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Genetic parameters estimation for growth traits in cultured tiger pufferfish (fugu), *Takifugu rubripes*

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Abstract

The aim of this study was to evaluate the genetic parameters of the growth performance of *Takifugu rubripes*. Heritabilities and genetic correlations were estimated for body weight (BW), body length (BL), total length (TL), chest measurement (CM) and trunk length (TKL) of *T. rubripes* from measurements of progeny at 6 months and 12 months. The results showed that the heritability was 0.37 for BW6, 0.19 for BL6, 0.35 for TL6, 0.29 for CM6, 0.26 for TKL6, 0.36 for BW12, 0.26 for BL12, 0.25 for TL12, 0.31 for CM12 and 0.15 for TKL12. The range of genetic correlations estimated at 6 months was 0.025–0.725 and –0.002–0.706 at 12 months. The results indicated that genetic improvement for faster growth rate or increased body weight in cultured *T. rubripes* was effective. Based on selection theory, the selection strategy for traits with medium heritability is flexible. Considering that these growth traits do not reach the high level of heritability, family selection should be expected. Given positive genetic correlations among BW, BL, TL, CM, and TKL at 6 months, the five traits could be improved simultaneously through selective breeding. As there was high genetic correlation only between BW12, BL12 and TL12, and negative correlations between TKL12 and BL12 as well as between CM12 and TL12, and only BW, BL and TL at 12 months could be improved simultaneously.

Key words: family, genetic evaluation, heritability, genetic correlation

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1 Introduction

Takifugu rubripes is a demersal species mainly distributed in Japan, the Korean Peninsula and the coastal areas of China in the western part of the North Pacific Ocean. *Takifugu rubripes* has high commercial value because its meat has a good flavor and is tender (Cui et al., 2006; Lin et al., 2020). Research on the breeding and cultivation of *T. rubripes* in China began in the early 1980s. Along with the technological breakthrough in the artificial breeding of this fish, by the mid-1990s, *T. rubripes* was beginning to be cultured on a large scale, and gradually became one of the main breeding species in the coastal areas of northern China. With the rapid development of the *T. rubripes* breeding industry, some problems impacting the development of the industry have emerged, including the lack of effective parent fish management and a reasonable breeding scheme. Declines in hatching rate, survival rate, growth rate and stress resistance pose serious problems for the industry (Ma et al., 2016). In order to ensure the healthy, stable and sustainable development of the *T. rubripes* culture industry, it is important to find effective methods to systematically select and breed new varieties with high quality, high yield and stress resistance (Li et al., 2013).

In order to carry out the genetic improvement of target traits, it is necessary to obtain accurate and reliable genetic parameters, which is the premise and foundation of breeding planning (Taylor et al., 2009; Fu et al., 2015; Sun et al., 2015; Liu et al., 2016; Ma et al., 2018; Wang and Ma, 2019; Wang et al., 2019). Heritability and genetic correlation are two of the most important genetic parameters in quantitative genetics (Ma et al., 2018; Wang et al., 2021). Heritability is a key quantitative index used to study the genetic essence of traits based on phenotypic variation. It plays an important role in the formulation of selection indices, prediction of selection response, comparison of selection methods and breeding planning decisions (Sun et al., 2015; Ma et al., 2018; Wang and Ma, 2019). Genetic correlation is another important basic genetic parameter, which can be used to describe the degree of correlation between different traits due to various genetic

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reasons. It plays an important role in determining the basis of indirect selection and predicting the response of indirect selection, comparing the selection effect under different environmental conditions, and formulating a comprehensive selection index (Sun et al., 2015; Ma et al., 2018; Wang and Ma, 2019).

In the current study, we used 2 400 and 2 011 individuals from 48 full-sib groups to evaluate the genetic parameters of body weight (BW), body length (BL), total length (TL), chest measurement (CM) and trunk length (TKL) at the age of 6 and 12 months. The purpose of this study is to estimate the genetic parameters of growth traits of *T. rubripes*, and discuss their potential impacts on the breeding planning of *T. rubripes*, so as to provide the basic parameters for formulating and optimizing the breeding planning of *T. rubripes*.

