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Estimation of genetic parameters for upper thermal tolerance and growth-related traits in turbot *Scophthalmus maximus* using the Bayesian method based on Gibbs sampling

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Abstract

In order to carry out the genetic improvement of turbot upper thermal tolerance, it is necessary to estimate the genetic parameters of UTT (upper thermal tolerance) and growth-related traits. The objective of this study was to estimate genetic parameters for BW (body weight) and UTT in a two-generational turbot (*Scophthalmus maximus* L.) pedigree derived from four imported turbot stocks (England, France, Denmark and Norway). A total of 42 families including 20 families from G_1 generation and 22 families from G_2 generation were used to test upper thermal tolerance (40–50 animals per family) in this study and the body weight of individuals were measured. The heritability of BW and UTT and the correlation between these two traits were estimated based on an individual animal model using Bayesian method based on two types of animal models with and without maternal effects. These results showed that the heritabilities for BW and UTT and phenotypic and genetic correlations between the two traits estimated from model without maternal effects were 0.239±0.141, 0.111±0.080, 0.075±0.026 and –0.019±0.011, respectively. The corresponding values from model with maternal effects were 0.203±0.115, 0.055±0.026, 0.047±0.034 and –0.024±0.028, respectively. The maternal effects of BW and UTT were 0.050±0.017 and 0.013±0.004, respectively. The maternal effects had a certain influence on the genetic evaluation of the two traits. The findings of this paper provided the necessary background to determine the best selection strategy to be adopted in the genetic improvement program.

Key words: heritability, genetic correlation, thermotolerance, body weight, Turbot, Bayesian inference

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1 Introduction

Turbot (*Scophthalmus maximus* L.) is an important commercial flatfish, which is widely distributed in the Baltic, Black, and Mediterranean Seas (Zhang et al., 2014; Wang et al., 2015; Wang and Ma, 2016). Although turbot industry in China has made great progress in recent years, there are still some problems to be solved about further promoting the industrialization development, for example, temperature tolerance. Turbot is a type of cold-water fish with strict requirements for environmental temperature. Therefore, it is particularly susceptible to thermal stress (Zhang et al., 2014). Suitable growth temperature for different size turbot is between 16°C and 24°C (Xu et al., 2015). In general, the tolerance to high temperatures for adult turbot, under ideal environmental conditions, for example, good air and flowing water, can reach 25–26°C but the temperatures can not been maintained for a long time. The high and low water temperatures on growth are 21–22°C and 7–8°C, respectively (Ma et al., 2012). Temperature, as the abiotic master factor for fishes, affects almost all biochemical, physiological and life history activities of fishes (Beitinger et al., 2000). The unsuitable high temperatures result in stress response against fish and cause low disease resistance, growth rate and reproductive activity (Dominguez et al., 2004). In culture areas of turbot in North China, the natural sea water temperatures usually exceed 26°C during the whole summer (May to September) (Zhang et al., 2014). Obviously, the temperatures are unsuitable for rearing turbot (optimal growth temperatures around 16°C). In order to solve the problem, the current cooling method was mainly used with seawater pumped

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from deep wells. This method was effective, but its shortcomings were also obvious. The extraction of groundwater is not only a waste of energy but also causes great environmental pressures; the groundwater exceeding extraction can cause a large-scale decrease in the water table and subsequent water shortage. Thus, the genetic improvement of turbot upper thermal tolerance is necessary to sustain the further development of the industry.

