



# Estimation of genetic parameters for growth traits in a breeding program for rainbow trout (*Oncorhynchus mykiss*) in China

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**ABSTRACT.** Genetic parameters and breeding values for growth traits were estimated in the first and, currently, the only family selective breeding program for rainbow trout (*Oncorhynchus mykiss*) in China. Genetic and phenotypic data were collected for growth traits from 75 full-sibling families with a 2-generation pedigree. Genetic parameters and breeding values for growth traits of rainbow trout were estimated using the derivative-free restricted maximum likelihood method. The goodness-of-fit of the models was tested using Akaike and Bayesian information criteria. Genetic parameters and breeding values were estimated using the best-fit model for each trait. The values for heritability estimating body weight and length ranged from 0.20 to 0.45 and from 0.27 to 0.60, respectively, and the heritability of condition factor was 0.34. Our results showed a moderate degree of heritability for growth traits in this breeding program and suggested that the genetic and phenotypic tendency of body length, body weight, and condition factor were similar. Therefore, the selection of phenotypic values based on pedigree information was also suitable in this research population.

**Key words:** Rainbow trout; Genetic parameter; Breeding value; China

## INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss*) originated in North America and was one of the first species of fish to be domesticated. The cultivation of rainbow trout has been distributed worldwide, making rainbow trout one of the most widely cultivated fishes (Gall and Crandell, 1992). A thorough understanding of the genetic control of growth traits in rainbow trout is key to genetic enhancements in production performance. On the basis of animal and plant breeding science, genetic improvement in aquaculture has been successfully implemented during the past three decades, particularly in salmonid farming, and is still in progress (Donaldson, 1969; Gall and Crandell, 1992; Janhunen et al., 2012; Kause et al., 2012; Sae-Lim et al., 2012). Cold-water fish culturing in China began in 1959, when eyed eggs and fry of rainbow trout were introduced from the Democratic People's Republic of Korea. Rainbow trout culture expanded rapidly throughout 22 provinces in China (Wang and Yang, 2002). According to statistical data provided by the Food and Agriculture Organization (2012), the production of rainbow trout in China was 16,397 tons in 2010. Because rainbow trout is the major cold-water fish farmed in China, accelerating selective breeding and preventing genetic degeneration are important, but the country has gotten a late start on this research. Programs have been established for 80 years in the United States, but the first selective breeding program for rainbow trout in China began in 2004 (Sun and Wang, 2010).

In 1978, the Bohai cold-water fish experimental station, which is affiliated with the Heilongjiang River Fishery Research Institute (HRFRI) of the Chinese Academy of Fishery Sciences became the center of rainbow trout culture studies in China (Wang and Yang, 2002). HRFRI has been conducting research and disseminating culture techniques for cold-water fish in collaboration with experts from Europe and Japan since the 1980s (Wang and Yang, 2002). In cooperation with the Finnish National Fisheries Innovation Centre, HRFRI established the first family breeding program in China for rainbow trout, which was based on passive integrated transponder tags at the Bohai cold-water fish experimental station in 2004 (Sun and Wang, 2010). Many estimations of genetic parameters and breeding values for growth traits have been published for rainbow trout, and previous genetic studies have revealed moderate levels of genetic variation for growth traits in salmon (Gunnes and Gjedrem, 1978; Gjerde and Gjedrem, 1984; Gjerde et al., 1994; Rye and Gjerde, 1996; Gjedrem, 1983, 2000), but they vary greatly among experiments (e.g., ranging from 0 to 0.58 for weight). Thus, a genetic estimation for growth traits in the breeding program for rainbow trout is needed for the common trout-farming environment in China.

In this study, we aimed to estimate genetic parameters and breeding values for growth traits in the first and, currently, the only family breeding program for rainbow trout in China. Genetic and phenotypic data were collected for growth traits from 75 full-sibling families with a 2-generation pedigree. Genetic parameters and breeding values for growth traits of rainbow trout were estimated using the derivative-free restricted maximum likelihood (DFREML) method.