2 Materials and methods

2.1 *Broodstock and experimental families*

Takifugu rubripes used as broodstock were collected from three different cultured populations (China Dalian Tianzheng Industrial Company Limited cultured population, a population introduced from Japan in 2010 and a wild population caught in the Yellow Sea in 2009), and brought to China Yantai Tianyuan Aquatic Limited Corporation. The genetic background of the three populations can be found in the literature (Ma et al., 2016). In April 2012, individuals with mature gonads were selected from these three populations as parent fish. The selected parent fish reached sexual maturity at the same time after artificial cultivation and reproductive regulation. The broodstock of *T. rubripes* was induced by injection of luteinizing hormone releasing hormone A3 (LRH-A3) 250–300 g/kg + human chorionic gonadotrophin (hCG) 500 IU/kg (Ningbo hormone factory, Ningbo, China). The gonadal maturation of the broodstock was examined 24–48 h after induction. The abdomen of mature brood fish was obviously swollen. The female's genital pore is filled with blood and slightly valgus, while milky semen flows out of the male fish when their abdomen is squeezed slightly. After gonadal maturation, the abdomen of female fish was squeezed to collect mature eggs in a dry white porcelain basin. The abdomen of the male was then squeezed to collect mature sperm. The sperm and eggs were then mixed. The sperm was activated by adding an appropriate amount of seawater, and the eggs were washed after standing for 5 min, until the fertilized eggs no longer adhered to the basin wall. The fertilized eggs were incubated in a 60 mesh sieve silk cone hatching net with a diameter of 80 cm. All the cone hatching nets were placed in a 40 m^3 pond, with aeration and micro flow incubation. The incubation temperature was 18–19℃. Families were produced according to a nested mating design with two females nested within a male among 24 males and 48 females (8 males and 16 females in each population). First, eggs were obtained from two females and stored in two different beakers. Subsequently, the male fish were stripped and the milt was divided in two. Each portion was used to fertilize one of the two females. In total, 48 full-sib families (24 half-sib families) were obtained through artificial insemination.

2.2 *Larval and juvenile rearing*

The larvae were fed with enriched rotifers on the 4th day after hatching (DAH), and enriched rotifers and *Artemia nauplii* on the 15th DAH. Larvae were fed a small amount of surimi on the 28th DAH, and only surimi was fed on the 45th DAH. On the 60th DAH the families were transferred to a sea cage for cultivation. In the early stages of family cultivation, individuals were too small to carry out tagging identification and polyculture, so each family had to be cultivated in a separate pond. So the families were inevitably affected by environmental factors. In order to reduce the differences in environmental effects among different families, environmental condition standardization and quantity standardization methods were used during breeding. In order to eliminate the effect of stocking density on each family at different stages of development, four levels of standardized treatment were carried out in combination with the ecological habits and culture modes of *T. rubripes*. According to the specifications of the breeding pool and sea net cage in the seedling workshop of the experimental site, quantity standardization was as follows: In the first level of quantity standardization, the larvae were cultured in a 5 m^3 round cultivation tank. On the 15th DAH, 15 000 larvae were retained for further cultivation, and the surplus larvae were transferred to production for cultivation. For the second level of quantity standardization, on the 30th DAH, 8 000 juveniles with fast growth and good vitality were selected and cultured in a 36 m^3 cement pond (6 m×6 m×l m). In the third level quantity standardization, on the 60th DAH, 5 000 juveniles with fast growth and good vitality were selected and placed in a 125 m^3 cage (5 m×5 m×5 m) for intermediate cultivation. The fourth level of quantity standardization involved 2 000 juveniles with fast growth and good vitality being selected and placed in a 125 m^3 cage (5 m×5 m×5 m) for intermediate cultivation on the 120th DAH. Intermediate cultivation lasted for 60 days. When the fish were 6 months old, 50 individuals from each family were randomly selected and individually tagged with passive integrated transponders (for distinguishing families and individuals). Individuals tagged with passive integrated transponders were transferred to a 400 m^3 concrete tank (20 m×20 m×l m) for polyculture, for another 6 months. Any dead individuals were removed from the tank once a day. The breeding conditions of each family were consistently maintained from the hatching of fertilized eggs to larval rearing and tagging polyculture. According to different developmental stages, the families were placed in the same workshop for unified breeding management. During the larval-culture period, water temperature, salinity, illumination intensity, pH, ammonia nitrogen, nitrite-nitrogen, and dissolved oxygen were maintained at 15℃ to 22℃, 25 to 32, 500 lx to 1 000 lx, 7.8 to 8.3, ⩽1 mg/L, ⩽0.4 mg/L, and 5 mg/L to 10 mg/L, respectively. During the juvenile- and adolescent-culture period, the above seven indices were 22℃ to 24℃, 15 to 32, 500 lx to 1 000 lx, 7.8 to 8.3, ⩽1 mg/L, ⩽0.4 mg/L, and ⩾6 mg/L, respectively (Li et al., 2013). During the larval- and adolescent-culture period, the bait is minced trash fish and pellet feed, and the feeding amount is 0.7%–1.5% of the total weight of the fish. It is fed once or twice a day. The nutritional components of pellet feed include protein, lipids, vitamins, minerals and carbohydrates.