Estimates of genetic parameters for selected traits are an important and fundamental work in fish breeding programs (Fu et al., 2015; Sun et al., 2015). As one of the most important genetic parameter, heritability is a key quantitative indicator in quantitative genetics, which is applied to the study of genetic mechanism of selected traits based on the phenotype data measuring. In addition, it also plays an extremely vital role in estimating breeding value, formulating selection index, predicting selection response, comparing breeding methods and determining reasonable breeding plans (Sun et al., 2015). Genetic correlation, in quantitative genetics, is another important basic genetic parameter, which is used to explore the correlations between different traits resulting and various genetic causes. It plays an important role in determining the genetic basis for indirect selection, predicting indirect selection response, comparing selection effects in different environments and formulating integrated selection index (Sun et al., 2015). The usual methods for estimating genetic parameters include maximum likelihood (ML) (Hartley and Rao, 1967), restricted maximum likelihood (REML) (Patterson and Thompson, 1971), average information restricted maximum likelihood (AI-REML) (Jensen et al., 1997), minimum variance quadratic unbiased estimation (MIVQUE) (Swallow and Searle, 1978), minimum norm quadratic unbiased estimation (MINQUE) (Rao, 1971) and Bayesian methods (Harville, 1974; Gianola and Fernando, 1986). Each has its advantages and disadvantages. Among them, maximum likelihood (ML), restricted maximum likelihood (REML) and Bayesian methods are often preferred over other methods for estimating variance components in animal breeding (Hoeschele, 1989). In recent years, with increasing attention being paid to genetic improvement in flatfish, some genetic parameters (mainly heritability and genetic correlation) for selected traits were reported for a variety of flatfish (Blonk et al., 2010; Wang et al., 2010; Liu et al., 2011a, b, 2015, 2016a, b, c; Tian et al., 2011; Zhang et al., 2014; Xu et al., 2015; Guan et al., 2016). The documents showed that these reported genetic parameters were estimated by restricted maximum-likelihood method (REML) (Blonk et al., 2010; Wang et al., 2010; Liu et al., 2011a, b, 2016a, b, c; Tian et al., 2011; Zhang et al., 2014; Xu et al., 2015; Guan et al., 2016), average information restricted maximum likelihood (AI-REML) (Liu et al., 2015) and minimum norm quadratic unbiased estimation (MINQUE) (Tian et al., 2011). However, the estimation of genetic parameters using Bayesian methods has not been reported in flatfish. Bayesian methods using Gibbs sampling (GS) and a Monte Carlo numerical integration technique by simulation are an important evaluation method of genetic parameters in the field of animal breeding (Wang et al., 2011). Gibbs sampling is a method of numerical integration that allows inferences to be made about joint or marginal densities, even when those densities cannot be evaluated directly (Wang et al., 2011). Compared with other evaluation methods, Bayesian method has a huge advantage in genetic parameters estimation, particularly when data do not satisfy normal distribution (Wang et al., 2011). Usually, thermotolerance can be regarded as a kind of threshold character. The threshold character data are difficult to meet normal distribution. Therefore, it is highly suitable to estimate the genetic parameters of thermotolerance character using Bayesian method.

The ultimate goal of genetic improvement, regardless of any selected traits, is to obtain greater economic benefits. Obviously, it is not important for thermotolerance selection without considering growth rate. Thus, turbot selective breeding program for thermotolerance and fast-growth was conducted at the Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences in 2007. In the present study, we evaluated the heritabilities of turbot body weight (BW) and upper thermal tolerance (UTT) as well as the genetic correlations among them by full- and half-sib family analysis using Bayesian method via Gibbs sampling. The main objective of this paper is to provide some fundamental insight for further selection through the genetic parameters of the two traits.

2 Materials and methods

2.1 *Genetic material and production of family*

The data were derived from a breeding program initiated in 2007 by the Yellow Sea Fisheries Research Institute, Qingdao, China. Four imported turbot stocks from England, France, Denmark and Norway from June 2002 to September 2003 were used to establish base populations for selective breeding by genetic background analysis of the four stocks. A total of 170 brood stocks including 68 males and 102 females were obtained. These brood stocks were individually tagged with the passive integrated transponders (PIT) in December 2006 (G_0 generation). In April 2007, 56 F_1 full-sib families were produced using a nested mating design with one male and two females by Yantai Tianyuan Aquatic Limited Corporation, Yantai, China. At 12 months of age, 20 randomly selected families from the F_1 families were used to test upper thermal tolerance (40–50 animals per family), and then the upper thermal tolerance (UTT) for each individual fish was calculated as cumulative thermal exposure in degree hours (deg hr) as followed Perry et al. (2005). An F_2 breeding program was developed based on UTT of the F_1 animals and pedigree relationship, and 42 full-sib families were obtained in April 2010. Follow the same procedure as F_1 thermal tolerance test, 22 randomly selected families from the F_2 families were selected to test upper thermal tolerance (40–50 animals per family) when the F_2 families were reared up to 12 months of age. The two-generation families were reared in separate tanks until tagging. When the fish were reared up to 3 months of age, samples of 250–300 fish were randomly selected from each tank for tagging using the visible implant elastomer (VIE) (for distinguishing different families) and then stocked communally. They were individually tagged with the passive integrated transponders (PIT) again (for distinguishing families and individuals) when all tagged fish with VIE were communally reared up to 9 months of age. To obtain similar rearing conditions for all F_1 and F_2 families at different breeding stages, some effective measures were taken to standardize both the stocking density of fish and the environment. The standard operating procedures were same as Wang et al. (2010).

