 2012AA10A410; the Zhejiang Science and Technology Project of Agricultural Breeding under contract No. 2012C12907-4; the Scientific and Technological Innovation Project financially supported by Qingdao National Laboratory for Marine Science and Technology under contract No. 2015ASKJ02.

*Corresponding author, E-mail: hxwang@qdio.ac.cn

research. In recent years, a major transition occurred in the statistical approaches for analyzing the variance component, shifting from analysis of variance (ANOVA) to likelihood-based methods (Littell, 2002). ANOVA has been a mainstay of statistical data analysis for several decades, but computer programs for this methodology have been encumbered with technical problems of estimation, weighting, and the handling of missing data (Littell, 2002). With the rapid development of computer technology, several methods based on maximum likelihood estimations have been developed. These include methods for the estimation of variance components, such as REML (restricted maximum likelihood), MIVQUE (minimum variance quadratic unbiased estimators) and MINQUE (minimum norm quadratic unbiased estimators). The implementation of REML estimation, which is widely used presently, heavily depends on the mixed model equations (MME) introduced by Henderson to construct the best linear unbiased predictors (BLUP) (Henderson, 1974). To accurately predict breeding values, the genetic relationships among all animals need to be accounted for. Therefore, animal models have been introduced that allow the specification of all additive variances among relatives by incorporating a random effect for the breeding value of each animal (Thompson et al., 2005). In addition to REML, Bayesian approach is another important method for analyzing genetic parameters with animal models; recently, this approach has attracted increased attention from researchers. REML is faster and easier to use than Bayesian analysis, but it has limitations. For example, parameter estimation and hypothesis testing becomes problematic when REML is used with non-Gaussian traits (Bolker et al., 2009). In contrast, these issues can be neatly solved by Bayesian inference via Markov chain Monte Carlo (MCMC) algorithms, but the computational speed can be slow and the analysis technically more challenging. For example, there are challenges in the specification of a sensible prior, which is a non-issue in REML analysis (Hadfield, 2010).

The aim of the present study was to estimate and compare the genetic parameters in three sample sizes of parents based on factorial mating designs (3×3, 4×4 and 5×5) through REML and Bayesian analysis. The accuracies of estimated breeding values (EBV) of growth traits were also compared from three families sizes using REML methods. Our results may be useful for identifying suitable mating schemes and analytical methods for a breeding improvement program of *M. meretrix*.

## 2 Materials and methods

### 2.1 *Experimental design*

The broodstock *M. meretrix* clams were the 3rd generation individuals under growth selection in the hatchery laboratory of Zhejiang Mariculture Research Institute (Wenzhou, China). The matured parent clams were treated by air-drying for 4–8 h, and each clam was placed in a 1 000 mL beaker containing 800 mL filtered seawater to induce spawning (Liu et al., 2006; Wang et al., 2011).

Twenty-five families were produced according to a factorial mating design in June 2012: typically five sires, each mated with five dams. Larvae rearing, juvenile nursing and grow-out were conducted following Wang et al. (2011). The 5×5 factorial design could be decomposed into one-hundred different 3×3 factorial designs, twenty-five different 4×4 factorial designs, thus, the three sizes of factorial designs (3×3, 4×4 and 5×5) could be used to estimate genetic parameters.

### 2.2 *Traits evaluated*

Four growth traits were measured at 12 months after fertilization for each size of factorial design: shell length (SL), shell height (SH), shell width (SW) and total body weight (TW). SL, SH and SW were measured using vernier calipers with each clam, and TW was measured using a digital balance. At least 25 individuals were chosen from each family.

### 2.3 *Genetic parameter estimation*

Genetic parameters were estimated using ASReml 3.0 (Gilmour et al., 2009) and the MCMCglmm package in R (Hadfield, 2010) with animal model. In matrix notation, the model is written as follows:

$$y = \boldsymbol{X}b + \boldsymbol{Z}_a a + \boldsymbol{Z}_c c + e,$$

where $y$ is the phenotypic measure of the trait being analyzed, $b$ is the vector of the fixed effects, $a$ is the additive genetic effect of the individual animal, and $c$ is the vector of common environment effects. $\boldsymbol{X}$, $\boldsymbol{Z}_a$ and $\boldsymbol{Z}_c$ are incidence matrices related to the fixed, additive genetic and common environment effects.

For the Bayesian analysis, the variance components were estimated using a Bayesian MCMC approach. The model was run with nitt=650 000, thinning interval=100, and burn-in period= 150 000. We assumed that the contribution of the genetic and residual effects were equivalent when setting the priors. Rerunning the model with a larger proportion (0.95 for the genetic effect) (Wilson et al., 2010) demonstrated that the prior had little effect on the outcome of the analysis.

Likelihood ratio tests and deviance information criterion (DIC) were used to test if the variance components of random effects were significant. For REML, we took off one random effect each time from the model above and run the programs to obtain log-likelihoods. Then compared twice the differences between these two log-likelihoods values (with and without one random effect) with Chi-squared values. For Bayesian analysis, deviance information criterion (DIC) was used to test the significance of random effects and lower DIC values indicated the random effect contributed to model.