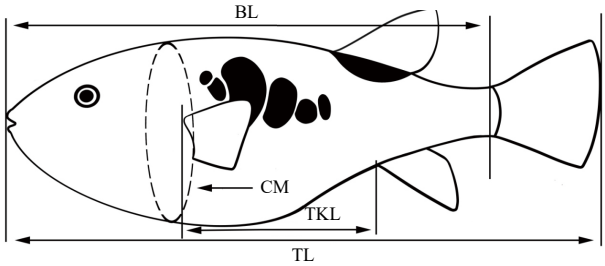

Fig. 1. Morphometric measurements of *Takifugu rubripes*. BL: body length; CM: chest measurement; TKL: trunk length; TL: total length.

2.3 *Data measurements*

Five growth traits, BW, BL, TL, CM, and TKL (Fig. 1), were evaluated at two growth stages. BL, TL and TKL of each *T. rubripes* were directly measured using Vernier calipers. With the help of the thin line, CM was indirectly measured using Vernier calipers. BW was obtained by weighing using a digital balance. Measurements were taken at 6 and 12 months. A total of 50 individuals were randomly sampled and measured in all 48 full-sib families at 6 months, and all individuals retained in the 48 families (some individuals died or escaped) were measured at 12 months. Prior to measurements, all individuals were anaesthetized with 100 μL/L MS222 (tricaine methane sulfonate) (Maya Reagent, Jiaxing, China).

2.4 *Statistical and genetic analysis*

The genetic parameters for BW, BL, TL, CM, and TKL were estimated using an animal model. The model can be written as

$$y_{ij} = \mu + a_i + f_j + e_{ij}, \tag{1}$$

where μ is the mean value of population; y_{ij} is the observation of each trait (BW, BL, TL, CM, and TKL); a_i is the random additive effect of individual i and is distributed $\sim N(0, \boldsymbol{A}\sigma_a^2)$, where $\boldsymbol{A}$ is the numerator relationship matrix; f_j is the full-sib family j as a random effect and e_{ij} is the random residual error of individual i. Heritability and genetic correlations were estimated using univariate animal model and bivariate animal model, respectively.

The narrow sense heritability was calculated as the proportion of additive genetic variance to total variance as follows:

$$h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_f^2 + \sigma_e^2), \tag{2}$$

where σ_a^2, σ_f^2 and σ_e^2 are additive variance components, the full-sib family variance component, and the residual variance component, respectively.

The phenotypic correlation and genetic correlation between the five growth traits were calculated based on phenotype value and breeding value.

Phenotypic correlation (r_p) can be written:

$$r_p = \mathrm{cov}(p_x, p_y)/\sqrt{\sigma_{p_x}^2 \cdot \sigma_{p_y}^2}. \tag{3}$$

Genetic correlation (r_g) can be written:

$$r_g = \mathrm{cov}(a_x, a_y)/\sqrt{\sigma_{a_x}^2 \cdot \sigma_{a_y}^2}, \tag{4}$$

where, p_x and p_y are the measurement results of x- and y- growth traits and cov(p_x, p_y) is covariance of p_x and p_y; a_x, a_y are additive genetic effects of x- and y- growth traits, and cov(a_x, a_y) is covariance of a_x and a_y.

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. Correlations could be classified as low (0–0.40), medium (0.45–0.55) and high (0.60–1), independent of the sign (Cardellino and Rovira, 1987). When p<0.05 or p<0.01, the correlation reached significant or highly significant level.

Variance components, heritabilities and genetic correlations for BW, BL, TL, CM, and TKL were estimated using derivative-free restricted maximum likelihood estimation as implemented in the MTDFREML package (Boldman et al., 1995). The phenotypic correlations among BW, BL, TL, CM, and TKL were estimated as Pearson's correlations using the SPSS 13.0 software package (Norušis, 2005). The t test was used to test the significance level of each correlation coefficient from zero. Before analysis, all data were checked for outliers using box plots.

3 Results

3.1 *Descriptive statistics of growth traits*

Five growth traits at two growth stages were included in these analyses: 6-month body weight (BW6), 6-month body length (BL6), 6-month total length (TL6), 6-month chest measurement (CM6), 6-month trunk length (TKL6), 12-month body weight (BW12), 12-month body length (BL12), 12-month total length (TL12), 12-month chest measurement (CM12) and 12-month trunk length (TKL12). The growth trait distributions are shown in Table 1. The coefficient of variation (CV) of the four growth traits was generally high at over 10%, with up to 19.238% and 17.649% for BW6 and BW12, respectively. The genetic diversity of BW was the highest. CV decreased gradually with the growth of juveniles. On the whole, the growth tendency of the 48 full-sib families remained the same at the 6-month and the 12-month stages (Figs 2–6).

3.2 *Heritabilities of growth traits*

Estimates of the variance component and the heritability of five growth traits are presented in Table 2. It was found that heritability was 0.37 for BW6, 0.19 for BL6, 0.35 for TL6, 0.29 for CM6, 0.26 for TKL6, 0.36 for BW12, 0.26 for BL12, 0.25 for TL12, 0.31 for CM12 and 0.15 for TKL12. The heritabilities of the other traits were moderate, except for BL6 and TKL12.