2.2 *Experimental procedure*

A total of 42 families including 20 families from G_1 generation and 22 families from G_2 generation were used to test upper thermal tolerance (40–50 animals per family) in April 2008 and April 2011, respectively. Fish from each family used in thermal tolerance challenges were reared in separate tanks for 1 week at 15°C before exposure to an acute thermal challenge. During the entire experimental period, the temperature of fish subjected to chronic thermal shock was increased by 13°C (1°C per 12 h up to

26°C and 1°C per 24 h between 26°C and 28°C), then held at 28°C until the end of the experiment (the lethal temperature for the turbot was 28°C). The experiment was finished when two-thirds of all individuals have lost their activity. The time to loss of activity (LOA) was determined based on the reaction of fish when the water is agitated for 10 s. In the experimental process, the still water, aerated cultures and automatic thermostat control were used to culture the tested fish. The fish activities were observed every hour and the individuals of loss of activity were timely removed. In the thermal challenge, some variability of the temperature of the time to loss of activity was observed. In order to correct for these differences, the upper thermal tolerance (UTT) was calculated as cumulative thermal exposure in degree hours (deg hr) as

$$UTT = \sum_{j} (T_j - T_{\mathrm{a}}),$$

where *j* represents each hour up to time to loss of activity (LOA) for each individual fish, T_j is the experimental temperature at each hour and T_{a} is the acclimation temperature (15°C). This method has been reported previously (Perry et al., 2005; Zhang et al., 2014). The body weight (BW, g) was also recorded for each individual fish at the beginning of the experiment. All the families shared the same environment and handing during the entire experimental period in the high temperature conditions to ensure that the eventual differences among them were detected.

2.3 *Statistical and genetic analysis*

The Kolmogorov-Smirnov test (K-S test) was used to test the normality of data for UTT and BW from each family before the data are analyzed. The Kolmogorov-Smirnov *Z* values and two-tailed probability (*P*) values of each family were calculated by using SPSS 13.0 software package (Norusis, 2009). The family data are considered to be normal distribution when P>0.05 and non-normal distribution when P<0.05.

Variance components, heritabilities, and genetic correlations with standard errors for UTT and BW traits were estimated using Gibbs sampling (GS) in Multiple Trait Gibbs Sampling in Animal Models (MTGSAM) programs (Harville, 1974; Gianola and Fernando, 1986) using the two types of animal models. Maternal genetic effect was included in Model 2 and was not included in Model 1. The two models can be written as

$$\begin{aligned}&\text{Model 1}: \ y_{ijk} = u + a_i + f_i + g_k + e_{ijk},\\&\text{Model 2}: \ y_{ijkl} = u + a_i + f_j + g_k + m_l + e_{ijkl},\end{aligned}$$

where *u* is the population mean, y_{ijk} is the measured values of UTT and BW, a_i is the additive genetic effect of individual as the random effect, f_j is full-sib family random effect, g_k is generation effect (k=1 or 2), m_l is maternal genetic effect, e_{ijk} and e_{ijkl} are the random residual. In matrix notation the model can be written:

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{b} + \boldsymbol{Z}\boldsymbol{u} + \boldsymbol{e},$$

where $\boldsymbol{y}$ is the vector of observations of each trait, $\boldsymbol{b}$ is the vector of fixed effects, $\boldsymbol{u}$ is the vector of random effects, $\boldsymbol{e}$ is a vector of random errors, $\boldsymbol{X}$ and $\boldsymbol{Z}$ are known design matrices assigning the observations to levels of $\boldsymbol{b}$ and $\boldsymbol{u}$, respectively. The mathematical expectation and variance was defined as

