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Dynamic genetic analysis for body weight and main length ratio in turbot *Scophthalmus maximus*

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Abstract

The objective of this study was to estimate genetic parameters of body width (BW) to body length (BL) ratio (BW/BL) and of body weight traits (BWT) in turbot, and to elucidate the genetic mechanism of the two traits during ontogeny by dynamic genetic analysis. From 3 to 27 months, BW, BL and BWT of each communally stocked fish were measured every 3 months. The BW/BL ratio was measured at different sampling ages. A two-trait animal model was used for genetic evaluation of traits. The results showed that the heritability values of BW/BL ratio ranged from 0.216 8 to 0.314 8, corresponding to moderate heritability. The BWT heritability values ranged from 0.270 2 to 0.347 9 corresponding to moderate heritability. The heritability of BW/BL ratio was lower than that of BWT, except at 3 months of age. Genetic correlation between BW/BL ratio and BWT decreased throughout the measurement period. Genetic correlations were higher than the phenotypic correlations. The current results for estimating genetic parameters demonstrate that the BW/BL ratio could be used as a phenotypic marker of fast-growing turbot, and the BW/BL ratio and BWT could be improved simultaneously through selective breeding.

Key words: turbot, dynamic genetic analysis, body weight, main length ratio, heritability, genetic correlation

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1 Introduction

Turbot (*Scophthalmus maximus* L.) is one of the most economically important flatfish species for aquaculture in the world. *Scophthalmus maximus* is widely distributed throughout the Baltic Sea, the Black Sea, and the Mediterranean Sea. *Scophthalmus maximus* has various advantages such as resistance to low temperatures, fast growth, polytrophy, and a unique taste (Zhang et al., 2014; Wang et al., 2015; Wang and Ma, 2016). Turbot was first introduced into China in 1992 (Wang et al., 2010; Ruan et al., 2011; Wang et al., 2015). The production of cultured turbot in China has been rapidly increasing due to a technological breakthrough in large-scale artificial breeding that occurred in 1999 (Ma et al., 2006; Wang et al., 2015). According to the literature, in the main production areas of turbot in China, the annual production of *S. maximus* ranged from 51 931.79 to 66 220.3 metric tonnes during 2009 to 2015 (Lei, 2010, 2012, 2013, 2014, 2015; National Technology Research and Development Center for Flounder Industry, 2011; Guan, 2016). Today, *S. maximus* is a commercially important fish, especially in North China (Wang et al., 2010). In China, turbot was originally imported from Europe. The number of parent fish was relatively small, and due to the lack of long-term and effective broodstock management programs, germplasm degenerated significantly (Wang et al., 2015). To promote a sustained development of the turbot industry for the Chinese aquaculture market, the Yellow Sea Fisheries Research Institute of the Chinese Academy of Fishery Sciences has carried out a turbot breeding program, which has made significant progress in achieving faster growth rates since 2006. A fast-growing strain was obtained by one generation of mass selection and three generations of family selection.

Within an aquaculture breeding program, breeding index should be readily observed or measured. Therefore, phenotypic markers can be used as breeding indicators for fast-growing traits when weight measurements are inconvenient, or when the difference between the true weight value and the measured value is large. In addition, phenotypic markers are also of great significance for farmers in the process of production, because they can also select fast-growing individuals in a simple and fast way, even without guidance of researchers. Studies on the dynamic changes of body shape during growth and development of turbot have shown that the ratio of body width/body length (BW/BL ratio) (Fig. 1) increased with age, indicating that the body of turbot changed from a narrow to a more rounded shape (Wang and Ma, 2015). Such rounded shape is not only considered more aesthet-

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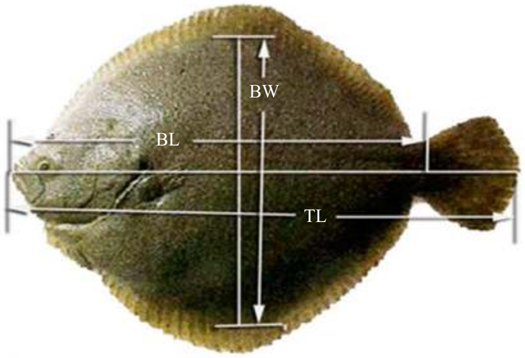

Fig. 1. Morphometric characteristics measured in turbot. BL represents body length, TL total length, and BW body width excluding dorsal and pelvic fins.

ic, but is also perceived as having a greater amount of edible flesh, which influences market preference. Phenotypic correlation analysis between BW/BL ratio and body weight showed highly significant positive correlation coefficients during 3 to 27 months of age (Wang and Ma, 2015). On the basis of this analysis, turbot BW/BL ratio could be considered as a phenotypic marker during selective breeding for body weight. Deep genetic analysis for BW/BL ratio, and for the corresponding growth traits, would be of great theoretical and practical significance to carry out selective breeding.