3.3 *Phenotypic and genetic correlations of growth traits*

Phenotypic and genetic correlations for all growth traits of 6-

Table 1. Descriptive statistics for all the variables included in the analysis

Trait	Number of *Takifugu rubripes*	Mean trait value	Standard deviation	Coefficient of variation/%	Minimum trait value	Maximum trait value
BW6	2 400	167.474 g	32.220 g	19.238	93.500 g	216.700 g
BL6	2 400	16.069 cm	1.144 cm	8.986	14.600 cm	19.200 cm
TL6	2 400	19.925 cm	1.176 cm	5.902	17.000 cm	21.300 cm
CM6	2 400	14.481 cm	1.408 cm	9.723	11.000 cm	16.200 cm
TKL6	2 400	5.908 cm	0.772 cm	13.067	5.000 cm	7.000 cm
BW12	2 011	353.379 g	62.369 g	17.649	176.000 g	513.700 g
BL12	2 011	20.625 cm	1.235 cm	5.987	17.900 cm	24.300 cm
TL12	2 011	23.957 cm	1.354 cm	5.651	19.600 cm	27.000 cm
CM12	2 011	19.479 cm	1.554 cm	7.977	18.000 cm	22.600 cm
TKL12	2 011	7.002 cm	0.783 cm	11.182	6.000 cm	8.800 cm

Note: BW, body weight; BL, body length; TL, total length; CM, chest measurement; TKL, trunk length.

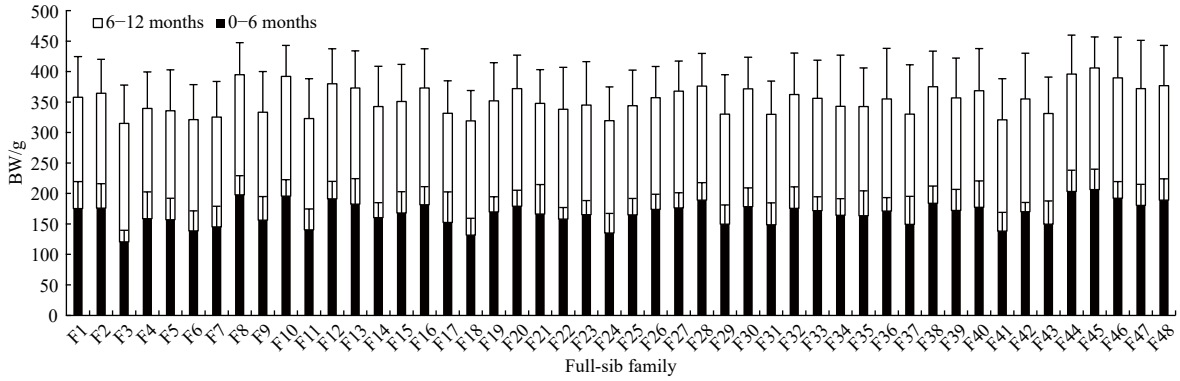

Fig. 2. Forty eight full-sib families' growth tendency in terms of body weight (BW) in the 0–12-month stage.

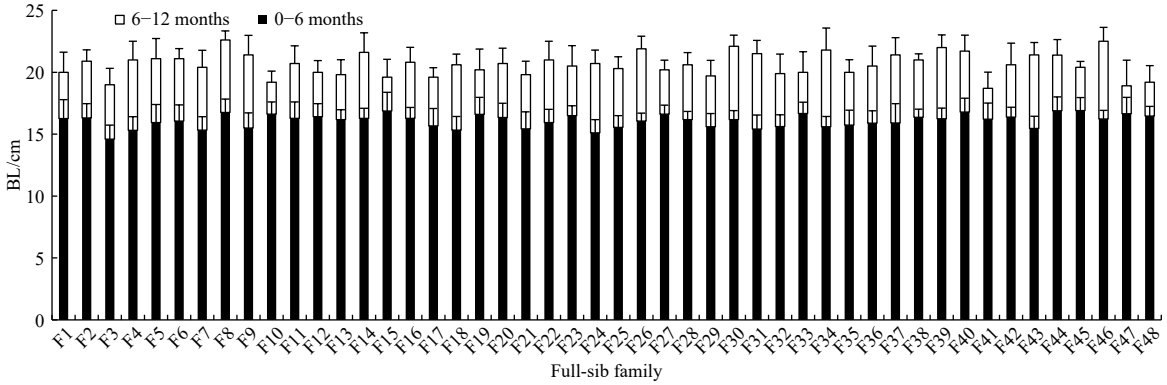

Fig. 3. Forty eight full-sib families' growth tendency in terms of body length (BL) in the 0–12-month stage.