$$\begin{aligned}&\boldsymbol{E}(\boldsymbol{u}) = 0, \ \boldsymbol{E}(\boldsymbol{e}) = 0, \ \boldsymbol{E}(\boldsymbol{y}) = \boldsymbol{X}\boldsymbol{b},\\&Var\begin{pmatrix}\boldsymbol{u}\\\boldsymbol{e}\end{pmatrix} = \begin{pmatrix}\boldsymbol{G}_0\otimes\boldsymbol{A} & 0\\ 0 & \boldsymbol{R}_0\otimes\boldsymbol{I}\end{pmatrix},\\&\boldsymbol{G}_0 = \begin{pmatrix}g_{11} & g_{12}\\ g_{21} & g_{22}\end{pmatrix}, \ \boldsymbol{R}_0 = \begin{pmatrix}r_{11} & r_{12}\\ r_{21} & r_{22}\end{pmatrix},\end{aligned}$$

where $\boldsymbol{G}_0$ is the genetic variances-covariances matrix of UTT and BW, $\boldsymbol{R}_0$ is the residual variance-covariance matrix of the two traits, $\otimes$ is Kronecker product, $Var(\boldsymbol{y}) = ZAZ'\sigma_A^2 + \boldsymbol{I}\sigma_e^2$. $\boldsymbol{A}$ is the additive genetic relationship matrix, $\boldsymbol{I}$ is an identity matrix, and σ_A^2 is additive genetic variance.

The equations of two-trait animal model are

$$\begin{bmatrix}X'R^{-1}X & X'R^{-1}Z'\\ Z'R^{-1}X & Z'R^{-1}Z + A^{-1}\otimes G^{-1}\end{bmatrix}\begin{bmatrix}\hat{b}\\ \hat{a}\end{bmatrix} = \begin{bmatrix}X'R^{-1}y\\ Z'R^{-1}y\end{bmatrix},$$

$\boldsymbol{X} = \begin{bmatrix}X_1 & 0\\ 0 & X_2\end{bmatrix}$, $\boldsymbol{Z} = \begin{bmatrix}Z_1 & 0\\ 0 & Z_2\end{bmatrix}$, $\hat{\boldsymbol{b}} = \begin{bmatrix}\hat{b}_1\\ \hat{b}_2\end{bmatrix}$, $\hat{\boldsymbol{a}} = \begin{bmatrix}\hat{a}_1\\ \hat{a}_2\end{bmatrix}$ and $\hat{\boldsymbol{y}} = \begin{bmatrix}\hat{y}_1\\ \hat{y}_2\end{bmatrix}$.

Heritability (h^2) and genetic correlation (r_g) can be written:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}, \quad r_g = \frac{\mathrm{cov}(a_x, a_y)}{\sqrt{\sigma_{a_x}^2 \cdot \sigma_{a_y}^2}},$$

where σ_a^2 is additive genetic variance, σ_p^2 is phenotype variance, a_x and a_y are additive genetic effects of x- and y-traits and $\mathrm{cov}(a_x, a_y)$ is covariance of a_x and a_y.

Bayesian inference facilitates obtaining the marginal posterior probability density of the genetic parameters, and from these densities, the calculation of the errors in the parameter estimates gets more information. In this study, a total Gibbs chain length of 5 000 samples for each analysis was defined with a burn-in period of 200 and a thinning interval of 30 uninformative (flat) priors were used for additive genetic and residual (co)variances. The phenotypic correlations between UTT and BW were estimated as Pearson's correlations by using SPSS 13.0 software package (Norusis, 2009).

3 Results

3.1 *The descriptive statistics of traits*

The descriptive statistics for UTT and BW were presented in Table 1. The values of UTT ranged from 962.000°C to 2 292.000°C and that of BW from 51.000 g to 153.000 g. The coefficient of variation (CV) of the two traits were high, greater than 15%, the trait BW even up to 20.370%, which indicated that there existed some very significant differences between individual in the two traits and had greater potential for genetic improvement.

3.2 *The normal distribution test for data*

The normal distribution test of the two variables was done with Kolmogorov-Smirnov test. Details of the parameters may be observed in Table 2. The Kolmogorov-Smirnov *Z* values for BW ranged from 0.477 to 0.819 and that for UTT from 1.330 to 1.559. All Asymp.Sig.(2-tailed) values (*P* value) for BW ranged from 0.616 to 0.973 and were higher than 0.05. On the contrary, most Asymp.Sig.(2-tailed) values for UTT were lower than 0.050 except for Family 22 (0.053), Family 3 (0.053), Family 5 (0.056) and Family 4 (0.058) from G_2 generation (the other *P* values ranged from 0.016 to 0.050).