Heritabilities for traits were calculated as $h^2 = \dfrac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + \sigma_e^2}$ from two univariate animal models. Here $\sigma_a^2$ is the additive genetic variance, $\sigma_c^2$ is the common environmental variance and $\sigma_e^2$ is the residual variance. Genetic and phenotypic correlations were estimated using the most appropriate animal model with the fixed and random effects as described above.

$$r = \frac{\sigma_{12}}{\sqrt{\sigma_1^2}\sqrt{\sigma_2^2}},$$

where $\sigma_{12}$ is the additive genetic or phenotypic covariance between the two traits, and $\sigma_1^2$ and $\sigma_2^2$ are the additive genetic or phenoypic variances of Traits 1 and 2, respectively.

### 2.4 *The accuracy of estimated breeding values*

The estimated breeding values (EBV) were also obtained through REML analysis. The accuracy ($r$) of each animal's EBV from each factorial design was calculated as

$$r = \sqrt{1 - \frac{PEV}{(1+F)\,\sigma_a^2}},$$

where $PEV$ is the prediction error variance of each EBV, $F$ is the inbreeding coefficient for each animal and $\sigma_a^2$ is the estimated additive genetic variance obtained from the mixed model analysis (Lewis et al., 2013). ASReml 3.0 provides both the estimates of the EBV and their associated PEVs.

## 3 Results

### 3.1 *Growth traits*

The number of observations, means, standard deviations and coefficients of variation (CV) for four traits in total 25 full-sib families were shown in Table 1. The number of measured offspring was 828. After one year growth, mean shell length of the clams was 18.48 mm, mean shell height was 15.52 mm, mean shell width was 8.94 mm and mean total weight was 1.92 g with high CV (60.47%).

### 3.2 *Heritabilities obtained from REML*

The narrow-sense heritability ($h^2_{\text{a}}$) of four growth traits have been estimatied 100 times for 3×3 factorial design, 25 times for 4×4 factorial design and one time for 5×5 factorial design based on different parent combination data. The distribution of heritability estimates for 3×3 and 4×4 factorial designs were shown in Fig. 1 and Fig. 2, respectively. In the case of 3×3 factorial designs, the heritabilities of four growth traits ranged from 0 to 1, with the standard error (SE) ranged from 0 to 0.37 (Fig. 1), while in the case of 4×4 factorial designs, the heritabilities of four growth traits ranged from 0 to 0.7 (SE, 0–0.34) (Fig. 2). From these histograms, it is visualized that normal distributions might be suitable approximation. The goodness of fit tests for normal distribution indicated that with the exception of TW of 3×3 factorial designs, the heritabilities of others obey the normal distributions. Generally, the variance of estimated heritabilities decreased with the number of parents increased in factorial designs. Such as, the average estimated heritabilities of SL were 0.29 for both 3×3 and 4×4 factorial designs. But in 3×3, 90% of the values fell within the range of 0.06–0.52 and the central 50% fell within the range of 0.20–0.38, versus in 4×4, the values of 90% confidence interval ranged from 0.11 to 0.47 and the central 50% fell within the range of 0.22–0.36. When the number of parents increased to 10, the estimation of heritability of the four growth traits obtained from REML analysis were 0.19–0.22 (Table 2), these values fell within the central 55% of the empirical heritability distribution of 3×3 or 4×4 factorial designs. The log-likelihood ratio tests for REML analysis in 5×5 factorial design showed that additive genetic variance components and common environment variance components in four growth traits were significant ($P$<0.01) (Table 3). For

**Table 1.** Descriptive statistics of four growth traits from 5×5 factorial design

| Traits | N | Mean | SD | CV/% |
|---|---|---|---|---|
| Shell length/mm | 828 | 18.48 | 5.36 | 29.02 |
| Shell height/mm | 828 | 15.52 | 4.19 | 26.98 |
| Shell width/mm | 828 | 8.94 | 2.81 | 31.47 |
| Total body weight/g | 828 | 1.92 | 1.16 | 60.47 |