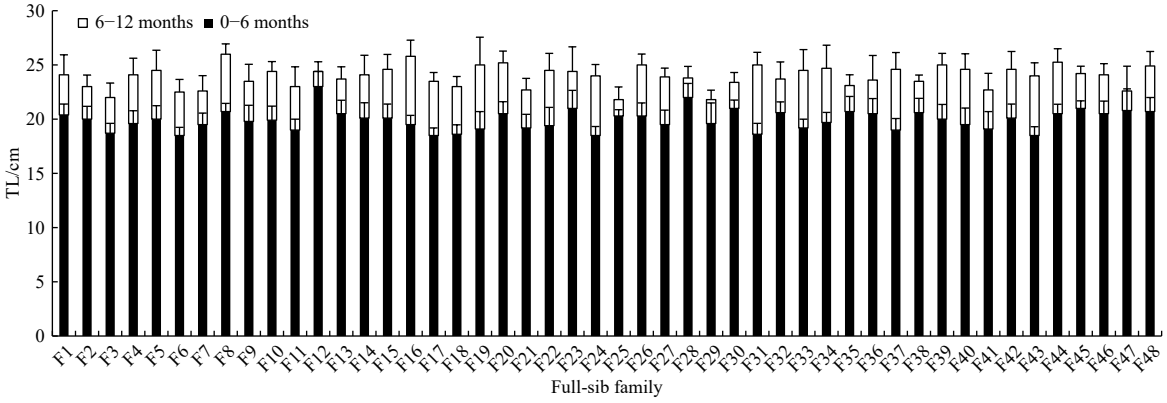

Fig. 4. Forty eight full-sib families' growth tendency in terms of total length (TL) in the 0–12-month stage.

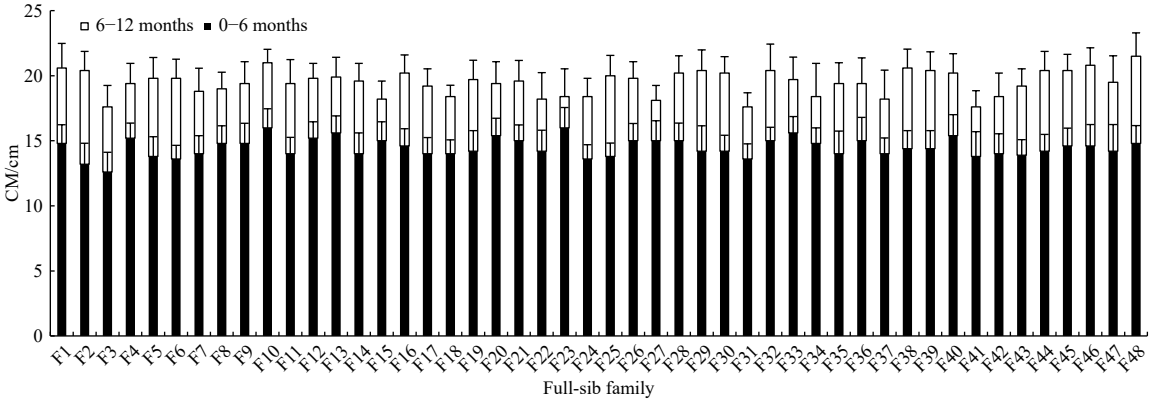

Fig. 5. Forty eight full-sib families' growth tendency in terms of chest measurement (CM) in the 0–12-month stage.

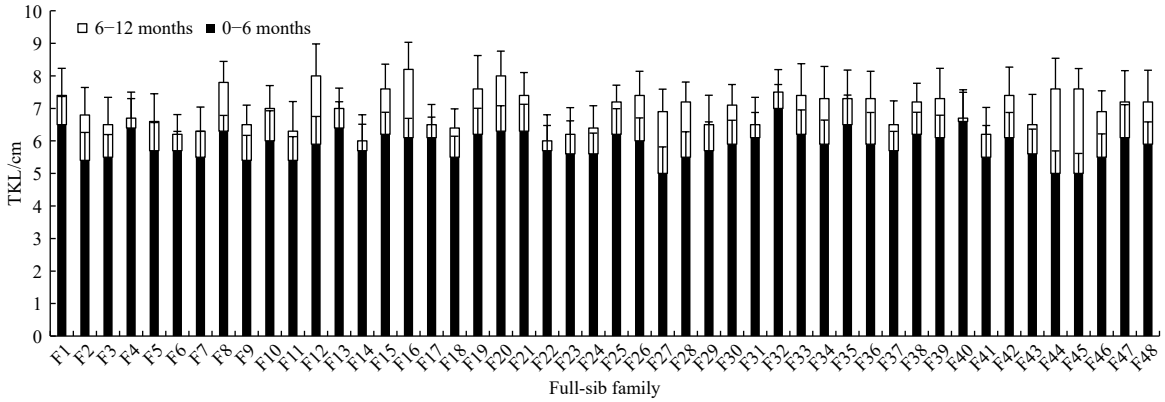

Fig. 6. Forty eight full-sib families' growth tendency in terms of trunk length (TKL) in the 0–12-month stage.