Table 1. Description statistics for UTT and BW traits in turbot (CV is coefficient of variation)

Trait	Mean trait value	Standard deviation	Coefficient of variation	Minimum trait value	Maximum trait value
UTT	1 873.692°C	293.943°C	15.690%	962.000°C	2 292.000°C
BW	82.712 g	16.845 g	20.370%	51.000 g	153.000 g

Table 2. Kolmogorov-Smirnov test for UTT and BW data in turbot

Generation	Family	BW		UTTC	
		Kolmogorov-Smirnov *Z*	Asympt.Sig.(2-tailed)	Kolmogorov-Smirnov *Z*	Asympt.Sig.(2-tailed)
G_1	1	0.638	0.829	1.456	0.029
	2	0.626	0.835	1.452	0.030
	3	0.633	0.831	1.448	0.030
	4	0.644	0.825	1.444	0.031
	5	0.629	0.833	1.498	0.023
	6	0.652	0.817	1.433	0.033
	7	0.517	0.952	1.431	0.033
	8	0.571	0.900	1.451	0.030
	9	0.587	0.881	1.447	0.030
	10	0.545	0.928	1.443	0.031
	11	0.510	0.957	1.406	0.038
	12	0.516	0.953	1.391	0.042
	13	0.523	0.947	1.462	0.028
	14	0.569	0.903	1.451	0.030
	15	0.499	0.959	1.457	0.029
	16	0.477	0.973	1.462	0.028
	17	0.486	0.969	1.413	0.037
	18	0.494	0.963	1.409	0.038
	19	0.481	0.971	1.413	0.037
	20	0.491	0.964	1.377	0.045
G_2	1	0.591	0.877	1.383	0.044
	2	0.590	0.878	1.396	0.040
	3	0.589	0.879	1.347	0.053
	4	0.588	0.880	1.330	0.058
	5	0.593	0.875	1.337	0.056
	6	0.592	0.876	1.508	0.021
	7	0.621	0.837	1.439	0.032
	8	0.608	0.859	1.423	0.035
	9	0.617	0.848	1.419	0.036
	10	0.819	0.616	1.493	0.023
	11	0.673	0.801	1.359	0.050
	12	0.781	0.689	1.374	0.046
	13	0.732	0.757	1.388	0.042
	14	0.772	0.713	1.377	0.045
	15	0.802	0.643	1.371	0.047
	16	0.604	0.861	1.559	0.016
	17	0.601	0.863	1.440	0.032
	18	0.599	0.868	1.455	0.029
	19	0.595	0.873	1.388	0.042
	20	0.594	0.874	1.415	0.036
	21	0.597	0.871	1.498	0.022
	22	0.596	0.872	1.349	0.053

3.3 *Estimation of genetic parameters*

Estimates of heritability for BW and UTT and the phenotypic and genetic correlations between the two traits estimated from two types of animal models were given in Table 3. The estimate of heritability for UTT, estimated from Model 1 that did not include maternal genetic effect, was low (0.111±0.080) and was no significant difference from zero ($P>0.05$), whereas that for BW was moderate (0.239±0.141) and was significant difference from zero ($P<0.05$). The phenotypic and genetic correlation between UTT and BW estimated from Model 1 was a low positive value (0.075±0.026) and a weak negative value (–0.019±0.011), respectively. The estimate of heritability for UTT, estimated from Model 2 that included maternal genetic effect, was lower (0.055±0.026) than that from Model 1 (0.111±0.080) and maternal genetic effect was 0.013±0.004, whereas that for BW was 0.203±0.115 and maternal effect was 0.050±0.017. The phenotypic and genetic correl-

Table 3. Heritability for the growth and upper thermal tolerance traits and phenotypic (r_p) and genetic (r_g) correlations between the two traits estimated from two animal models

Mode l	Trait	Heritability (h^2)	Maternal effects	r_g	r_p
Model 1	UTT	0.111±0.080		–0.019±0.011	0.075±0.026
	BW	0.239±0.141			
Model 2	UTT	0.055±0.026	0.013±0.004	–0.024±0.028	0.047±0.034
	BW	0.203±0.115	0.050±0.017		

ation between UTT and BW estimated from Model 2 was 0.047±0.034 and –0.024±0.028, respectively.