## MATERIAL AND METHODS

### Data collection

Samples were obtained from the rainbow trout breeding program at the Bohai cold-

water fish experimental station affiliated with HRFRI of the Chinese Academy of Fishery Sciences. Five cultured strains, established in 2001, including the Bohai, Denmark, Norway, American Donaldson, and California strains, were used to create the basic populations [generation 0 ( $G_0$ )]. The Bohai strain originated with the first introduction of rainbow trout from North Korean in 1959. The Demark and other strains were introduced from Denmark, Norway, and the United States, respectively. Four-year-old fish from these strains were used in a complete diallel cross and a self-breeding experiment in 2004 (Griffing, 1956). The offspring from the  $G_0$  population, as the first generation ( $G_1$ ), were cultivated in a natural flowing spring at a temperature ranging from 5.2° to 16.0°C at the Bohai experimental station. The parental fish were cultured in earth pond with 15 m in width, 120 m in length, and 0.8 m in water depth, water flow of 20-30 L/s, and dissolved oxygen saturation range from 42 to 80%. All the fish were fed by manual work in the experiment, the feeding rate per day depends on the water temperature and dissolved oxygen saturation according to “The Feed Catalogue For Trout from BioMar Company”.

Seventy-five male and 75 female fish from  $G_1$  were used between October 2007 and January 2008 to establish 75 full-sibling  $G_2$  families. After floating until March 2008, all fry were reared in the aquarium for 10 months until reaching the size when could be implanted the passive-integrated transponder tag, the aquarium with 1 m in diameter, 0.5 m in water depth, in which there was average water temperature range from 6.5 to 12, water flow of 6-8 L/min. During 10 months rearing, there were 3 times for randomly screened for fish in order to satisfy the environmental requirement for the fry in the aquarium.

When average body weight reached >50 g, we selected 50 fish with no deformity and defeature from each tank and mixed them in a cemented pool after implanting passive-integrated transponder tags to avoid the influence of environmental factors on the cross. The concrete pond with flow through spring water, water flow of 20-30 L/s, 5 m in width, 30 m in length, and 0.7 m in water depth. Body length and body weight were measured three times for each fish during 2009 and 2010. The condition factors (CFs) were calculated for all fish:  $CF = \text{ungutted body weight} / (\text{body length})^3 \times 100\%$ . After the abnormal and wrong records were deleted, the  $G_2$  consisted of 2157 individuals; each fish had 3 records made at 1, 1.5, and 2 years of age.

## Statistical model

Simple descriptive statistics for data collected are summarized in Table 1. The selection of fixed effects fitted to the model was carried out using the general linear model procedure of SAS (SAS Institute, Cary, NC, USA). All possible interactions among fixed effects were tested. Fixed effects with a P value of >0.05 were excluded from the final model. Significant fixed effects on body weight and body length included year, season, sire, dam, and water temperature. The fixed effect of CF excluded temperature from the model owing to statistical insignificance. Variance components and heritability for each trait were estimated for a single trait, two traits, and a repeatability animal model using DFREML with a simplex algorithm using multiple-trait DFREML (Boldman et al., 1995).

**Table 1.** Descriptive statistics for growth traits of rainbow trout.

Traits	Mean	SD	Minimum	Maximum	CV
Weight <sub>(1 year)</sub>	63.014	34.269	51	150	0.544
Weight <sub>(1.5 year)</sub>	176.41	41.993	121	330	0.238
Weight <sub>(2 years)</sub>	624.467	129.923	238.5	1090	0.208
Length <sub>(1 year)</sub>	15.485	7.467	13.75	88	0.482
Length <sub>(1.5 year)</sub>	24.105	7.654	15.1	50.4	0.318
Length <sub>(2 years)</sub>	35.869	9.182	16.1	54.01	0.256
CF <sub>(1 year)</sub>	0.9293	0.4672	0.442	1.899	0.503
CF <sub>(1.5 year)</sub>	1.0957	0.9714	0.345	1.91	0.8865
CF <sub>(2 years)</sub>	1.6278	2.462	0.28	2.85	1.512

SD = standard deviation; CV = coefficient of variation.

The single-trait animal model (model I) used is as follows:

$$y_{ijkl} = \mu + E_i + s_j + d_k + a + e_{ijkl} \quad (\text{Equation 1})$$

where  $y_{ijkl}$  is the observation in individual animals,  $\mu$  is the population mean,  $E_i$  is the fixed effect of common environmental effects including year and season,  $s_j$  is the fixed effect of dam family,  $d_k$  is the fixed effect of sire family,  $a$  is the random animal effect, and  $e_{ijkl}$  is the random residual error for animal individual.