Table 2. Variance components and heritability (h^2) of five growth traits in *Takifugu rubripes*

Growth traits	Variance components			
	σ_a^2	σ_f^2	σ_e^2	h^2
BW6	265.967 9 g	360.891 0 g	95.155 0 g	0.37±0.040
BL6	0.102 2 cm	0.265 6 cm	0.172 8 cm	0.19±0.023
TL6	0.580 6 cm	0.820 8 cm	0.274 0 cm	0.35±0.037
CM6	0.288 1 cm	0.487 0 cm	0.216 9 cm	0.29±0.032
TKL6	0.092 0 cm	0.170 5 cm	0.092 1 cm	0.26±0.026
BW12	345.567 4 g	524.396 0 g	96.666 0 g	0.36±0.041
BL12	0.413 9 cm	0.824 89 cm	0.341 9 cm	0.26±0.031
TL12	0.485 7 cm	0.959 3 cm	0.535 0 cm	0.25±0.025
CM12	0.519 0 cm	0.869 2 cm	0.311 0 cm	0.31±0.034
TKL12	0.093 1 cm	0.305 8 cm	0.242 8 cm	0.15±0.020

Note: BW6, 6-month body weight; BL6, 6-month body length; TL6, 6-month total length; CM6, 6-month chest measurement; TKL6, 6-month trunk length; BW12, 12-month body weight; BL12, 12-month body length; TL12, 12-month total length; CM12, 12-month chest measurement; TKL12, 12-month trunk length; σ_a^2, additive genetic variance; σ_f^2, full-sib variance; σ_e^2, residual variance; h^2, heritability.

Table 3. Phenotypic (r_p) (above the diagonal) and genetic (under the diagonal) correlations (r_g) of growth traits in 6-month-old *Takifugu rubripes*

Trait	BW6	BL6	TL6	CM6	TKL6
BW6		0.727**	0.727**	0.580**	0.155**
BL6	0.725**		0.454**	0.461**	0.010
TL6	0.721**	0.445**		0.438**	0.105**
CM6	0.578**	0.464**	0.420**		0.344**
TKL6	0.146**	0.025	0.074**	0.357**	

Note: BW6, 6-month body weight; BL6, 6-month body length; TL6, 6-month total length; CM6, 6-month chest measurement; TKL6, 6-month trunk length. ** Correlation is significant at the 0.01 level (2-tailed).

and 12- month old *T. rubripes* are shown in Tables 3 and 4. The ranges of phenotypic and genetic correlations estimated for the traits at 6 months were 0.010–0.727 and 0.025–0.725, respectively. The phenotypic correlation between BW6 and BL6 (0.727), and the genetic correlation between BW6 and BL6 (0.725) were the strongest. The ranges of phenotypic and genetic correlations estimated for traits at 12 months were 0.001–0.697 and –0.002–0.706, respectively. The phenotypic correlation between BW12 and TKL12 (0.697) as well as the genetic correlation between BW12 and TKL12 (0.706) were the strongest.

Table 4. Phenotypic (r_p) (above the diagonal) and genetic (under the diagonal) correlations (r_g) of growth traits in 12-month-old *Takifugu rubripes*

Trait	BW12	BL12	TL12	CM12	TKL12
BW12		0.145**	0.482**	0.581**	0.697**
BL12	0.146**		0.462**	0.075**	0.001
TL12	0.495**	0.466**		0.026	0.453**
CM12	0.547**	0.072**	–0.020		0.376**
TKL12	0.706**	–0.002	0.453**	0.373**	

Note: BW12, 12-month body weight; BL12, 12-month body length; TL12, 12-month total length; CM12, 12-month chest measurement; TKL12, 12-month trunk length. ** Correlation is significant at the 0.01 level (2-tailed).

4 Discussion

In recent years, the genetic improvement of the main economic traits of *T. rubripes* in China has led to the estimation of genetic parameters of breeding traits of *T. rubripes* being estimated using AI-REML (Liu et al., 2014, 2017) and ANOVA (Yu et al., 2016). The results showed that the heritability of 6-month old individuals was 0.54 for BW, 0.38 for BL, and 0.52 for TL. The heritability of 12-month old fish was 0.46 for BW, 0.37 for BL, and 0.44 for TL (Yu et al., 2016). There was a genetic correlation of 0.99 between BW and BL, 0.99 between BW and TL, and 0.98 between BL and TL at 6 months of age. In 12-month old fish, the genetic correlation was found to be 0.97 between BW and BL, 0.97 between BW and TL, and 0.96 between BL and TL (Yu et al., 2016). Heritabilities of BW and BL of *T. rubripes* have been estimated using AI-REML with three different animal models (in model 1 the additive genetic effect, the maternal genetic effect and the family effect were considered; in model 2 the additive genetic effect and the maternal genetic effect were included; and in model 3 the additive genetic effect and the family effect were analyzed). The results showed that the estimated heritabilities for BW and the BL at 200 days were 0.16 and 0.14, respectively (Liu et al., 2014). Heritabilities of BW and BL of *T. rubripes* have been estimated using a marker-based pedigree animal model. The results showed that the estimated heritabilities for BW and the BL at 150 days were 0.17 and 0.15, respectively, and 0.21 and 0.18 at 240 days (Liu et al., 2017).