4 Discussion

In a successful breeding program, genetic parameters of the selected traits should be correctly estimated so that suitable breeding programmes could be planned (Narinc et al., 2010). The accuracy estimations of genetic parameters depend on the use of a correct model, a large sample size and reliable statistical methods (Wang et al., 2011). During the experiment (12 months of age), the sex of turbot was unable to be distinguished and the difference between female and male turbot in growth was not significant (P>0.05) (Wang et al., 2014), so the effect was not taken into account in the model. The heritabilities of traits were generally estimated using two types of models with and without maternal genetic effects. The documents showed that the maternal effects in some studies, for example, estimation of genetic parameters for growth-related traits in common carp (Vandeputte et al., 2004; Ninh et al., 2011), were negligible; on the contrary, there were statistically significant maternal effects in other studies, for example, genetic parameters for growth and survival in common carp (Nielsen et al., 2010; Ninh et al., 2011; Dong et al., 2015). In the present study, two types of animal models with excluding and including maternal genetic effects (Model 1 and Model 2) (the two models all include additive genetic effect, full-sib family effect and generation effect) were used to estimate genetic parameters. Appropriate family numbers and large sample sizes are generally required to estimate heritabilities and genetic correlations accurately. Simulation studies revealed that the estimation value was more accurate for larger sample size (Wang et al., 2011). In this paper, a total of 1 260 individuals from 42 families (two generations) were used to estimate genetic parameters for UTT and BW. The sample size was moderate for genetic evaluation due to the limitation of experimental conditions. There are two main reasons for the limitation: firstly, for the sake of ensuring common conditions in the entire experiment and secondly the consumption of expensive experimental materials. In addition, the body weight data from each family fit the normal distribution based on Kolmogorov-Smirnov test but the UTT data mostly do not (only three sets of UTT data were accorded with normal distribution). Based on the data characteristics in this study (sample size and normality), it is very important to choose reasonable approach for accurate genetic evaluation. In the context of animal breeding, restricted maximum likelihood (REML) and Bayesian method have been found preferable over others for estimating variance and covariance components in mixed liner models in recent years. Bayesian analysis via Gibbs sampling is an appropriate alternative for estimating (co)variance components and genetic parameters. It can provide reasonable estimates and greater flexibility than the usual likelihood estimates, mainly because of the inferences obtained by employing the posterior marginal distributions (Faria et al., 2007). Any features of this distribution can be computed including probability statements. Obviously, Bayesian analysis method has a huge advantage in heritability estimation, particularly when data do not fit a normal distribution. Based on the data characteristics in this study, it is more reasonable to select Bayesian analysis for more accurate genetic evaluation.

In this study, a total of 1 260 individuals from 42 families (two generations) were used to estimate genetic parameters for UTT and BW using Bayesian method based on two types of animal models with and without maternal effects. Heritabilities for BW and UTT and phenotypic and genetic correlations between the two traits estimated from model without maternal effects (Model 1) were 0.239±0.141, 0.111±0.080, 0.075±0.026 and –0.019±0.011, respectively. The corresponding values from model with maternal effects (Model 2) were 0.203±0.115, 0.055±0.026, 0.047±0.034 and –0.024±0.028, respectively. Obviously, the maternal effects had a certain influence on the genetic evaluation of the two traits. The existence of maternal effects should be the reason for separate family rearing before tagging. This speculation was consistent with the conclusion of some studies that maternal effects were detected when families were reared separately until tagging size (Nielsen et al., 2010; Ninh et al., 2011; Dong et al., 2015). In addition, other studies reported that the maternal effects were negligible when families were reared communally from newly hatched larvae (Vandeputte et al., 2004; Ninh et al., 2011), which further confirmed that maternal effects could be eliminated when fish were reared in communal stocks. Therefore, it is necessary, for genetic evaluation of breeding traits, to take into account maternal effects in analysis model when all families were not reared communally from newly hatch.