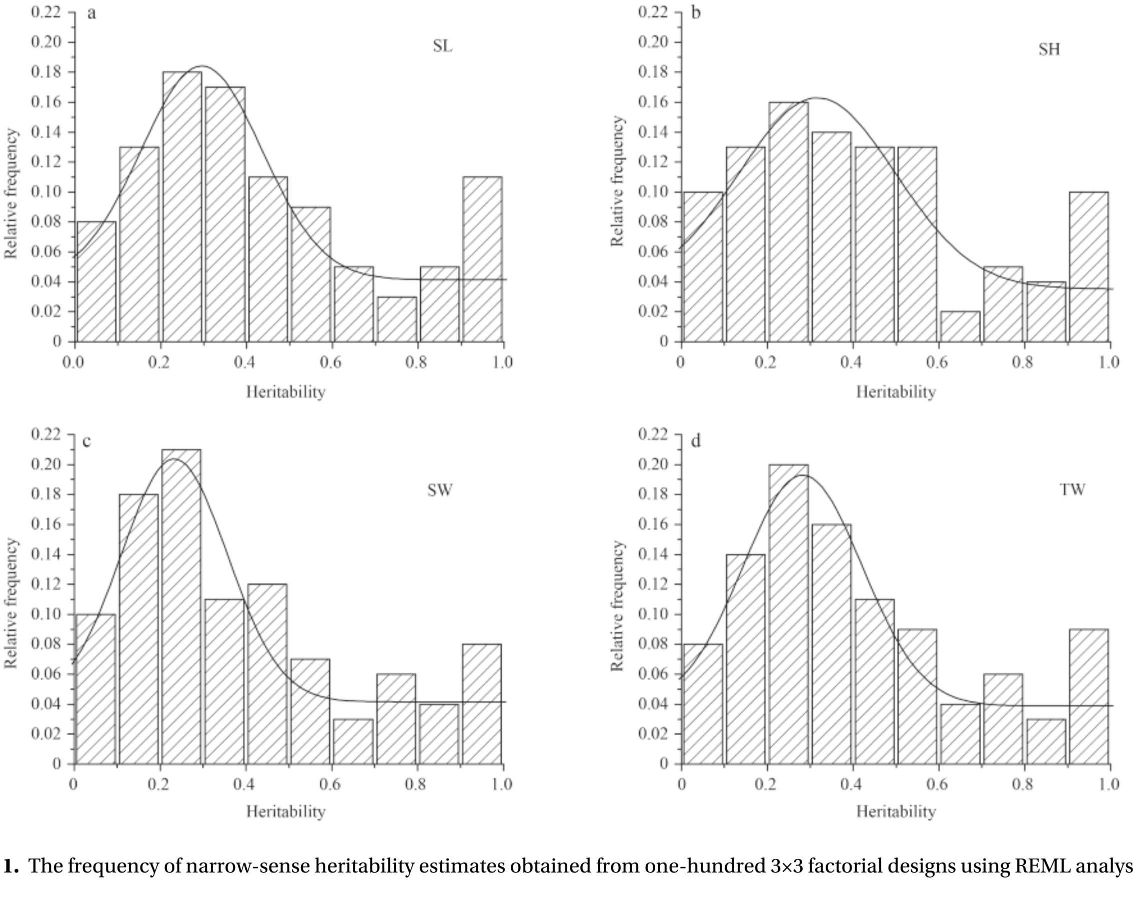

**Fig. 1.** The frequency of narrow-sense heritability estimates obtained from one-hundred 3×3 factorial designs using REML analysis.

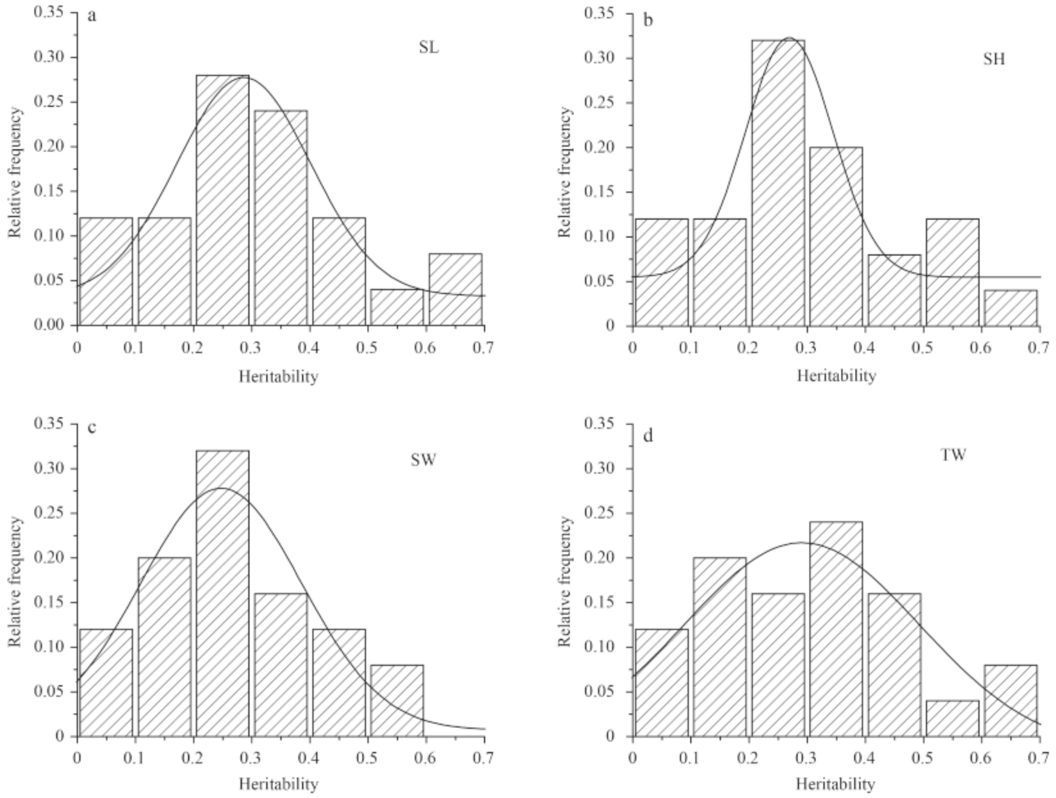

**Fig. 2.** The frequency of narrow-sense heritability estimates obtained from twenty-five 4×4 factorial designs using REML analysis.

