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Developmental dynamics of genetic effects for body weight in *T. rubripes* at different growth periods

Jiang Zemin Chiang

Laboratory for Marine Biology and Biotechnology, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, China.

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To elucidate the genetic mechanism of growth trait in *Takifugu rubripes* during ontogeny, developmental genetic analysis of body weight was conducted by mixed genetic model with additive-dominance effects, using complete diallel cross with three different strains of *T. rubripes* from Laizhou Shandong, Tangshan Hebei and Dalian Liaoning. Unconditional genetic analysis revealed that the unconditional dominance effects with very significant P<0.01 were detected during 8 to 20 months and the unconditional additive effects were detected only at 17 and 20 months. This suggests that the body weight trait was mainly controlled by dominance effects from 8 to 17 months and by both dominance and additive effects from 17 to 20 months. Conditional analysis showed that the net dominance effects were ascertained during growth from 0 to 8, 8 to 11, and 11 to 14 months, and the net additive effects were detected only during growth from 14 to 17 months. The following conclusions could be drawn from the results: the selection period should be considered during 14 to 17 months if the genetic improvement of *T. rubripes* is conducted using selective breeding, and the selection period should be considered during 8 to 14 months if cross breeding is used. The conditional genetic procedure is a useful method to elucidate the dynamics of genes action governing the variability of quantitative traits during ontogenetic development. In addition, the study is also highly important to determine the appropriate developmental period (*t*-1→*t*) for trait measurement in developmental quantitative genetic analysis in fish.

Key words: *Takifugu rubripes*, body weight, genetic parameters, gene effects.

INTRODUCTION

Takifugu rubripes belongs to teleost, Tetraodontiformers, Tetraodontoidei, Tetraodontidae, and Takifugu. It is distributed mainly in Japan of the Western North Pacific, the Korean Peninsula and China Coast (Wang et al.,

*Corresponding author: E-mail: zemin.ch09@mail.com
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2016). Due to its appealing taste, rich nutrition, low fat content and numerous trace elements, *T. rubripes* represents one of the fish species with high economic value (Wang et al., 2016). In recent years, T. rubripes are extensively farmed in Dalian, Qinhuangdao, Tangshan, and Tianjin regions, and have become the main cultured species of China puffer fishery. However, with the expansion of the scale of farming, serious germ plasm degeneration has appeared owing to lack of scientific and reasonable parent fish mating programmes, which has led to high mortality and retarded growth. Production of *T. rubripes* showed large fluctuations and the total yield decreased gradually, which severely restricted the development of *T. rubripes* aquaculture. Therefore, the genetic improvement of *T. rubripes* is necessary to sustain the development of the industry in a highly competitive aquaculture market.

For animal breeding, it is the foundation of the breeding work for studies on the genetic mechanism of breeding traits. These studies have important academic significance and application value to elucidate thoroughly the genetic mechanism of breeding traits and improve the predictability and selection efficiency of genetic breeding. In fish breeding, the genetic analysis of many quantitative traits was reported. Generally, these studies mostly utilized the data collected from one single time point to estimate the genetic effects (Gjerde et al., 1997; Martínez et al., 1999; Shikano, 2007; Tian et al., 2011; Liu et al., 2011, 2013; Zhang et al., 2014). However, the genetic mechanism of quantitative traits changes with temporal and spatial patterns (Zhu, 1995). Genes, based on developmental theory, are selectively expressed during the different growing stages in specific spatio-temporal patterns, and the mechanism that controls complex traits would be significantly changed in developmental process (Atchley, 1984; Cowle et al., 1992; Atchley et al., 1994; Atchley and Zhu, 1997). Clearly, the entire process of genetic regulation in the process of development cannot be disclosed using the data sampled at a particular point in time and the dynamics of gene expression need to be studied in different growth phases during ontogenetic development.

In the past, there were two common methods used for genetic analysis of developmental behavior: one by analyzing the phenotypic value at various periods; the other by using the difference ($y_{(d)}= y_{(t)}- y_{(t-1)}$) between two phenotypic values at time *t* and *t*-1. For quantitative traits, the genetic effects at time *t* were the sum of the genetic effects at time (*t*-1) and the extra genetic effects in the period (*t*-1) to *t* (Zhu, 1995). Obviously, the two methods ignored the dissimilar gene actions at different stages which is an important factor influencing the development of the quantitative traits and have not revealed the net genetic effects of gene expression during developmental stages. A conditional analysis method developed by Zhu (1995) can solve this problem well and can estimate the extra genetic effects in specific developmental intervals.

