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Genetic parameters and response to selection for body weight in turbot (*Scophthalmus maximus*, Linnaeus)

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Abstract

Genetic parameters and response to selection were estimated for harvest body weight in turbot. The data consisted of 10 952 individuals of 508 full-sib families from three generations (G0, G1, and G2). The heritability estimates for G0, G1, and G2 were 0.11±0.08, 0.18±0.09, and 0.17±0.07, respectively. Over three generations, the heritability estimate was 0.19±0.04. Maternal and common environmental effects were 0.10±0.04, 0.14±0.04, and 0.13±0.03 within each generation and 0.12±0.01 across generations. The selection differential in growth was 18.24 g in G0 and 21.19 g in G1 corresponding to an average of 19.72 g per generation. The genetic gains were also calculated, they were 22.06 g in G1 and 11.93 g in G2, corresponding to 6.36% and 3.52% body weight. The total genetic gain after two generations was 10.10% body weight, which indicated that the selective breeding program for the body weight trait in turbot was successful.

Key words: turbot, genetic parameter, selective breeding, body weight, *Scophthalmus maximus*

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1 Introduction

Turbot (*Scophthalmus maximus*, Linnaeus, 1758) is a marine fish distributed on the Atlantic coasts of Europe, including the Baltic Sea, Black Sea, and Mediterranean Sea (Blanquer et al., 1992; Lei and Liu, 1995). With the advantages of fast growth, high cold resistance, rich taste, and good nutrition, turbot is the most widely cultured commercial flatfish globally. Since its introduction into China from Britain as juvenile by the Yellow Sea Fisheries Research Institute in 1992, turbot aquaculture has developed into an important industry with an annual production of 56 300 t in 2013 (National Technology Research and Development Center of Flatfish Culture Industry, 2014). To promote the development of the turbot aquaculture industry and increase turbot production, there is a major effort in genetic improvement programs aimed at body weight traits to breed fast-growing varieties, because the commercial value of a turbot depends primarily on its body weight.

Selective breeding is a basic approach for genetic improvement that can offer the opportunity of continuous genetic gain; any gain in a core breeding group can be multiplied and expressed in millions of progeny (Lind et al., 2012). Selective breeding has been conducted for many aquatic species to improve the body weight trait (O'Flynn et al., 1999; Bentsen et al., 2012; Luan et al., 2012; Sui et al., 2015). In China, turbot breeding began more than a decade ago and two cross varieties, Danfa Turbot (Registration No. GS-02-001-2010) and Duobao No.1 (Registration No. GS-02-001-2014), have been ratified by the National Certification Committee for Aquatic Varieties of China. However, there have been no reports, to date, on genetic gains for any traits in either turbot or the newly selected turbot varieties.

A selective breeding program based on best linear unbiased prediction (BLUP) to improve harvest body weight for cultured turbot carried out by the Yellow Sea Fisheries Research Institute was initiated in 2006. The selective breeding program for turbot has now been underway for over ten years and phenotypic data for harvest body weight has been obtained for two selective generations (G1 and G2). Here, the heritability for harvest body weight was estimated based on within and across generation datasets using the restricted maximum likelihood (REML) method; the response to selection after two generation selection was calculated in the form of selection differential and genetic gains. The results provide a reference point with directive significance for further turbot selection breeding work.

2 Materials and methods

2.1 *The environment*

The breeding program was performed at the Genetic Breed-

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ing Center of Seawater Flatfish (36°40′24″N, 121°09′00″E), Yellow Sea Fisheries Research Institute, Haiyang City, Shandong Province, China. The progenies were cultured in two farms: one in the Genetic Breeding Center of Seawater Flatfish and the other one (36°54′14.10″N, 121°48′37″E) in Rushan City, Shandong Province, China.

2.2 *Production of base generation (G0)*

The base turbot generation (G0) was bred by introduced populations from five countries (Denmark, France, Spain, Britain, and Chile), all of which were introduced as about 5 cm long juvenile in 2003 and 2004. Healthy individuals that fed well and exhibited normal morphology were chosen as the brood stock. The brood stock were reared in 5 m×5 m×0.6 m ($L \times W \times H$) ponds at a density of 2–3 kg/m^2. Three months before breeding, illumination and water temperature in the culture ponds were controlled to stimulate gonad development. Illumination intensity on the water was 200–600 lx and the time increased gradually from 8 h to 10 h per day. Water temperature increased from 8°C to 14°C. The pond water was exchanged by continuous running water.

The base generation (G0) was established in 2006 and 2007 using hybridization between populations and artificial insemination. Lively individuals, which had no trauma and body weight of more than 1 kg, could be selected as parent fish. Full- and half-sib families were produced via an unbalanced nested mating design by randomly mating selected males and females from different populations. The numbers of turbot from different populations used to produce the base generation (G0) are show in Table 1, and the numbers of family in each hybridized combination were shown in Table 2.