The matrix notation is as follows:

$$Y = Xb + Za + e \quad (\text{Equation 2})$$

where  $Y$  is a vector of phenotype observations of animals,  $a$  is a vector of random breeding values,  $b$  is a vector of the fixed effects of the common environmental effect dam family and sire family,  $X$  and  $Z$  are the corresponding incidence matrices relating the effects to  $Y$ , and  $e$  is the vector of random residuals.

$$\text{Then, } E(y) = Xb, E(a) = 0, E(e) = 0 \quad \text{Var} \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} A\delta_a^2 & 0 \\ 0 & I\delta_e^2 \end{bmatrix} \quad (\text{Equation 3})$$

If  $A$  is the matrix of additive genetic relationships among individuals, the mixed model equation (MME) used is as follows:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}k \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \quad (\text{Equation 4})$$

The multiple-trait animal model (model II) is as follows:

$$y_{ijkl} = \mu + E_{ti} + s_{ij} + d_{tk} + a + e_{ijkl} \quad (\text{Equation 5})$$

where  $t$  represents the traits of body weight, body length, and condition factor,  $y_{ijkl}$  is the observation of trait  $t$  for individual animals, and other definitions are the same as those described for the single-trait animal model.

The MME is as follows:

$$\begin{bmatrix} X'_1 X_1 r^{11} & X'_1 X_2 r^{12} & X'_1 Z_1 r^{11} & X'_1 Z_2 r^{12} \\ X'_2 X_1 r^{12} & X'_2 X_2 r^{22} & X'_2 Z_1 r^{12} & X'_2 Z_2 r^{22} \\ Z'_1 X_1 r^{11} & Z'_1 X_2 r^{12} & Z'_1 Z_1 r^{11} + A^{-1} g^{11} & Z'_1 Z_2 r^{12} + A^{-1} g^{12} \\ Z'_2 X_1 r^{12} & Z'_2 X_2 r^{22} & Z'_2 Z_1 r^{12} + A^{-1} g^{12} & Z'_2 Z_2 r^{22} + A^{-1} g^{22} \end{bmatrix} \begin{bmatrix} \hat{b}_1 \\ \hat{b}_2 \\ \hat{a}_1 \\ \hat{a}_2 \end{bmatrix} = \begin{bmatrix} X'_1 y_1 r^{11} + X'_1 y_2 r^{12} \\ X'_2 y_2 r^{12} + X'_2 y_2 r^{22} \\ Z'_1 y_1 r^{11} + Z'_1 y_2 r^{12} \\ Z'_2 y_2 r^{12} + Z'_2 y_2 r^{22} \end{bmatrix} \quad (\text{Equation 6})$$

The repeatability animal model (model III) is as follows:

$$y_{ijkl} = u + E_i + s_j + d_k + a + p + e_{ijkl} \quad (\text{Equation 7})$$

where  $p$  is the permanent environment effect. Other symbols are the same as those described for the single-trait animal model.

The MME is as follows:

$$\begin{bmatrix} X'X & X'Z & X'W \\ ZX & Z'Z + A^{-1}k_2 & Z'W \\ W'X & W'Z & W'W + A^{-1}k_2 \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \\ \hat{p} \end{bmatrix} = \begin{bmatrix} X'y \\ W'y \\ W'y \end{bmatrix} \quad (\text{Equation 8})$$

### Estimation of genetic parameters and breeding values

Calculations were carried out with the multiple-trait DFREML (Boldman et al., 1995), a set of programs using the simplex procedure to locate the maximum of the log of likelihood. Convergence was considered to have been reached when the variance of function values in the simplex was less than  $10^{-9}$ . Variance and heritability for each trait were estimated for three animal models using DFREML with a simplex algorithm. Phenotypic and genetic correlations were estimated using a multivariate linear model. To calculate genetic trends, breeding values across generations were estimated with the best linear unbiased prediction method by using the repeatability animal model. Means of animal estimated breeding values were regressed across years to predict annual genetic trends for growth traits.

## Model selection

To test the goodness-of-fit among the three models, Akaike information criterion (AIC) and Bayesian information criterion (BIC) were chosen to determine the optimal models. The AIC and BIC were also chosen because likelihood ratio tests tend to favor models with multiple parameters (Jensen, 2001), whereas these criteria penalize models with many parameters.