In recent years, genetic analysis for quantitative developmental traits has achieved important progress in terrestrial animals (Atchley, 1984, 1994; Atchley and Zhu, 1997; Cowley and Atchley, 1992) and plants (Zhu, 1995; Shi et al., 2001, 2002) based on the conditional analysis method. However, the aquatic organisms have attracted very limited attention (Wang et al., 2006). The objective of this study is to evaluate the developmental dynamics of genetic effects for body weight in *T. rubripes* at different growth periods based on the method and to explore the preliminary investigations on developmental quantitative genetics in fish.

MATERIALS AND METHODS

Cross mating and rearing conditions

During April 21 to 24 2011, a complete 3×3 diallel cross was conducted on three strains of *T. rubripes* collected from Laizhou Shandong, Tangshan Hebei and Dalian Liaoning in Laizhou Mingbo Fisheries Limited Company. Laizhou strain (LZ) came from Mingbo Fisheries Limited Company in Laizhou Shandong; Tangshan strain (TS) came from Tanghai Nanpu Salt Farm in Tangshan Hebei; Dalian strain (DL) came from Tianzheng Industrial Limited Company in Dalian Liaoning. The cross mating experiments were performed in nine concrete tanks filled with air-pumped circulating seawater with five females and five males in each tank. The quantity of fish and the environment were standardized to obtain similar rearing conditions for all cross combinations at the early breeding stage. After hatching at 15, 30, 60, and 120 days, the quantity of larvae or juveniles in each cross combination was standardized using random samples of 15000, 8000, 5000, and 2000, respectively. At 6 months of age, 400 samples were randomly selected from each stocking tank for tagging using Visible Implant Fluorescent Elastomer (VIE) tags. Polyculture was used with two parent fish and their reciprocal cross combinations in one tank (72 m^3 each); for example, the parents Laizhou and Tangshan and their reciprocal hybrids Laizhou(♀)×Tangshan(♂) and Tangshan(♀)×Laizhou(♂) with 300 fish each were combined in a single tank with a total of 1200 fish. Clearly, 3 kinds of polycultures were obtained by diallel crossing resign of 3×3. Nine of such tanks were used in this study with three replicates for each polyculture. Thus, a total of 10800 fish were initially tagged using VIE tags. The environmental conditions were standardized for the different rearing stages. During the larval-culture period, water temperature, salinity, illumination intensity, pH, ammonia nitrogen, nitrite-nitrogen, and dissolved oxygen were 5 to 22°C, 25 to 32, 500 to 1000 lx, 7.8 to 8.3, ≤1 mg/L, ≤0.4 mg/L, and 5 to 10 mg/L, respectively. During the juvenile- and adolescent-culture period, the above seven indices were 22 to 24°C, 15 to 32, 500 to 1000 lx, pH 7.8 to 8.3, ≤1 mg/L, ≤0.4 mg/L and ≥6 mg/L, respectively.

From 8 to 20 months, the body weights (BW) of all fish in each tank were measured every three months. Each data collection was synchronous with moving ponds. Body weights were measured using an electronic balance with a precision of 0.01 g. More than 90% survival rates were obtained for each tank due to well-maintained culture conditions.

Genetic analysis methods

The statistical analysis model including additive and dominance genetic effects was adopted to calculate the genetic components of additive (V_A) and dominance variance (V_D) of body weights of *T.*

Table 1. Estimates of unconditional variance components and their proportions to phenotype variance for body weight in *Fugu rubripes* at different growth stages.