**Table 2.** Narrow-sense heritability estimates ($h_a^2$) of each growth trait estimation obtained from 5×5 factorial design using either REML or Bayesian inference

|  | Traits | REML |  | Bayesian |  |
|---|---|---|---|---|---|
|  |  | $h_a^2$±SE | $h_c^2$±SE | $h_a^2$ (95% HPID) | $h_c^2$ (95% HPID) |
| 5×5 | SL | 0.19±0.10 | 0.20±0.002 | 0.13 (0.05–0.64) | 0.27 (0.17–0.47) |
|  | SH | 0.19±0.10 | 0.20±0.002 | 0.16 (0.05–0.61) | 0.28 (0.16–0.47) |
|  | SW | 0.21±0.11 | 0.10±0.002 | 0.13 (0.05–0.57) | 0.27 (0.17–0.44) |
|  | TW | 0.22±0.11 | 0.10±0.002 | 0.15 (0.05–0.66) | 0.26 (0.17–0.45) |

Note: $h_c^2=\sigma_c^2/\left(\sigma_a^2+\sigma_c^2+\sigma_e^2\right)$. The standard error (SE) is shown for REML $h_a^2$ and $h_c^2$ estimates. The 95% highest posterior density interval (HPDI) is shown for Bayesian $h_a^2$ and $h_c^2$ estimates.

**Table 3.** Log-likelihoods (LL) and deviance information criterion (DIC) for four traits with or without random effect in 5×5 factorial design

| Method | Effect | Traits |  |  |  |
|---|---|---|---|---|---|
|  |  | SL | SH | SW | TW |
| REML-LL | without $\sigma_a^2$ | –1 250.600 | –1 113.550 | –894.390 | –591.223 |
|  | with $\sigma_a^2$ | **–1 240.610** | **–1 102.240** | **–886.734** | **–575.947** |
|  | without $\sigma_c^2$ | –1 242.670 | –1 104.410 | –889.080 | –577.951 |
|  | with $\sigma_c^2$ | **–1 240.610** | **–1 102.240** | **–886.734** | **–575.947** |
| MCMCglmm-DIC | without $\sigma_a^2$ | 4 788.816 | 4 374.664 | 3 760.327 | 2 811.288 |
|  | with $\sigma_a^2$ | **4 768.367** | **4 259.403** | **3 704.877** | **2 803.536** |
|  | without $\sigma_c^2$ | 5 079.828 | 4 683.189 | 4 022.281 | 3 106.760 |
|  | with $\sigma_c^2$ | **4 788.816** | **4 374.664** | **3 760.327** | **2 811.288** |

Note: Significance of variance components were tested using likelihood ratio tests for REML. The values in bold mean that the random effect was significant ($P<0.01$). Significance of variance components were tested using DIC values for Bayesian and lower DIC (in bold) indicated the random effect contributed to model.

both 3×3 and 4×4 factorial designs, the common environment effects obtained from REML were about 0–0.02, which were lower than 5×5 factorial design (0.10–0.20) (Table 2).

### 3.3 *Heritabilities obtained from Bayesian inference*

Distribution of estimated heritabilites obtained from 3×3 and 4×4 factorial designs using Bayesian inference were shown in

Figs 3 and 4. The Bayesian estimated heritabilties of 4×4 factorial designs were normally distributed, whereas 3×3 factorial designs were not strictly obey normal distribution under one sample Kolmogorov-Smirnov test. The estimated heritabilities of 4×4 factorial designs ranged from 0.04 to 0.36 (Fig. 4). For SL, SH and SW, the averages of heritabilities were 0.11, and the 90% confid-

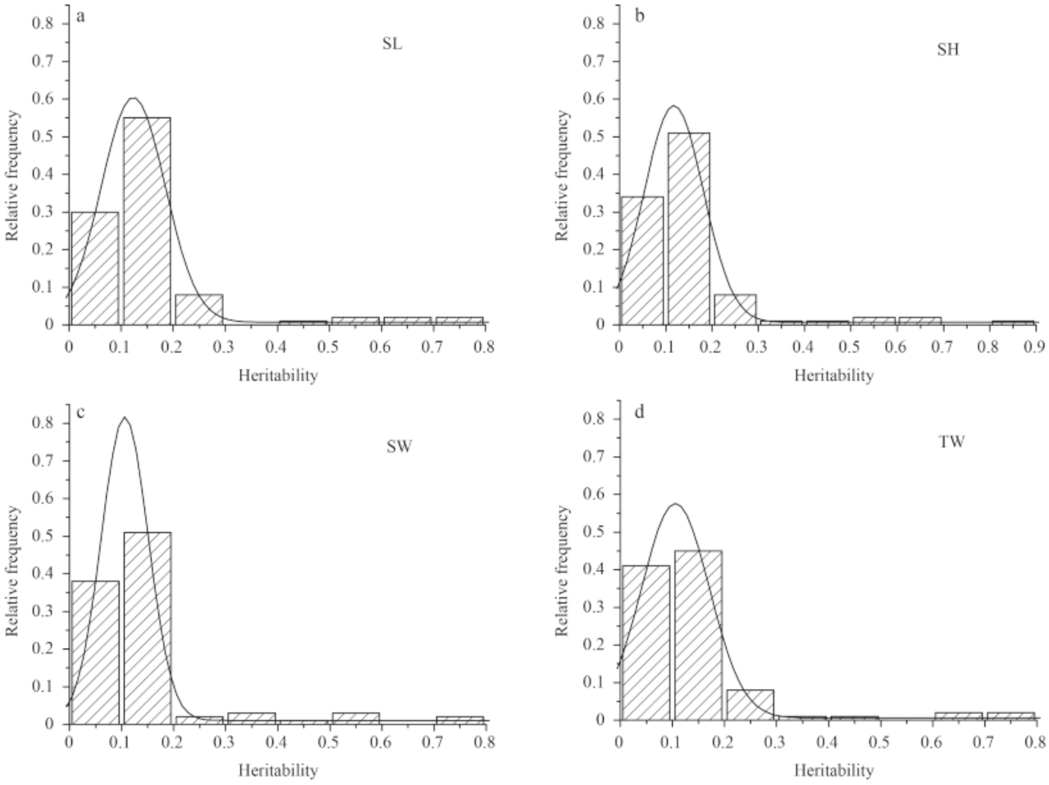

**Fig. 3.** The frequency of narrow-sense heritability estimates obtained from one-hundred 3×3 factorial designs using Bayesian inference.