AIC and BIC were defined as

$$\text{AIC} = -2\log(L_i) + 2t_i, \text{ and } \text{BIC} = -2\log(L_i) + t_i \log(v) \quad (\text{Equation 9})$$

where  $t_i$  is the number of variance parameters in the model  $i$ , and  $v = n - p$  is the number of residual degrees of freedom. AIC and BIC were calculated for each model, and the model with the lowest value was assumed to be optimal.

## RESULTS

### Parameter selection for models

The importance of including particular fixed effects in our model is accommodated by F-tests. For growth traits, the effects of season, sire family, dam family, year, and temperature were highly significant ( $P < 0.001$ ), and they were therefore included in the model (Table 2). In fact, the effects of season, year, and temperature were highly consistent and were considered a common environmental effect.

**Table 2.** Generalized linear model variance analyses of growth traits.

Factor	Weight (g)			Length (cm)			CF		
	MS	d.f.	F	MS	d.f.	F	MS	d.f.	F
Year	271233007.9	1	7133.06**	308041.637	1	7382.39**	625.1064	1	2.88
Season	327319616.6	2	54945.6**	276658.374	2	13401.6**	773.5372	2	3.57*
Sire family	535690.602	4	8.85**	948.753844	4	14.12**	510.2611	4	2.35*
Year x sire	30425712.8	9	804.22**	312216.886	9	837.84**	411.711	9	1.90*
Season x sire	46983586.9	14	8241.31**	39844.0426	14	1910.25**	551.084	14	2.54**
Dam family	591690.396	4	9.78**	634.34382	4	9.43**	187.366	4	0.86*
Year x dam	30454425.0	9	805.44**	34520.1045	9	831.14**	190.428	9	0.88
Season x dam	47022682.2	14	8315.01**	39733.331	14	1893.16**	266.323	14	1.23
Sire x dam	312.185.83	19	5.18**	487.7671	19	7.30**	228.215	19	1.05
Temperature	25575145.6	2	52100.4**	275505.82	2	12870.3**	574.386	2	2.48
Year temperature	2171404.17	3	34871.6**	183862.874	3	86707.87**	516.5411	3	2.38
Season temperature	163686266.7	4	27513.5**	138333.741	4	6520.40**	387.5155	4	1.79

CF = condition factors; MS = mean square values; d.f. = degrees of freedom. \* $P < 0.05$ . \*\* $P < 0.01$ .

## Model selection

The model selection results for AIC and BIC are presented in Table 3. AIC and BIC rank models and the models with the lowest values are the preferred models. Results indicate that for body weight, model I was superior to models II or III (rank I > II > III); for length,

model II was superior (rank II > I > III); and only for CF did model III have the lowest scores (rank III > II > I).

**Table 3.** Estimates of Akaike information criterion (AIC) and Bayesian information criterion (BIC) comparing different models across different growth traits.

Trait	Model	Number of parameter	Log	AIC	BIC
Weight	Model I	5	4.795	0.77	8.459521
	Model II	5	4.340	1.96	9.369562
	Model III	5	4.556	0.88	8.937264
Length	Model I	5	3.223	3.90	11.60212
	Model II	5	3.981	2.68	10.08662
	Model III	5	2.065	5.87	13.91927
CF	Model I	5	3.107	4.44	11.83403
	Model II	5	3.565	3.51	10.91803
	Model III	5	3.446	3.11	10.89201

CF = condition factors.

### Genetic parameters

The genetic parameter of body weight estimated using the single-trait animal model showed moderate heritability estimates ranging from 0.2 to 0.45. The genetic parameter of body length was estimated using the 2-trait animal model and showed slightly higher heritability estimates ranging from 0.27 to 0.60. CF exhibited moderate heritability, with a value of 0.34, and the repeatability of CF, which was the breeding evaluation of individuals, was 0.35. The variance components and heritability on the observed scale for these three traits are shown in Table 4.