Months	Unconditional variance components			Proportions of unconditional variance components	
	V_A	V_D	V_p	V_A/V_p	V_D/V_p
8	0	102.626**	1312.09*	0	0.0782156
11	0	1238.52**	9109.13**	0	0.135965
14	0	1890.38**	11472.8**	0	0.1647*
17	1331.02**	2307.09**	19834.7**	0.0671054	0.116316+
20	1490.4**	3474.56**	20490.7**	0.0727356	0.169568*

V_A, unconditional additive variance; V_D, unconditional dominance variance; V_p, unconditional phenotypic variance; +, * and ** are significant at 0.10, 0.05 and 0.01 levels, respectively. The means of abbreviations and symbols in Tables 2, 3 and 4 are the same as those in Table 1.

rubripes. The unconditional genetic analysis model can be written as (Zhu, 1995; Atchley and Zhu, 1997; Wang et al., 2006):

$Y_{ij(t)} = u_{(t)} + A_{i(t)} + A_{j(t)} + D_{ij(t)} + e_{ij(t)}$

where $Y_{ij(t)}$ is the unconditional phenotypic value of the individual from maternal line i × paternal line j at time t;$u_{(t)}$ is the unconditional population mean at time t; $A_{i(t)}$ or ($A_{j(t)}$) is the unconditional additive effect from maternal line i (or paternal line j) at time t, $A_{i(t)}\sim(0, \sigma^2 A_{i(t)})$, $A_{j(t)}\sim(0, \sigma^2 A_{j(t)})$; $D_{ij(t)}$ is the unconditional dominance effect from the cross of line $i \times j$ at time t, $D_{ij(t)}\sim(0, \sigma^2 D_{(t)})$; and $e_{ij(t)}$ is the unconditional residual error at time t, $e_{ij(t)}\sim(0, \sigma e^2_{(t)})$.

For body weight, genetic effect at time t includes cumulative genetic effects at time (t-1) and added genetic effects in the period (t-1 → t) (Zhu, 1995; Atchley and Zhu, 1997; Wang et al., 2006). The measured values at time t were conditioned on measured values at time t – 1. Thus, the conditional genetic model can be written as follows (Zhu, 1995; Atchley and Zhu, 1997; Wang et al., 2006):

$Y_{ij(t|t-1)} = u_{(t|t-1)} + A_{i(t|t-1)} + A_{j(t|t-1)} + D_{ij(t|t-1)} + e_{ij(t|t-1)}$

where $Y_{ij(t|t-1)}$, $u_{(t|t-1)}$, $A_{i(t|t-1)}/A_{j(t|t-1)}$, $D_{ij(t|t-1)}$ and $e_{ij(t|t-1)}$ is the conditional measured value of the individual from female parent fish i ×male parent fish j at time t, the conditional population mean value at time t, the conditional additive effect from female parent fish i / male parent fish j at time t, the conditional dominance effect from the hybridization of line $i \times j$ at time t and the conditional residual error $\sigma^2 A_{i(t|t-1)}$ $\sigma^2 A_{j(t|t-1)}$, $D_{ij(t|t-1)}\sim(0, \sigma^2 D_{(t|t-1)})$ and $e_{ij(t|t-1)}\sim(0, \sigma e^2_{(t|t-1)})$.

According to the estimated unconditional and conditional variance components, phenotypic unconditional and conditional variance can be obtained by $V_{P(t)} = V_{A(t)} + V_{d(t)} + V_{e(t)}$ and $V_{P(t|t-1)} = V_{A(t|t-1)} + V_{d(t|t-1)} + V_{e(t|t-1)}$, respectively. The unconditional ($V_{A(t)}$ and $V_{D(t)}$) / conditional ($V_{A(t|t-1)}$ and $V_{D(t|t-1)}$) variance components were estimated using the MINQUE(1) method (Rao, 1970, 1971; Zhu, 1995; Wang et al., 2006) with 1 for all prior components (Zhu, 1993; Zhu and Weir, 1996; Wang et al., 2006). The Jackknifing re-sampling method (Miller, 1974; Zhu and Weir, 1996) was employed to estimate the standard errors of variance components. The t-test was applied to test the significance of all estimated parameters. All data were calculated and analyzed using the statistical programs supplied by Zhu (Zhu, 1995).