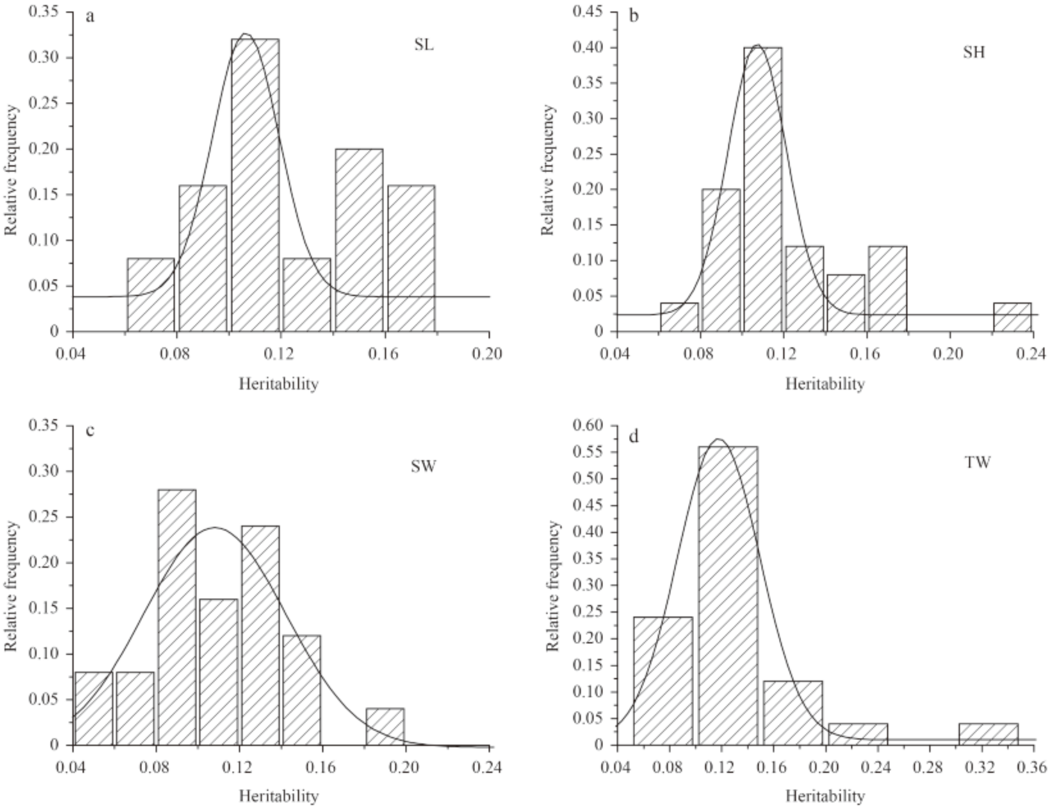

**Fig. 4.** The frequency of narrow-sense heritability estimates obtained from one-hundred 4×4 factorial designs using Bayesian inference.

ence interval of the averages values were 0.09–0.13. As for TW, the averages of heritability was 0.12±0.002, and the 90% confidence interval ranged from 0.07 to 0.17.

Compared with the REML, the distribution heritabilities of Bayesian inference were more concentrated. Take SL for example, 90% confidence interval of the averages values obtained from Bayesian analysis (0.09–0.13) were smaller than those obtained from REML (0.11–0.47) in 4×4 factorial designs. The heritabilities of four traits obtained from 5×5 designs ranged from 0.13 to 0.16 which were similar with 5×5 factorial design when using REML analysis (Table 2). Deviance information criterion for each trait also suggested that the additive genetic variance components and common environment variance components were significant and these random effects should be added into the model (Table 3).

### 3.4 *Correlations among growth traits*

The phenotypic and genetic correlations among the four growth traits using the two different methods of analysis are presented in Tables 4 and 5. The estimated genetic correlations of the traits were higher than the phenotypic correlations, ranging from 0.94 to 0.96 with REML analysis and 0.85 to 0.91 with Bayesian analysis in 5×5 factorial design. All these phenotypic and genetic correlations for growth traits were highly significant. Most of the phenotypic and genetic correlation values estimated from the 5×5 factorial design were slightly lower than those from the 3×3 and 4×4 factorial design with REML. For Bayesian inference, the genetic correlation values of growth traits from three factorial designs were similar except TW in 4×4 factorial design. Overall, the four growth traits were highly correlated with each other in the three sizes of factorial designs and both two methods of analysis.

### 3.5 *The accuracy of estimated breeding values*

The individual estimated breeding values (EBV) of growth traits in three different sample sizes of parents were obtained through REML analysis and the mean accuracies of EBV of the four growth traits were also compared to analyze the influence of different parental sample sizes on the accuracy of EBV. The results showed that the mean accuracies of EBV of the four growth traits in the 5×5 factorial design ranged from 64.2%–65.7%, which were significantly higher ($p<0.01$) than those in 3×3 and 4×4 factorial design (Fig. 5). In addition, TW was significantly higher than ($p<0.01$) other three traits (Fig. 5) in 5×5 factorial design.