Length ratios associated with morphological traits are quantitative in nature. From the point of view of classical quantitative genetics, the additive effects of these ratios are inheritable, according to subjective categorical scoring or to digital image analysis (Kirkpatrick et al., 1989; Kirkpatrick et al., 1990; Blonk et al., 2010; Schaeffer, 2004; Shimada et al., 2007; Liu et al., 2014). Therefore, genetic evaluation of length ratio traits can be carried out using animal models with different fixed and random effects (Liu et al., 2014). In the present study we estimated heritability of the BW/BL ratio during different periods (3 to 27 months), and estimated genetic correlations between BW/BL ratio and body weight, using the two-traits animal model AIREML, using ASReml-R software (Gilmour et al., 2009). The objective of this study was to elucidate the genetic mechanism of BW/BL ratio and of BWT in turbot during ontogeny by dynamic genetic analysis. These genetic parameters would provide the most direct theoretical basis for using the BW/BL ratio as phenotypic marker of fast-growing turbot.

2 Materials and methods

2.1 *Production of S. maximus families and rearing*

The data used in this paper were derived from 54 F_2 full-sib families created in 2010 by the Yellow Sea Fisheries Research Institute of the Chinese Academy of Fishery Science. The dynamic genetic analysis of body weight and main length ratio was carried out using 54 full-sib families. These families were produced using a nested mating design, depending on the availability of well-liking breeders in Yantai Tianyuan Aquatic Limited Corporation. The artificial fertilization method was used to obtain eggs and sperm from breeders injected with Ovaprim (Battaglene, 1996). 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. After fertilization, individual full-sib families were incubated at 13–14°C in separate rectangular incubation net cages (80 cm×60 cm×60 cm). After ~110 h in the incubation net cages, spawn from individual full-sib families was collected and stocked in separate concrete tanks (3 m×1 m×1.5 m). To obtain similar feeding conditions, the stocking density of fish and the environmental variables were maintained at standard conditions, during the early breeding stage of all families. At the 15, 30 and 45 days after hatching, the quantity of fish in each family was normalized by randomly sampling 10 000, 5 000 and 2 000 individuals, respectively. At the 60 days after hatching, random samples of 1 000 young fish from each full-sib family were transferred to separate 12 m^3 concrete tanks. At 3 months of age, 250–300 individuals were selected randomly from each family for tagging, using a visible implant elastomer (four different tags and combinations were used to distinguish different families). Fish were then transferred to a 650 m^3 concrete tank with air-pumped circulating seawater for polyculture. When individuals tagged with the visible implant elastomer were 9 months of age, random samples of 50–60 individuals from each family were individually tagged again with passive integrated transponders (for distinguishing families and individuals). Individuals tagged with passive integrated transponders were transferred to a 200 m^3 concrete tank for polyculture, until they reached 18 months of age. From 18 to 27 months, individuals tagged with passive integrated transponders were reared in two 400 m^3 concrete tanks. Dead individuals were removed from the tank once a day. The environmental conditions were standardized during the larval and juvenile culture period at: water temperature 13–18°C, salinity 30–40, illumination intensity 500–2 000 lx, pH 7.8–8.2, and dissolved oxygen >6 mg/L. During the period 3 to 27 months, the above five indices were 15–18°C, 25–30, 500–1 500 lx, pH 7.6–8.2 and >6 mg/L, respectively.

2.2 *Data collection and analysis*

From 3 to 27 months of age, the BW, BL and body weight (BWT) of fish were measured every three months. Each data collection was synchronous with moving ponds. A total of 50–60 individuals from each family were collected randomly at 3 and 6 months of age, and all fish tagged with passive integrated transponders were collected from 9 to 27 months of age (months of age are counted from hatching). BWT was measured using a 0.01 g precision electronic balance, and BL was measured using a Vernier caliper to the nearest 0.01 cm. The BW/BL ratio was calculated at different sampling ages. The descriptive statistics for BW/BL ratio and BWT at different growth periods are shown in Table 1.