RESULTS

Unconditional and conditional variance components

The unconditional genetic variances for body weight including V_A and V_D (The genetic variances for body weight at a fixed age) showed that the unconditional additive variances can be significantly detected only at 17 and 20 months and the value at 17 months was greater than that at 20 months (Table 1); and the unconditional dominance variances with very significant P<0.01 can be detected from 8 to 20 months; it appears that there was systematically increased trends with the development of *T. rubripes* (range: 102.626-3474.56). The proportions of unconditional additive/dominance variance showed that, the changes of the proportions of unconditional additive variance were basically identical to those of unconditional dominance variance except for a lower proportion at 17 months, and the proportions of unconditional dominance variance were greater than that of the unconditional additive variance at 17 and 20 months (Table 1). This indicates that the phenotypic variability of body weight was controlled by dominance effects from 8 to 14 months and controlled by both additive and dominance effects from 8 to 20 months.

For body weight, the genetic effect at time t includes both cumulative genetic effects at time (t-1) and added genetic effects within the period (t-1 → t) (Zhu, 1995; Wang et al., 2006). In the present paper, the unconditional genetic effects described earlier at different months of age were the cumulative genetic effects of many genes expressed at specific age periods from the initial month to the month when the body weights were measured. The unconditional genetic analysis can estimate the cumulative but cannot estimate the added genetic effects in a certain

Table 2. Estimates of conditional variance components and their proportions to phenotype variance for body weight in *Fugu rubripes* at different growth stages.

Month interval	Conditional variance components			Proportions of conditional variance components	
	$V_{A\ (t\mid t-1)}$	$V_{D\ (t\mid t-1)}$	$V_{p\ (t\mid t-1)}$	$V_{A\ (t\mid t-1)} / V_{p\ (t\mid t-1)}$	$V_{D\ (t\mid t-1)} / V_{p\ (t\mid t-1)}$
8 | 0	0	102.626**	1312.09*	0	0.0782156
11 | 8	0	646.951**	6166.78**	0	0.104909
14 | 11	0	791.852**	2372.14**	0	0.333813**
17 | 14	539.608**	0	3412.21**	0.15814**	0
20 | 17	0	0	2228.55**	0	0

$V_{A(t\mid t-1)}$, conditional additive variance; $V_{D(t\mid t-1)}$, conditional dominance variance; $V_{e(t\mid t-1)}$, conditional residual variance; $V_{p(t\mid t-1)}$, conditional phenotypic variance.

Table 3. Unconditional and conditional additive effects for body weight in *Fugu rubripes* parents at different growth stages.

Months	Unconditional additive effects			Month interval	Conditional additive effects		
	$A_{(TS)}$	$A_{(DL)}$	$A_{(LZ)}$		$A_{(TS)\ (t\mid t-1)}$	$A_{(DL)\ (t\mid t-1)}$	$A_{(LZ)\ (t\mid t-1)}$
8	0	0	0	8 | 0	0	0	0
11	0	0	0	11 | 8	0	0	0
14	0	0	0	14 | 11	0	0	0
17	25.615422	-25.975728	0.359682	17 | 14	14.579467	-17.796248+	3.215729
20	23.328032	-30.023141	6.694391	20 | 17	0	0	0

$A_{(TS)}$, unconditional additive effects of TS parents; $A_{(DL)}$, unconditional additive effects of DL parents; $A_{(LZ)}$, unconditional additive effects of LZ parents; $A_{(TS)\ (t\mid t-1)}$, conditional additive effects of TS parents; $A_{(DL)\ (t\mid t-1)}$; conditional additive effects of DL parents; $A_{(LZ)\ (t\mid t-1)}$; conditional additive effects of LZ parents.

period; the conditional genetic analysis developed by Zhu (1995) provides a useful method to elucidate the dynamics of genes action governing the variability of quantitative traits during ontogenetic development (Zhu, 1995; Atchley and Zhu, 1997) and could estimate the extra genetic effects. The conditional genetic variances showed that the conditional dominance variances with very significant $P<0.01$ were detected only at the intervals of 0 to 8, 8 to 11 and 11 to 14 months, and the conditional additive variances only at the intervals of 14 to 17 months (Table 2). Obviously, the net additive/ dominance genetic variances (conditional genetic variance) at different developmental stages were different and detected only at some time intervals. It is very difficult to elucidate these genetic characteristics using traditional genetic analysis methods.