## 4 Discussion

### 4.1 *Effect of parental sample sizes on estimates of heritability*

In our study, a full factorial mating design was used to estimate the genetic parameters and breeding values. Furthermore, we compared the distribution of heritabilities of four growth traits that obtained from different sample sizes of parents. The relationship of the number of families and the accuracy of heritabilty have been studied using simulation data, such as Dupont-Nivet et al. (2002) found that the number of breeders and families seems significantly affect the accuracy of the heritabilities when the total number of offspring is held constant in fully factorial designs. That is the larger the number of families are, the higher the accuracy of the heritability estimation will be. But in experi-

**Table 4.** Genetic (above the diagonal) and phenotypic (below the diagonal) correlations among growth traits using REML analysis

| | Traits | SL | SH | SW | TW |
|---|---|---|---|---|---|
| 3×3 | SL | | 0.98±0.06 | 0.96±0.34 | 0.98±0.23 |
| | SH | 0.95±0.03 | | 0.99±0.04 | 0.99±0.01 |
| | SW | 0.90±0.01 | 0.87±0.01 | | 0.98±0.49 |
| | TW | 0.90±0.01 | 0.86±0.01 | 0.82±0.01 | |
| 4×4 | SL | | 0.96±0.04 | 0.96±0.04 | 0.98±0.02 |
| | SH | 0.98±0.01 | | 0.99±0.05 | 0.98±0.01 |
| | SW | 0.96±0.03 | 0.97±0.004 | | 0.98±0.02 |
| | TW | 0.93±0.01 | 0.93±0.01 | 0.94±0.01 | |
| 5×5 | SL | | 0.96±0.02 | 0.96±0.04 | 0.95±0.05 |
| | SH | 0.96±0.003 | | 0.95±0.04 | 0.95±0.05 |
| | SW | 0.94±0.004 | 0.94±0.004 | | 0.94±0.06 |
| | TW | 0.89±0.008 | 0.89±0.008 | 0.89±0.008 | |

**Table 5.** Genetic (above the diagonal) and phenotypic (below the diagonal) correlations among growth traits using Bayesian inference

| | Traits | SL | SH | SW | TW |
|---|---|---|---|---|---|
| 3×3 | SL | | 0.93 (0.35–0.98) | 0.89 (0.22–0.96) | 0.90 (0.18–0.97) |
| | SH | 0.91 (0.35–0.98) | | 0.87 (0.19–0.94) | 0.88 (0.16–0.94) |
| | SW | 0.86 (0.18–0.96) | 0.82 (0.19–0.94) | | 0.89 (0.16–0.95) |
| | TW | 0.86 (0.18–0.97) | 0.82 (0.16–0.95) | 0.82 (0.16–0.95) | |
| 4×4 | SL | | 0.94 (0.43–0.98) | 0.91 (0.43–0.97) | 0.77 (0.16–0.96) |
| | SH | 0.92 (0.43–0.98) | | 0.83 (0.17–0.98) | 0.78 (0.16–0.97) |
| | SW | 0.89 (0.43–0.97) | 0.87 (0.16–0.98) | | 0.79 (0.17–0.97) |
| | TW | 0.85 (0.16–0.96) | 0.86 (0.16–0.97) | 0.87 (0.17–0.98) | |
| 5×5 | SL | | 0.87 (0.47–0.98) | 0.91 (0.15–0.96) | 0.91 (0.15–0.96) |
| | SH | 0.92 (0.47–0.97) | | 0.85 (0.35–0.97) | 0.85 (0.16–0.97) |
| | SW | 0.89 (0.15–0.96) | 0.90 (0.35–0.97) | | 0.85 (0.13–0.97) |
| | TW | 0.81 (0.15–0.96) | 0.83 (0.16–0.97) | 0.83 (0.13–0.97) | |

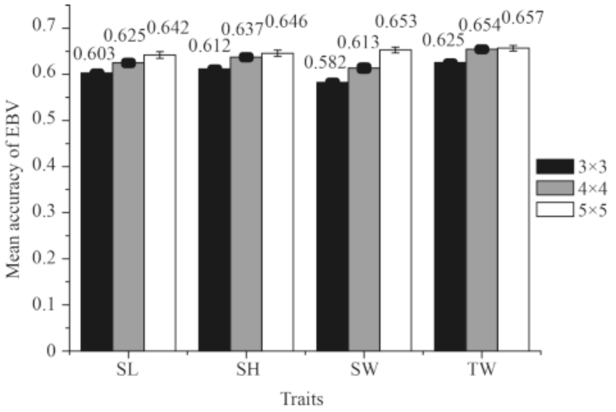

**Fig. 5.** Mean accuracies of EBV of growth traits in three different sample sizes of parents using REML analysis.

mental practice, the number of rearing facilities and the number of progeny per dam limit the number of families to increase infinitely. What's more, as the family number increase, the environment factors are more difficult to control, so the environmental heterogeneity will influence the accuracy of genetic parameter analysis. Our result showed that several factorial crosses with smaller size for estimation heritabilty of confidence intervals perform, on the average, quite satisfactorily, though the reliability for a single experiment may be quite low. It indicates that a large number of families could be replaced by several small number of families in studies estimating heritability, as a small size of factorial design can be better controlled and easier to implement in a practical breeding program.