For BW/BL ratio and BWT traits, variance components, heritability, and genetic correlations with standard errors, were estim-

Table 1. Ratio of body width/body length (BW/BL ratio), and mean body weight (BWT) for each family of turbot at different sampling ages (mean±standard deviation)

Months of age	BW/BL ratio	BWT/g
3	0.605 6±0.022 9	2.979 1±0.916 2
6	0.784 4±0.025 0	31.125 0±9.181 8
9	0.786 1±0.024 2	164.718 8±21.533 3
12	0.813 0±0.034 5	376.412 0±47.118 2
15	0.795 4±0.0314	593.113 1±76.325 6
18	0.827 9±0.0572	2 996.683 4±107.853 4
24	0.819 3±0.048 9	1 776.437 8±183.442 1
27	0.856 7±0.332 1	2 031.383 2±279.890 1

ated using the two-trait animal model AIREML, using ASReml-R software (Gilmour et al., 2009). The model can be written as:

$$y_{ij} = u + a_i + f_j + e_{ij},$$

where u is the population mean, y_{ij} is the measured value of BW/BL and BWT, a_i is the additive genetic effect of individual as a random effect, f_j is the full-sib family random effect, e_{ij} is the random residual. In matrix notation the model can be written:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Zu} + \boldsymbol{e},$$

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 assigned to the observations to levels of $\boldsymbol{b}$ and $\boldsymbol{u}$, respectively. The mathematical expectation and variance were defined as:

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

where $\boldsymbol{G}_0$ is the genetic variance-covariance matrix of BW/BL ratio and BWT, $\boldsymbol{R}_0$ is the residual variance-covariance matrix of the two traits, $\otimes$ is the Kronecker product defined by $Var(\boldsymbol{y}) = \boldsymbol{ZAZ}'\sigma_a^2 + \boldsymbol{I}\sigma_e^2$, $\boldsymbol{A}$ is the additive genetic relationship matrix, $\boldsymbol{I}$ is an identity matrix, σ_a^2 is additive genetic variance, and σ_e^2 is residual variance.

The equations of the two-trait animal model are:

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

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

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

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

where σ_p^2 is phenotype variance, a_x and a_y are additive genetic effects of x- and y-traits, and cov(a_x, a_y) is covariance of a_x and a_y. Before statistical analysis, outliers were checked using box plots and the normality of data was assessed using the Shapiro–Wilk test.

3 Results

3.1 *Descriptive statistics of BW/BL ratio and BWT*

All data sets were confirmed to be normally distributed by passing the Shapiro–Wilk normality test. The descriptive statistics for BW/BL ratio and BWT are presented in Table 1. During the period of 3 to 27 months of age, the values of BW/BL ratio ranged from 0.605 6 to 0.856 7, and the BWT value from 2.979 1 to 2 031.383 2 g. In general, the BW/BL ratio increased with body weight, except at 15 and 24 months when it decreased slightly.

3.2 *Genetic evaluation for BW/BL ratio and BWT*

The results of genetic evaluation for BW/BL ratio of turbot at different sampling ages are shown in Table 2. From 3 to 27 months of age, the ranges of variance components (σ_a^2, σ_f^2 and σ_e^2) were 0.122 9–27.350 8, 0.083 4–0.130 0 and 0.213 7–47.807 3, respectively. Both σ_a^2 and σ_e^2 raised throughout the measurement period, whereas σ_f^2 did not change significantly in a specific direction. The heritability values of BW/BL ratio ranged from 0.216 8 to 0.314 8, corresponding to moderate heritability. Heritability did not change significantly in a specific direction either.

The results of genetic evaluation for BWT of turbot at different sampling ages are shown in Table 3. From 3 to 27 months, the ranges of variance components (σ_a^2, σ_f^2 and σ_e^2) were 0.101 5–49 368.553 2, 0.126 6–0.240 6 and 0.050 7–113 783.300 1, respectively. The BWT heritability values ranged from 0.270 2 to 0.347 9, corresponding to moderate heritability. Similarly to the BW/BL ratio, both $\sigma_a^2$and σ_e^2 raised throughout the measurement period; neither σ_f^2 or h^2 changed significantly in a specific direction.