**Table 4.** Variance component and heritability for body weight, body length and condition factors (CF).

Traits	V <sub>A</sub>	V <sub>PE</sub>	V <sub>R</sub>	h <sup>2</sup>	Genetic model
Weight <sub>(1 year)</sub>	27.912	33.752	61.65	0.45 ± 0.03	Model I
Weight <sub>(1.5 year)</sub>	4770.85	6324.15	11094.66	0.41 ± 0.02	Model I
Weight <sub>(2 years)</sub>	5952.72	23454.8	29407.6	0.20 ± 0.05	Model I
Length <sub>(1 year)</sub>	196.262	127.13	323.399	0.60 ± 0.01	Model II
Length <sub>(1.5 year)</sub>	6437.05	4422.42	10859.4	0.54 ± 0.02	Model II
Length <sub>(2 years)</sub>	3.83	30.28	34.218	0.27 ± 0.04	Model II
CF	72.28	2.208	140.92	0.34 ± 0.02	Model III

### Phenotypic and genetic correlations

Phenotypic correlation among body weight, body length, and CF of 1-year-old fish was positive and high. This finding was similar to that of the genetic correlations. Phenotypic correlation among the growth traits of 1.5-year-old fish was close to 0, whereas body length and condition showed negative correlation. Estimation of genetic correlation was very similar to that of phenotypic correlation. The phenotypic and genetic correlations of body weight and body length in 2-year-old fish were moderate and positive. The phenotypic correlation between body weight, body length, and CF was low and negative, but the genetic correlation was high. The results are shown in Table 5.

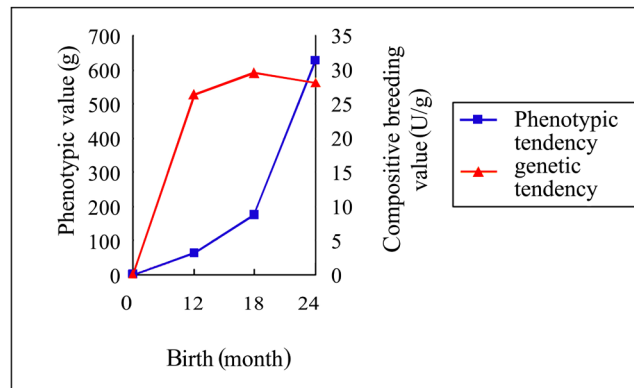
**Table 5.** Genetic correlations among growth traits in rainbow trout.

	Weight	Length	CF
Weight <sub>(1 year)</sub>	1	0.923	0.838
Length <sub>(1 year)</sub>	0.92	1	0.8794
CF <sub>(1 year)</sub>	0.90	0.917	1
Weight <sub>(1.5 year)</sub>	1	0.22	0.0646
Length <sub>(1.5 year)</sub>	0.53	1	-0.223
CF <sub>(1.5 year)</sub>	0.51	-0.43	1
Weight <sub>(2 years)</sub>	1	0.366	-0.026
Length <sub>(2 years)</sub>	0.31	1	-0.1337
CF <sub>(2 years)</sub>	-0.908	-1	1

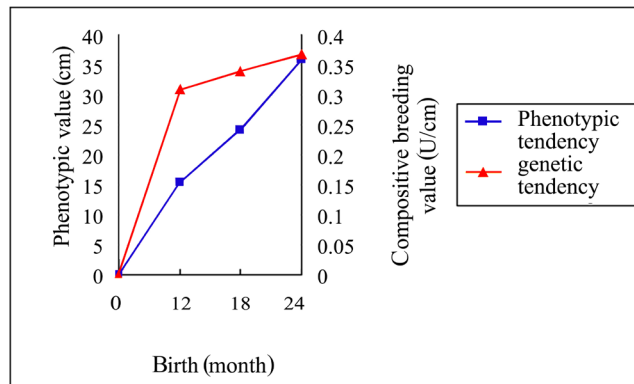
CF = condition factors.

### Phenotypic and genetic tendency of all traits

The annual phenotypic and genetic trends for body weight, body length, and CF are presented in Figures 1-3. Estimated phenotypic trends for all traits were relatively large ( $P < 0.05$ ) and favorable. However, for each growth trait, certain regions had large and undesirable phenotypic trends.