The heritabilities at high frequency obtained from three sample sizes of parents based on factorial designs through REML and Bayesian inference ranged from 0.1 to 0.2; these were medium levels. However, we have noticed that, for most bivalves, the heritabilities estimated from nested designs are high relative to those from factorial designs. For example, Wang et al. (2011) found high-magnitude heritabilities (0.64–0.85) in 6- and 12-month-old *M. meretrix* using a nested mating design established in 2007. Strömgren and Nielsen (1989) reported high heritabilities ($h_D^2$ >0.6, $h_S^2$ >0.5) for growth in both larvae and juveniles of *Mytilus chilensis* in a nested design (27 females, 9 males). Similar values (0.62–0.92) were reported by Mallet et al. (1986), who estimated the heritabilities of shell length in juveniles and adults using 30 full-sib and 10 half-sib families. Toro et al. (2004) studied the heritabilities of larval size in *Mytilus chilensis* based on a nested design and obtained half-sib heritability estimates of shell height ranging between 0.38±0.33 and 0.84±0.45. High estimated heritabilities for growth were also found in *Ruditapes philippinarum* (0.87±0.24) through 33 full-sib families nested within 11 half-sib families generated from the cultured population (Dégremont et al., 2007).

The difference might reflect study differences in mating design, model and method of analysis. The nested design, although it has been frequently used, its additive effects may be inflated by non-additive genetic such as dominant, maternal or common environmental effects. So the proper and practical experimental designs and suitable analysis models were important when estimate genetic parameters. In the present study, we excluded the common environment effects from additive genetic effects to obtain reliable estimates of heritability using a full factorial design.

### 4.2 *Comparison of the REML and Bayesian analysis*

With the advances in computer technology, complex algorithms can easily be implemented. A common method for variance components estimation uses restricted maximum likelihood (REML) (Patterson and Thompson, 1971). However, Bayesian prediction of genetic parameters has also been widely employed. Mathew et al. (2012) used a Markov chain Monte Carlo sampling algorithm to estimate genetic parameters in a linear mixed model with several random effects. They observed that the Bayesian estimates of variance components were close to the REML estimates for simulated data and as accurate as the REML estimates for barley field data. Silva et al. (2013) also established a Bayesian framework for mixed models analysis and demonstrated that the Bayesian inference was as adequate as REML/BLUP for genetic evaluation. In our study, the estimated heritabilities at highest frequency of growth traits based on REML and Bayesian methods were similar, remained approximately constant at a medium level ($h^2$ ranging from 0.10 to 0.20). However, when six and eight parents were used to estimate the heritabilities of growth traits, the distributions of the heritabilities obtained from Bayesian inference were more convergence than the results got from REML analysis. The results showed that Bayesian inference has better performance than REML when facing small size of mating design. When ten parents were used to produce factorial design, the heritabilities using Bayesian inference were slightly lower than using REML. In the present study, the high standard errors for REML and the wide credible intervals for Bayesian analysis were found for both the heritabilities and the correlations. These results were likely due to the limited sample size, mass spawning practices and the impacts of other environmental factors arising during rearing and grow-out.

### 4.3 *Prediction of breeding values*

Best linear unbiased prediction (BLUP) (Henderson, 1974) has been widely used for genetic evaluation in animal breeding programs. Many theoretical studies have compared ANOVA/BLUE (best linear unbiased estimation), REML/BLUP and Bayesian inference in predicting genetic parameters. However, no method is clearly superior in all situations. Waldmann and Ericsson (2006) compared genetic parameters obtained with REML and Bayesian Gibbs sampling using simulated data and real data of Scots pine. They found that the REML estimates were accurate and that the mode of posterior distribution from Gibbs sampling can be overestimated depending on the heritability. Schenkel et al. (2002) found that the breeding values obtained from Bayesian and REML/BLUP did not differ over the range of simulated situations with respect to Spearman's rank correlations between true and predicted breeding values, but that the correlations were not strong (0.48–0.57) when the heritability was 0.2.

In our study, individual breeding values were estimated using REML/BLUP in three different sample sizes of families and the mean accuracies of EBV of the four growth traits were also compared to analysis the influence of different parental sample sizes on the accuracy of EBV. When using BLUP to estimate the breeding values, it is important that the pedigree and phenotype data are correct, complete and credible, and that the variance components are estimated accurately. The accuracy of heritability estimation greatly influences the breeding value estimates. From the results, we found that the mean accuracies of EBV of the four growth traits in the 5×5 factorial design were significantly higher ($p$<0.01) than those in 3×3 and 4×4 factorial design, which showed good agreement with Dupont-Nivet et al. (2002). These results indicated that the 5×5 factorial design may be more reliable in its estimates of breeding value. Furthermore, the mean accuracy of EBV of TW was significantly higher ($p$<0.01) than other three traits in 5×5 factorial design, which might suggest that TW in a 5×5 factorial design should be reliable for improve the genetic progress in future studies.

## 5 Conclusions

In summary, we compared the genetic parameters and accuracies of EBV of four growth traits by three sizes of factorial designs in REML and Bayesian inference. The estimated heritabilities of growth traits based on Bayesian inference were a little lower than REML, but still remained at a medium level. Genetic correlations among traits were positive and high, and had no significant difference between different sizes of designs. The mean accuracies of EBV of the four growth traits estimated from 25 full-sib famlies were significantly higher than those from 9 and 16 full-sib famlies, especially the total body weight. Our results provide a basic genetic evaluation of growth traits and should be useful for the design and operation of a practical selective breeding program in the clam *M. meretrix*.