Conditional and conditional genetic effects

The additive effects of *T. rubripes* parents and dominance effects of their cross combinations are different at different growth stages (Tables 3 and 4). The results indicated that the genetic effects at different developmental stages were different; therefore, the traditional genetic analysis (unconditional) using the phenotypic values measured at a fixed age cannot reveal the differences of the genetic effects in specific development intervals. But, the differences can be clearly elucidated using developmental genetic analysis method and the optimal parents and optimal mating combinations could be selected for genetic improvement.

The unconditional and conditional additive effects of parents at different growth stages are summarized in Table 3. The unconditional additive effects of three *T. rubripes* parents can be detected only at 17 and 20 months, but the two values were not statistically significant ($P>0.10$). The unconditional additive effect value of TS parents was the largest and that of DL parents was the lowest. The conditional additive effects can be only detected at the intervals of 14 to 17 months and the new expression of additive effect genes was turned-off at other four development intervals.

The unconditional and conditional dominance effects of different mating combinations at different growth stages are summarized in Table 4. The unconditional dominance effects of different mating combinations can all be detected at five development intervals and were not statistically significant ($P>0.10$), but the three sets values showed different change trends, that is, the unconditional

Table 4. Unconditional and conditional dominance effects for body weight in *Fugu rubripes* crosses at different growth stages.

Months	Unconditional dominance effects			Month interval	Conditional dominance effects		
	$D_{(TS\times DL)}$	$D_{(TS\times LZ)}$	$D_{(DL\times LZ)}$		$D_{(TS\times DL)\ (t\mid t-1)}$	$D_{(TS\times LZ)\ (t\mid t-1)}$	$D_{(DL\times LZ)\ (t\mid t-1)}$
8	12.531387	-6.894688	11.535862	8 | 0	12.531387	-6.894688	11.535862
11	59.224261	-33.516730	-14.718509	11 | 8	30.433316	-17.150900	-34.844647
14	45.838099	-67.665930	10.208108	14 | 11	-18.260171	-38.848113+	29.084396*
17	48.592290	-71.303413	10.043455	17 | 14	0	0	0
20	77.881972+	-73.870438	-3.207248	20 | 17	0	0	0

$D_{(TS\times DL)}$, unconditional dominance effects of TS×DL mating combination; $D_{(TS\times LZ)}$, unconditional dominance effects of TS×LZ mating combination; $D_{(DL\times LZ)}$, unconditional dominance effects of DL×LZ mating combination; $D_{(TS\times DL)\ (t\mid t-1)}$, conditional dominance effects of TS×DL mating combination; $D_{(TS\times LZ)\ (t\mid t-1)}$, conditional dominance effects of TS×LZ mating combination; $D_{(DL\times LZ)\ (t\mid t-1)}$, conditional dominance effects of DL×LZ mating combination.

dominance effects of TS×DL, TS×LZ and DL×LZ mating combinations showed increasing, decreasing and fluctuant change, respectively. The conditional dominance effects of different mating combinations can be detected only at the intervals of 0 to 8, 8 to11, and 14 to 17 months, but the three values were not statistically significant (P>0.10). The net dominance effects of both TS×DL and DL×LZ mating combinations have two positive and one negative value and that of TS×LZ mating combination has three decreasing negative values. The conditional dominance effects cannot be detected at the intervals of 14 to 17 and 17 to 20 months, and the new expression of dominance effect genes was turned-off at the two development intervals.

DISCUSSION

The body weight at a time point, as a typical quantitative trait, depends on the genes expression, regulation and their interactions during growth and development. The genetic analysis using the body weight measured at a specific moment in time can only reflect the accumulative genetic effects of multiple genes controlling body weight, but cannot reveal the extra genetic effects in specific development intervals. Therefore, it is necessary to study the differences in gene expression for body weight in specific development intervals, which can deeply understand the genetic architecture of quantitative traits and provide more detailed theory evidences for the genetic improvement of body weight (Zhu, 1995). In this study, the developmental genetic analysis was conducted for body weight in *T. rubripes* by using the statistical methods of the conditional genetic variance component estimation and conditional genetic effect prediction (Zhu, 1995). This method can overcome the drawback of the traditional genetic analysis that cannot estimate the extra genetic effects in specific development intervals and was widely applied in terrestrial animals (Atchley, 1984; Cowley and Atchley, 1992; Atchley et al., 1994; Atchley and Zhu, 1997) and plants (Zhu, 1995; Ye and Zhu, 2000; Fan et al., 2000; Shi et al., 2001). But, little research in this field has been conducted in fish (Wang et al., 2006).