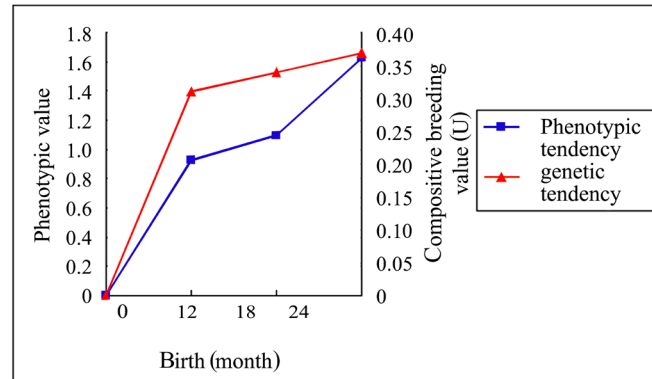


**Figure 1.** Phenotypic and genetic change tendency of body weight.



**Figure 2.** Phenotypic and genetic change tendency of body length.





**Figure 3.** Phenotypic and genetic change tendency of condition factors.

In contrast to the phenotypic trends, all of the estimated genetic trends in both data sets were relatively small and sometimes undesirable (see Figures 1-3). Although some of the trends were desirable and significant, the magnitude of the change over time was of limited practical importance.

## DISCUSSION

The genetic parameter of body weight estimated using the single-trait animal model showed moderate-to-high heritability estimates ranging from 0.2 to 0.45. The heritability estimates of body length ranged from 0.27 to 0.6. These results followed similar trends reported in other studies, which generally averaged 0.2-0.3 for Atlantic salmon aged 2-3 years (Gunnæs and Gjedrem, 1978; Gjerde and Refstie, 1984; McKay, 1986; Gjerde, 1988; Gjerde and Schaeffer, 1989; Rye and Gjerde, 1996). The heritability for CF estimated at 0.35 in the present study was similar or slightly higher than that of previous reports in rainbow trout ( $h^2 = 0.19-0.45$ ) (McKay, 1986; Kauser et al., 2002). Furthermore, bidirectional mass selection for the body height:body length ratio in common carp has resulted in a strong selection response after one generation of selection, with a realized heritability of 0.33-0.47 (Ankorion et al., 1992). The magnitude of the calculated values from the present study tended to be smaller than those found in other studies. Although the reasons for these differences are unknown, multiple grow-out sites with various environmental conditions leading to additional environmental variance may have caused lower than expected heritability estimates. However, such site differences should have been largely accounted for by site-fixed effects in the model. Moreover, regarding expected environmental effects, the estimates may also have been influenced by factors that could not be recorded during these experiments, including genetic differences among populations (Roff and Moousseau, 1987; Roff, 1997, 2000), genotype-by-environment interactions (Stearns, 1992), sample errors in family assignment, and stage of sexual maturation.

Genetic correlations among the growth traits were similar in both multiple-trait analyses. Elvingson and Nilsson (1994) found that the largest genetic and environmental correlations are obtained between body weight and body length at 1.5-2.5 years. These correlations decreased as differences in weight and length increased with age. The genetic correlations

between weight and CF were slightly negative to moderately positive at 2.5 years of age. These results were mostly in agreement with those of previous studies (McKay, 1986; Standal and Gjerde, 1987; Gjerde et al., 1994; Kause et al., 2002). Body weight, body length, and CF showed medium-to-high genetic correlation, in the range of 1.0-1.5 years indicating that exploiting the variation in early growth would be profitable if weight at 2.5 years were the trait of interest. However, late maturity is a desirable trait in many fish breeding programs (Gjerde, 1988; Crandell and Gall, 1993; Su et al., 1996). Although growth and age at maturity are interrelated, whether rapid growth induces maturation or maturation stimulates growth is unclear. We predict that strong selection for rapid growth advances the initiation of maturity as correlated with genetic change, which might further motivate fish breeders to select for late maturity. Although late maturity is genetically connected with slow growth, much variation accompanies this trend.

Significant positive direct trends for body weight and body length indicated effective selection for the improvement of these traits. The gains in body weight observed in the present study are similar to previously reported values (O'Flynn et al., 1999; Thodesen et al., 1999; Bolivar and Newkirk, 2002; Vandeputte et al., 2002). In a Finnish breeding program, genetic gains in weight ranged from 4.8 to 12.5% per generation. However, estimates of genetic progress showed that the trends for CF were not as well defined as those for performance traits because they were lower between 1.0 and 1.5 years. Thus, genetic trend estimates for the direct additive genetic values indicated that the currently used selection program has achieved favorable results.

In summary, our results elucidated the genetic parameters of growth traits in the breeding program for rainbow trout in China. Although they seemed to be the same as those for cultured rainbow trout in other countries, the results may be helpful in furthering the understanding of the genetic architecture of the phenotypic variation of growth traits in rainbow trout and may guide rainbow trout breeding practice in China.

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