## References

Blanc J M. 2003. Comparison of experimental designs for estimating quantitative genetic parameters in fish. Aquaculture Research, 34(12): 1099–1105

Bolker B M, Brooks M E, Clark C J, et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution, 24(3): 127–135

Busack C, Knudsen C M. 2007. Using factorial mating designs to increase the effective number of breeders in fish hatcheries. Aquaculture, 273(1): 24–32

Dégremont L, Ernande B, Bédier E, et al. 2007. Summer mortality of hatchery-produced Pacific oyster spat (*Crassostrea gigas*): I. Estimation of genetic parameters for survival and growth. Aquaculture, 262(1): 41–53

Dupont-Nivet M, Vandeputte M, Chevassus B. 2002. Optimization of factorial mating designs for inference on heritability in fish species. Aquaculture, 204(3–4): 361–370

Dupont-Nivet M, Vandeputte M, Haffray P, et al. 2006. Effect of different mating designs on inbreeding, genetic variance and response to selection when applying individual selection in fish breeding programs. Aquaculture, 252(2–4): 161–170

Engström G, McMillan I, McKay L, et al. 1996. Comparison of mating systems in a fish population: a simulation study. Journal of Animal Breeding and Genetics, 113(1–6): 559–566

Falconer D S, Mackay T F C. 1996. Introduction to Quantitative Genetics. 4th ed. Harlow: Longman, 464

Gilmour A R, Gogel B J, Cullis B R, et al. 2009. ASReml User Guide Release 3.0. Hemel Hempstead, UK: VSN International Ltd

Hadfield J D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistic Software, 33(2): 1–22

Henderson C R. 1974. General flexibility of linear model techniques for sire evaluation. Journal of Dairy Science, 57(8): 963–972

Lewis T W, Blott S C, Woolliams J A. 2013. Comparative analyses of genetic trends and prospects for selection against hip and elbow dysplasia in 15 UK dog breeds. BMC Genetics, 14(1): 1471–2156

Littell R C. 2002. Analysis of unbalanced mixed model data: a case study comparison of ANOVA versus REML/GLS. Journal of Agricultural, Biological, and Environmental Statistics, 7(4): 472–490

Liu Baozhong, Dong Bo, Tang Baojun, et al. 2006. Effect of stocking density on growth, settlement and survival of clam larvae, *Meretrix meretrix*. Aquaculture, 258(1–4): 344–349

Mallet A L, Freeman K R, Dickie L M. 1986. The genetics of production characters in the blue mussel *Mytilus edulis*: I. A preliminary analysis. Aquaculture, 57(1–4): 133–140

Mathew B, Bauer A M, Koistinen P, et al. 2012. Bayesian adaptive Markov chain Monte Carlo estimation of genetic parameters. Heredity, 109(4): 235–245

Nguyen T T T, Hayes B J, Guthridge K, et al. 2011. Use of a microsatellite-based pedigree in estimation of heritabilities for economic traits in Australian blue mussel, *Mytilus galloprovincialis*. Journal of Animal Breeding and Genetics, 128(6): 482–490

Patterson H D, Thompson R. 1971. Recovery of inter-block information when block sizes are unequal. Biometrika, 58(3): 545–554

Schenkel F S, Schaeffer L R, Boettcher P J. 2002. Comparison between estimation of breeding values and fixed effects using Bayesian and empirical BLUP estimation under selection on parents and missing pedigree information. Genetics Selection Evolution, 34(1): 41–59

Silva F F E, Viana J M S, Faria V R, et al. 2013. Bayesian inference of mixed models in quantitative genetics of crop species. Theoretical and Applied Genetics, 126(7): 1749–1761

Strömgren T, Nielsen M V. 1989. Heritability of growth in larvae and juveniles of *Mytilus edulis*. Aquaculture, 80(1–2): 1–6

Thompson R, Brotherstone S, White I M S. 2005. Estimation of quantitative genetic parameters. Philosophical Transactions of the Royal Society B: Biological Sciences, 360(1459): 1469–1477

Toro J E, Alcapán A C, Vergara A M, et al. 2004. Heritability estimates of larval and spat shell height in the Chilean blue mussel (*Mytilus chilensis* Hupe 1854) produced under controlled laboratory conditions. Aquaculture Research, 35(1): 56–61

Waldmann P, Ericsson T. 2006. Comparison of REML and Gibbs sampling estimates of multi-trait genetic parameters in Scots pine. Theoretical and Applied Genetics, 112(8): 1441–1451

Wang Hongxia, Chai Xueliang, Liu Baozhong. 2011. Estimation of genetic parameters for growth traits in cultured clam *Meretrix meretrix* (Bivalvia: Veneridae) using the Bayesian method based on Gibbs sampling. Aquaculture Research, 42(2): 240–247

Wilson A J, Réale D, Clements M N, et al. 2010. An ecologist's guide to the animal model. Journal of Animal Ecology, 79(1): 13–26

Yan Xiwu, Huo Zhongming, Yang Feng, et al. 2014. Heritability of larval and juvenile growth for two stocks of Manila clam *Ruditapes philippinarum*. Aquaculture Research, 45(3): 484–490