In present study, heritabilities of BW, BL, TL, CM, and TKL in 6- and 12-month old *T. rubripes*, as well as the genetic correlations among them were estimated using the derivative-free restricted maximum likelihood method applied to an animal model. The estimated heritabilities for growth traits of *T. rubripes* in the present study were lower than those reported by Yu et al.

(2016), but higher than those reported by Liu et al. (2014, 2017). In addition, the estimated genetic correlation of growth traits was also lower than that estimated by Yu et al. (2016). In addition to the different analysis methods used, these differences were also attributed to the intraspecific differences, sample size, number of families and sample time. Heritability is one of the main bases to determine the selection method of traits. It is widely accepted that a trait with medium and high heritability (h^2>0.2) is suitable for individual or group phenotypic selection, whereas a trait with low heritability (h^2<0.2) is suitable for family selection or within-family selection (Sun et al., 2015). In the present study, the heritabilities of the other traits were moderate, except for BL6 and CM12. Therefore, the method of genetic improvement for these growth traits is flexible. In selective breeding, some traits can obtain satisfactory breeding results through direct selection, while it is difficult to obtain ideal breeding results for some traits through direct selection. Then, indirect selection will be used through the selection of traits with higher correlations with these traits (Sun et al., 2015). Heritable traits usually include morphological, behavioral, physiological and life-history traits. For most morphological/production traits, genetic correlations tend to be highly positive (Perry et al., 2005). In fact, in the field of aquatic animals, there are many reports of positive genetic correlation between economic traits of different species (Liu et al., 2011; Wang et al., 2011; Fu et al., 2015; Sun et al., 2015; Yu et al., 2016; Ma et al., 2018; Srimai et al., 2019; Wang and Ma, 2020). At 6 and 12 months, with the exception of two negative genetic correlations between TKL12 and BL12 as well as between CM12 and TL12, the phenotypic correlations and genetic correlations among the other traits were positive. The results of the current study are consistent with this conclusion.

In conclusion, the results of this study indicate that genetic improvement is effective in improving the growth rate or weight gain of *T. rubripes*, as can be expected from moderate heritabilities. The selection strategy for the traits with medium heritability is flexible. However, these growth traits have not yet reached high heritability level. Based on this consideration, family selection should be an ideal method. At 6 and 12 months, with the exception of two negative genetic correlations between TKL12 and BL12 as well as between CM12 and TL12, the phenotypic correlations and genetic correlations among the other traits were positive. There were positive genetic correlations among BW, BL, TL, CM, and TKL at 6 months, which indicated that collecting data on one trait could promote the evaluation of other traits. Therefore, the five traits can be improved simultaneously by selective breeding. However, at 12 months, only BW12, BL12 and TL12 could be improved simultaneously because of the negative correlations between TKL12 and BL12 as well as between CM12 and TL12.

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References

Boldman K G, Kriese L A, Van Vleck L D, et al. 1995. A manual for use of MTDFREML—A set of programs to obtain estimates of variances and covariances (draft). Clay Center: U. S. Department of Agriculture-Agricultural Research Service

Cardellino R, Rovira J. 1987. Mejoramiento Genético Animal (in Spanish). Buenos Aires: Hemisferio Sur, 253

Cui Jianzhou, Shen Xueyan, Gong Qingli, et al. 2006. Identification of sex markers by cDNA-AFLP in *Takifugu rubripes*. Aquaculture, 257(1–4): 30–36, doi: 10.1016/j.aquaculture.2006.03.003

Fu Jianjun, Shen Yubang, Xu Xiaoyan, et al. 2015. Genetic parameter estimates and genotype by environment interaction analyses for early growth traits in grass carp (*Ctenopharyngodon idella*). Aquaculture International, 23(6): 1427–1441, doi: 10.1007/s10499-015-9894-7

Li Weiye, Ma Aijun, Wang Xin'an, et al. 2013. The study of *Takifugu rubripes* breeding family establishment and the early standardized cultivation technique. Oceanologia et Limnologia Sinica, 44(4): 944–952