Genetic and phenotypic correlations between BW/BL ratio and BWT are shown in Table 4. At different sampling ages, the ranges of genetic and phenotypic correlations were 0.437 8–0.821 3 and 0.336 1–0.638 3, respectively. All genetic and phenotypic correlation coefficients were significantly different from zero at the 1% level. Genetic correlations had only two medium correlations (24 and 27 months of age) and the others belonged to high correlations (from 3 to 18 months of age), and phenotypic correlations had three low correlations (12, 24 and 27 months of age), five medium correlations (3, 6, 9 and 15 months of age) and one high correlation (18 months of age). In general, genetic

Table 2. Variance components and heritability (h^2) with standard errors (mean±SE) of BW/BL ratio of turbot at different sampling ages

Months of age	σ_a^2	σ_f^2	σ_e^2	h^2
3	0.150 0±0.003 8	0.112 8±0.000 1	0.213 7±0.002 7	0.314 8±0.197 1
6	0.122 9±0.012 6	0.083 4±0.000 3	0.293 6±0.013 5	0.245 8±0.121 5
9	0.256 3±0.017 1	0.100 0±0.002 4	0.825 9±0.057 8	0.216 8±0.103 2
12	1.265 2±0.135 9	0.130 0±0.018 4	3.413 4±0.179 3	0.263 1±0.140 6
15	5.580 3±1.274 9	0.089 0±0.001 3	13.729 5±2.458 1	0.287 6±0.154 3
18	18.720 2±3.946 6	0.100 0±0.003 5	47.807 3 ±7.073 4	0.280 9±0.117 2
24	27.350 8±5.001 2	0.095 1±0.001 4	61.501 1±10.713 0	0.307 5±0.168 3
27	33.331 1±8.701 1	0.016 0±0.001 1	80.312 1±12.673 2	0.293 3±0.159 8

Note: σ_a^2 represents additive genetic variance, σ_f^2 full-sib variance, σ_e^2 residual variance, h^2 heritability, BW body width, and BL body length.

Table 3. Variance components and heritability (h^2) with standard errors (mean±SE) of BWT of turbot at different sampling ages

Months of age	σ_a^2	σ_f^2	σ_e^2	h^2
3	0.101 5±0.019 3	0.223 4±0.001 1	0.050 7±0.040 2	0.270 2±0.114 3
6	12.365 1±6.124 1	0.194 4±0.001 2	29.685 3±11.365 1	0.293 1±0.123 6
9	276.341 6±66.606 0	0.210 6±0.001 4	638.884 3±105.131 6	0.301 9±0.130 8
12	700.260 0±101.098 6	0.240 6±0.001 7	2 218.330 0±283.817 3	0.315 6±0.149 0
15	1 950.150 0±196.814 1	0.199 6±0.001 1	3 858.514 0±415.443 1	0.335 6±0.157 7
18	4 047.030 0±527.378 4	0.210 6±0.001 4	7 584.000 1±994.087 2	0.347 9±0.156 5
24	29 679.150 0±3 043.887 7	0.205 7±0.001 5	59 496.430 0±6 211.432 1	0.332 816±0.148 8
27	49 368.553 2±6 003.087 0	0.126 6±0.001 2	113 783.300 1±2 0583.076 3	0.302 5±0.140 1

Note: σ_a^2 represents additive genetic variance, σ_f^2 full-sib variance, σ_e^2 residual variance, h^2 heritability, and BWT body weight.

Table 4. Genetic and phenotypic correlations between BW/BL ratio and BWT

Months of age	Genetic correlation ($r_{A_1A_2}$)	Phenotypic correlation ($r_{P_1P_2}$)
3	0.821 3±0.021 6**	0.534 0±0.000 3**
6	0.666 7±0.013 7**	0.402 7±0.000 1**
9	0.635 5±0.012 1**	0.435 9±0.000 2**
12	0.701 4±0.017 8**	0.392 9±0.000 0**
15	0.685 4±0.014 2**	0.581 2±0.000 0**
18	0.655 5±0.011 9**	0.638 3±0.000 1**
24	0.437 8±0.012 2**	0.336 1±0.000 0**
27	0.480 4±0.012 9**	0.340 1±0.000 0**

Note: * A significant correlation ($P<0.05$); ** a highly significant correlation ($P<0.01$). BW represents body width, BL body length, and BWT body weight.

correlations decreased throughout the measurement period, but phenotypic correlations did not change significantly in a specific direction.