The unconditional genetic variances for body weight at different developmental stages in *T. rubripes* showed that the unconditional additive variances can be significantly detected only at 17 and 20 months, and the unconditional dominance variances can be significantly detected during all stages and appeared systematically increased trends with the development of *T. rubripes*. The conditional genetic variances showed that the conditional additive variances only at the intervals of 14 to 17 months and the conditional dominance variances which were very significant (P<0.01) were detected only at the intervals of 0 to 8, 8 to 11 and 11 to 14 months. Obviously, the genetic effects of controlling body weight at some developmental stages displayed alternative expressions. The following conclusions could be drawn from the results described earlier: the selection period should be considered during 14 to 17 months if the genetic improvement of *T. rubripes* is conducted using selective breeding, and the selection period should be considered during 8 to 14 months if using cross breeding.

The unconditional additive effects of three *T. rubripes* parents at different growth stages showed that it can be detected only at 17 and 20 months and that of TS, LZ and DL parents were the largest, larger and negative, respectively. The conditional additive effects showed that it can be only detected at the intervals of 14 to 17 months and the new expression of additive effect genes was turned-off at other development intervals. The unconditional dominance effects of different mating combinations at different growth stages showed that it can all be detected at five development intervals, and the change trends of the dominance effects of TS×DL, TS×LZ and DL×LZ mating combinations showed increasing, decreasing and fluctuating changes, respectively. The conditional dominance effects of different mating combinations showed that it can be detected only at the intervals of 0 to 8, 8 to 11 and 14 to 17 months, and that of both TS×DL and DL×LZ mating combinations have two positive and one negative values

and that of TS×LZ mating combination three decreasing negative values. The results described earlier showed that the preferred parents should be from TS and LZ strains if the genetic improvement of *T. rubripes* is conducted using selective breeding and the preferred mating combinations should be TS×DL and DL×LZ if using cross breeding, whereas DL strain and TS×LZ mating combination were unsuitable for selective breeding and cross breeding.

Using conditional genetic analysis method can obtain the net genetic effects between two development periods, investigate the dynamic genetic expression of a certain period under condition of eliminating early interference, and further explain the results of unconditional analysis (Ye and Zhu, 2000). For conditional genetic analysis, the test interval (t-k) plays an important role in investigating the gene activity of quantitative traits at various stages. Previous studies showed that the genetic effects of opposite direction counteracted each other and were not detected due to a long test interval when the intensity of gene activity varied from weak to strong (Ye and Zhu, 2000). The developmental genetic analysis of body weight in T. rubripes was conducted using the data measured during 8 to 20 months. Obviously, the developmental interval used in this study is in the period that the intensity of gene activity varied from weak to strong, and the fast-growth is likely to continue for some time after 20 months. In this study, the unconditional and conditional genetic effects (additive and dominance effects) cannot be significantly detected except for the conditional additive effects of DL parents at the intervals of 14 to 17 months and the conditional dominance effects of TS×LZ and DL×LZ mating combination at the intervals of 11 to 14 months. This could be because the test interval of 3 months is too long for the genetic analysis of body weight in *T. rubripes ; it is* not an optimal interval.

From breeding viewpoint, the studies on the genetic mechanism of breeding traits provided the necessary background to determine the best selection strategy (for example, determining breeding method, clarifying breeding period, identifying the best individuals for mating and predicting response to selection, etc.) to be adopted in the genetic improvement program in order to allow the selection response and efficient advancement predicted. In addition, it could also provide some basis for quantitative trait loci (QTLs) analysis and marker assisted selection (MAS) of *T. rubripes* quantitative traits improvement at different developmental stages.

Conclusion

The following conclusions could be drawn from the results described earlier: the selection period should be considered during 14 to 17 months if the genetic improvement of *T. rubripes* is conducted using selective breeding and the selection period should be considered during 8 to 14 months if cross breeding is used.

Conflicts of Interests

The authors have not declared any conflict of interests.

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