Lin Zijie, Hosoya S, Sato M, et al. 2020. Genomic selection for heterobothriosis resistance concurrent with body size in the tiger pufferfish, *Takifugu rubripes*. Scientific Reports, 10(1): 19976, doi: 10.1038/s41598-020-77069-z

Liu Feng, Li Yangzhen, Wang Xiaoxia, et al. 2016. Estimation of genetic parameters for disease-resistance traits in *Cynoglossus semilaevis* (Günther, 1873). Journal of Applied Ichthyology, 32(4): 643–651, doi: 10.1111/jai.13067

Liu Xiande, Sui Banliang, Wang Zhiyong, et al. 2011. Estimated reproductive success of brooders and heritability of growth traits for large yellow croaker (*Larimichthys crocea*) using microsatellites. Chinese Journal of Oceanology and Limnology, 29(5): 990–995, doi: 10.1007/s00343-011-0266-5

Liu Yongxin, Zhou Qin, Zhang Hongtao, et al. 2014. Estimation of genetic parameters of growth traits of redfin puffer (*Takifugu rubripes*). Progress in Fishery Sciences, 35(6): 39–44, doi: 10.11758/yykxjz.20140606

Liu Yongxin, Zhou Qin, Zhang Hongtao, et al. 2017. Genetic analysis of redfin puffer (*Takifugu rubripes*) for growth traits by using a marker-based pedigree. Journal of Fisheries of China, 41(1): 21–30, doi: 10.11964/jfc.20160210282

Ma Aijun, Wang Xin'an, Huang Zhihui, et al. 2018. Estimation of genetic parameters for upper thermal tolerance and growth-related traits in turbot *Scophthalmus maximus* using the Bayesian method based on Gibbs sampling. Acta Oceanologica Sinica, 37(6): 40–46, doi: 10.1007/s13131-018-1185-5

Ma Aijun, Wang Xin'an, Sun Zhibin, et al. 2016. Morphological variations among three different populations of *Takifugu rubripes*. Oceanologia et Limnologia Sinica, 47(1): 166–172, doi: 10.11693/hyhz20150300083

Norušis M J. 2005. SPSS 13.0 Guide to Data Analysis. Upper Saddle River: Prentice Hall

Perry G M L, Martyniuk C M, Ferguson M M, et al. 2005. Genetic parameters for upper thermal tolerance and growth-related traits in rainbow trout (*Oncorhynchus mykiss*). Aquaculture, 250(1–2): 120–128, doi: 10.1016/j.aquaculture.2005.04.042

Srimai W, Koonawootrittriron S, Manee-Aphai W, et al. 2019. Genetic parameters and genotype-environment interaction for growth traits of North African catfish, *Clarias gariepinus* (Burchell, 1822). Aquaculture, 501: 104–110, doi: 10.1016/j.aquaculture.2018.10.064

Sun Miaomiao, Huang Jianhua, Jiang Shigui, et al. 2015. Estimates of heritability and genetic correlations for growth-related traits in the tiger prawn *Penaeus monodon*. Aquaculture Research, 46(6): 1363–1368, doi: 10.1111/are.12290

Taylor R S, Kube P D, Muller W J, et al. 2009. Genetic variation of gross gill pathology and survival of Atlantic salmon (*Salmo salar* L.) during natural amoebic gill disease challenge. Aquaculture, 294(3–4): 172–179, doi: 10.1016/j.aquaculture.2009.06.007

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, doi: 10.1111/j.1365-2109.2010.02617.x

Wang Xin'an, Ma Aijin. 2019. Genetic parameters for resistance against *Vibrio anguillarum* in turbot *Scophthalmus maximus*. Journal of Fish Diseases, 42(5): 713–720, doi: 10.1111/jfd.12973

Wang Xin'an, Ma Aijun. 2020. Dynamic genetic analysis for body weight and main length ratio in turbot *Scophthalmus maximus*. Acta Oceanologica Sinica, 39(2): 22–27, doi: 10.1007/s13131-020-1551-y

Wang Xin'an, Ma Aijun, Huang Zhihui, et al. 2019. Estimation of genetic parameters for upper thermal tolerances and growth-related traits in turbot *Scophthalmus maximus*. Journal of Oceanology and Limnology, 37(5): 1736–1745, doi: 10.1007/s00343-019-7267-1

Wang Xin'an, Ma Aijun, Sun Zhibin. 2021. Genetic parameters of seven immune factors in turbot (*Scophthalmus maximus*) infected with *Vibrio anguillarum*. Journal of Fish Diseases, 44(3): 263–271, doi: 10.1111/jfd.13320

Yu Hailong, Gu Chenlei, Kong Derong, et al. 2016. Heritability estimating and correlativity of growth traits in redfin puffer *Takifugu rubripes*. Journal of Dalian Ocean University, 31(4): 357–361, doi: 10.16535/j.cnki.dlhyxb.2016.04.002