3.3 *Comparison of heritability of BW/BL ratio and BWT*

A comparison of heritability of BW/BL ratio and BWT are shown in Fig. 2 for different sampling ages. Heritability of BW/BL ratio was lower than that of BWT, except at 3 months of age. Differences of heritability between BW/BL ratio and BWT from 6 to 18 months of age were larger than those at 3, 24, and 27 months of age.

3.4 *Comparison of genetic and environmental correlations between BW/BL ratio and BWT*

A comparison of genetic and environmental correlations between BW/BL ratio and BWT is shown in Fig. 3 for different sampling ages. Genetic correlations were higher than environmental correlations throughout the measurement period. Differences between genetic and environmental correlations from 3 to 12 months of age were larger than from 15 and 27 months of age. The maximum of genetic correlations appeared at 12 months of age and the minimum at 18 months.

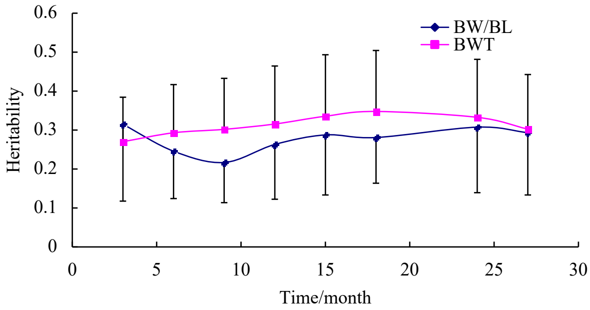

Fig. 2. Comparison of heritability of body width/body length (BW/BL) ratio, and body weight (BWT).

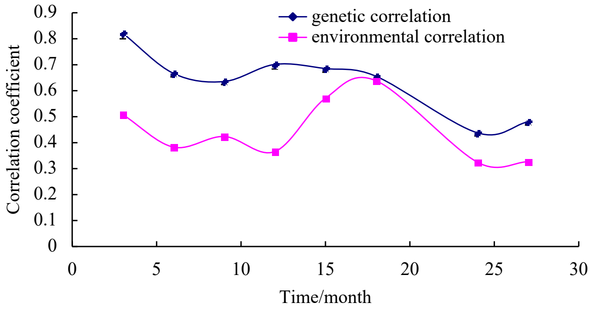

Fig. 3. Comparison of genetic and environmental correlations between body width/body length (BW/BL) ratio and body weight (BWT) at different sampling ages.

4 Discussion

Although growth is the highest economically important trait in fish improvement programmes, body shape is also very important for marketing of fish (Kause et al., 2003; Blonk et al., 2010; Liu et al., 2015). Therefore, a few aquaculture breeding programmes incorporate shape traits into the breeding goal (Ankorion et al., 1992; Liu et al., 2014, 2015). Genetic parameters of length ratio associated with body shape have been reported in the literature (Gjerde and Schaeffer, 1989; Ankorion et al., 1992; Shikano, 2007; Liu et al., 2014, 2015; De Oliveira et al., 2016). Gjerde and Schaeffer (1989) reported that heritabilities based on the sire component for BS2 and BS3 (BS2=THD/BL and BS3=WD/BL, where THD is the body height and WD is the BW, and BL is the body length) in Rainbow Trout were 0.14 and 0.13, respectively, and 0.44 and 0.40 respectively, based on the dam component. The heritability based on the dam components for BS2 and BS3 was higher than that based on the sire components. For the height/length ratio, Ankorion et al. (1992) reported that estimates of realized heritability measured in common carp were 0.47, 0.33, and 0.42 for up-selection, down-selection, and for simultaneous bidirectional selection, respectively. In an analysis of *Paralichthys olivaceus*, Shikano (2007) reported that heritability for the proportion of body length to body depth in hatchery-reared juveniles and in released individuals was 0.50 and 0.51, respectively. Subsequently, Liu et al. (2014) reported that 15 length ratios exhibited moderate to high heritability and their estimates at 180 and 360 days of age were 0.590 and 0.480 for $L5$:$L6$, 0.800 and 0.670 for $L5$:$L3$, 0.710 and 0.490 for $L5$:$L4$, 0.630 and 0.470 for $L5$:$L2$, 0.460 and 0.450 for $L5$:$L1$, 0.630 and 0.440 for $L6$:$L3$, 0.580 and 0.540 for $L6$:$L4$, 0.650 and 0.410 for $L6$:$L2$, 0.600 and 0.500 for $L6$:$L1$, 0.710 and 0.550 for $L3$:$L4$, 0.700 and 0.600 for $L3$:$L2$, 0.600 and 0.620 for $L3$:$L1$, 0.480 and 0.330 for $L4$:$L2$, 0.510 and 0.440 for $L4$:$L1$ as well as 0.650 and 0.440 for $L2$:$L1$ ($L1$, $L2$, $L3$, $L4$, $L5$, and $L6$ for total length, BL, head length, trunk length, caudal peduncle length at the insertion of the caudal fin, and caudal fin length measured on the midline, respectively). Moreover, Liu et al. (2015) also reported that four length ratio traits showed low to moderate heritability. Their estimates at 180, 240 and 360 days of age were 0.27, 0.19 and 0.28 for $L3$:$L1$; 0.25, 0.19 and 0.13 for $L2$:$L1$; 0.25, 0.13 and 0.12 for $L5$:$L1$ as well as 0.25, 0.28 and 0.16 for $L4$:$L3$ ($L1$, $L2$, $L3$, $L4$ and $L5$ for BL, head length, body depth, caudal peduncle depth, and caudal peduncle length, respectively). De Oliveira et al. (2016) reported that heritability for DL-R (depth to length ratio) in Nile tilapia was 0.189 and the genetic correlations between DL-R and BWT was 0.281.