The economic importance of upper thermal tolerance in aquaculture species has given rise to some experiments in the last few decades with the aim of genetic improvement (Perry et al., 2005; Liu et al., 2011b; Zhang et al., 2014). Perry et al. (2005) estimated genetic (co)variance parameters for body weight (BW) and upper thermal tolerance (UTT) in a three-generational rainbow trout (*Oncorhynchus mykiss*) pedigree derived from two commercial strains using restricted maximum likelihood (REML). The heritability for BW and UTT is 0.460±0.040 and 0.410±0.070, respectively. The genetic correlation between two traits is –0.030±0.080 and the phenotypic correlation is 0.060±0.013 (Perry et al., 2005). Liu et al. (2011b) used 753 animals from 40 families (G_1 generation) of turbot to estimate the genetic parameters of juvenile BW (mean value: (7.300±3.600) g) and UTT with average information restricted maximum likelihood method (AIREML). The heritability of BW and UTT is 0.220±0.090 and 0.026±0.034, respectively. The standard error for the estimated heritability of upper thermal tolerance (0.034) is larger than the estimated heritability (0.026). The phenotypic and genetic correlation between the two traits is 0.040 and –1.000, respectively (Liu et al., 2011b). Zhang et al. (2014) used 1 725 individuals from 53 families (G_2 generation) to estimate the genetic parameters of juvenile BW (mean value: 7.500 g) and UTT using the average information restricted maximum likelihood method (AIREML). The heritability for UTT is 0.087±0.032 and that for BW is 0.303±0.074. The phenotypic correlation between the two traits is 0.093±0.029 and the genetic correlation is –0.044±0.239. From these results, it can be seen that the differences of four parameters (including two heritabilities, phenotypic correlation and genetic correlation) between current research (the conclusions from models including maternal effects) and rainbow trout (*Oncorhynchus mykiss*) are greater than the differences between current research and turbot (*Scophthalmus maximus* L.). We speculated that this discrepancy is mainly due to the differences between species. Compared with two kinds of conclusions from turbot, the estimated heritability of UTT, in the present study, is higher than the estimates of both Liu et al. (2011b) and Zhang et al. (2014), and the heritability of BW is less than the estimates of both Liu et al. (2011b) and Zhang et al. (2014). The phenotypic correlation between UTT and BW is situated between Liu et al. (2011b) and Zhang et al. (2014) estimates and the genetic correlation is higher than the estimates of both Liu et al. (2011b) and Zhang et al. (2014). It is speculated that this kind of intraspecific differences is mainly attributed to the number of individuals contributing to the estimates, the use of different statistical methods and models, different source populations and different developmental periods of samples used. Among these factors, special attention should be paid to the difference of developmental periods of samples used. Liu et al. (2011b) and Zhang et al. (2014) have studied upper thermal tolerance of juvenile turbot, and this paper has explored upper thermal tolerance of adult turbot.

Estimated heritability could be classified as low (0.05–0.15), medium (0.20–0.40), high (0.45–0.60) and very high (>0.65) levels (Cardellino and Rovira, 1987; Xu et al., 2015). This study determined that the heritability of BW and UTT were 0.203±0.115 and 0.055±0.026, respectively. According to this grading standard, the heritability of BW and UTT could be defined as medium and low heritability, respectively. Moderate heritability on the BW trait demonstrated promising effects on genetic improvement in select breeding programs of the turbot industry. Clearly, the selection methods are very flexible for genetic improvement of BW. For the UTT traits with low heritability, the determination of the selection strategy requires careful consideration, and family selection is to be preferred, provided that common environmental effects are kept at a low level (Rye et al., 1990; Wang et al., 2010). The magnitude of correlations was categorized as low (0–0.40), medium (0.45–0.55) and high (0.60–1), independent of the sign (Cardellino and Rovira, 1987; Xu et al., 2015). In this study, the genetic and phenotypic correlations between BL ((body length) and BW were –0.024±0.028 and 0.047±0.034, respectively. Obviously, it was positive and low in magnitude for the phenotypic correlation but negative and low for the genetic correlation. It is very important to obtain the phenotypic and genetic correlations among breeding traits for the design of breeding programs (Zhang et al., 2014). Negative genetic correlation between traits might cause offsets in genetic gain from selection on single characters by economic losses in correlated traits. Additionally, the multi-trait selection breeding also has difficulty obtaining good breeding results due to offsets between the two traits. Clearly, the BW and UTT traits cannot be improved simultaneously in a selection programme. Given the negative genetic correlations between the two traits, methods of achieving simultaneous improvement of both traits require further investigation. A breeding method by first cultivating two new strains and then hybridization between the two strains may be a strategy worthy of consideration. From a breeding viewpoint, the estimated genetic parameters provided the necessary background to determine the best selection strategy to be adopted in the genetic improvement program in order to allow the selection response and efficient advancement predicted by this study.

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