In this study, the heritability of the BW/BL, and genetic correlations between BW/BL ratio and body weight were estimated using a two-trait animal model. The values of heritability ranged from 0.216 8 to 0.314 8. Compared with other fish species, the estimated heritabilities for BW/BL were lower than those in Rainbow Trout based on the dam component (Gjerde and Schaeffer, 1989), common carp (Ankorion et al., 1992) and *Paralichthys olivaceus* (Shikano, 2007), and similar to those estimated by Liu et al. (2015) in *P. olivaceus* but higher than those for Rainbow Trout based on the sire component (Gjerde and Schaeffer, 1989) and Nile tilapia (De Oliveira et al., 2016). With one exception, the present heritability was similar to that estimated by Liu et al. (2015) in *P. olivaceus*. These differences should be mainly attributed to the fish species selected, to family numbers, to sample size, to the trait analyzed, and to the statistical model used. The genetic correlations between BW/BL ratio and BWT ranged from 0.437 8–0.821 3. In comparison to other fish species, the estimated genetic correlations between BW/BL ratio and BWT were higher than in Nile tilapia (De Oliveira et al., 2016). On the whole, the present genetic correlations exhibited a decreasing trend throughout the measurement period, which is consistent with the estimates of Liu et al. (2015). Generally, genetic correlations are higher than the phenotypic correlations because of the efficient masking of the environment which modified the expression of a character lead to reduction of the phenotypic expression (Islam et al., 1993; Rana and Pandit, 2011), which has been confirmed in plant and poultry-breeding (Saatci et al., 2003; Rana and Pandit, 2011; Awan et al., 2015; Said and Fatiha, 2015; Kumar et al., 2017). Our present study confirmed this conclusion. In our study, the magnitude of genotypic correlation coefficients was higher than phenotypic coefficients indicating that the two traits are under genetic control rather than under environmental control. In addition, heritability of BW/BL ratio was lower than that of BWT, which indicated that additive genetic effects had a greater impact on BWT than on BW/BL ratio. At the same time, we showed that the selection methods for BWT were more flexible than for BW/BL ratio.

Estimated heritability was classified as low (0.05–0.15), moderate (0.20–0.40), high (0.45–0.60), and very high (>0.65) (Cardellino and Rovira, 1987; Xu et al., 2015). The BW/BL ratio heritability values of ranged from 0.216 8 to 0.314 8. According to this grading standard, the heritability of BW/BL was moderate. Moderate heritability on the BW/BL ratio trait demonstrated promising effects on genetic improvement in specific breeding programs, and improvement of the BW/BL ratio would be achieved through selection. The magnitude of correlations was categorized as low (0–0.40), moderate (0.45–0.55), and high (0.60–1), independently of the sign (Cardellino and Rovira, 1987; Xu et al., 2015). The genetic correlations between BW/BL ratio and BWT ranged from 0.437 8–0.821 3. According to this grading standard, these genetic correlations were high, indicating that the two traits were possibly controlled by the same number of genes, so that the two traits could be improved simultaneously through selective breeding. Based on our comprehensive analysis, we consider that the BW/BL ratio could be used as phenotypic marker of fast-growing turbot.

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