Table 1. Number of turbot from different introduced populations used to produce the base population

Population type	Numbers for sires	Numbers for dams
Denmark	8	34
France	21	6
Britain	9	19
Spain	21	0
Chile	8	8

Table 2. Number of families used to produce the base population from each cross combination

Cross combinations (♂×♀)	Number of families
Denmark×Britain	4
Denmark×Chile	3
France×Denmark	32
France×Britain	15
France×Chile	5
Spain×Denmark	15
Spain×France	2
Spain×Britain	5
Spain×Chile	4
Britain×Denmark	12
Chile×Britain	5
Chile×Denmark	10
Total	112

Fertilized eggs were incubated in mini flow water at 13.5–15°C until hatching (~3–5 d). All of the families were then reared separately in fiberglass-reinforced plastic tanks (0.5 m^3) at a density of thirty thousand larvae (~50 mL fertilized eggs). The temperature of the larvae culture was maintained at 16–20°C. Salinity was 25–30 and dissolved oxygen was maintained at 4.9–8.0 mg/L. The rearing procedure was kept as consistent as possible for the different families. At the 35th and 70th days after hatching, 1 000 larvae and 400 juvenile fish per family were selected randomly and reared in new fiberglass-reinforced plastic tanks (0.5 m^3). At the 3rd months after hatching, 80 individuals with a greater body weight than the mean from each family were selected randomly, weighed, and marked with a VIE tag. The fish were then randomly distributed into either one or several 5 m×5 m×0.6 m ($L \times W \times H$) test ponds in two farms. The VIE tag was updated once every three months. Approximately 15 months post-hatching, all of the surviving individuals were landed, toweled dry and measured harvest body weight using electronic scale in turn. The progenies were genetically evaluated for the harvest body weight trait.

2.3 *Production of selection generation (G1 and G2)*

The subsequent generations (G1 and G2) were established by family and within-family selection strategy. From G0 to G2, all the full-sib families were ranked according their average family breeding values and about 40 families with high average family breeding values were selected as the parents of the next generation. Selected brood individuals were injected with passive integrated transponder (PIT) markers to distinguish them. Full- and half-sib families in G1 and G2 were produced via an unbalanced nested mating design by mating selected males and females from different families. Families with high average family breeding values were mated first and the candidate parents with higher breeding values were mated first. Brood individuals was mated randomly and inbreeding coefficient was maintained at <1%. Rearing and tagging of families in G1 and G2 were the same as G0.

2.4 *Data analysis*

Because we used PIT markers and VIE tags, a complete pedigree containing all phenotypically measured individuals was available and used in this study. The mixed model should include all effects that potentially played a role on the harvest body weight. The fixed effects considered in this study were year and farm. Each effect contains different factors that impact growth. The year effect contained annual breeding environment factors (e.g., water temperature and quality) and breeding operation. The farm effect contained raising environment, management level, stocking density, etc. A factor at different levels may have different effects on another factor, so their interaction was also included. The animal model was used to estimate the variance component using REML method with ASREML software (Gilmour et al., 2009) as follows:

$$y_{ijkm} = \mu + a_i + F_j + Y_k + F_j \times Y_k + A_i\left(F_j \times Y_k\right) + d_m + e_{ijkm},$$

where y_{ijkm} is the phenotypic observation for harvest body weight, μ is the overall mean, a_i is the random additive genetic effect of animal i, F_j is the fixed effect of farm j (two levels), Y_k is the fixed effect of year (seven levels), $F_j \times Y_k$ is the interaction between farm and year, $A_i(F_j \times Y_k)$ is a linear covariate nested within the interaction between year and farm, d_m is the random maternal and common environmental effects on full-sib m, and e_{ijkm} is the random error term.

The distribution of the random effects a, d, and e were assumed to be normal, with means of zero. The variance-covariance matrix was as follows:

$$\boldsymbol{V}\begin{bmatrix} a \\ d \\ e \end{bmatrix} = \begin{bmatrix} \boldsymbol{A}\sigma_a^2 & 0 & 0 \\ 0 & \boldsymbol{I}_d\sigma_d^2 & 0 \\ 0 & 0 & \boldsymbol{I}_e\sigma_e^2 \end{bmatrix},$$

where σ_a^2, σ_d^2, and σ_e^2 are the variance of the random effects a, d, and e, respectively. $\boldsymbol{A}$ is the $n{\times}n$ matrix of additive genetic relationship, and $\boldsymbol{I}_d$ and $\boldsymbol{I}_e$ are $n{\times}1$ identity matrices. n is the number of individuals.

Total phenotypic variance (σ_p^2) was calculated as the sum of the additive genetic variance (σ_a^2), the maternal and common environmental effects variance (σ_d^2), and the error variance (σ_e^2). The heritability (h^2) was computed as σ_a^2/σ_p^2, and maternal and common environment effects (c^2) as σ_d^2/σ_p^2. All of the calculations were carried out in ASREML software (Gilmour et al., 2009).

The z-score was used to test whether the heritability significantly varied from zero:

$$z = \frac{h^2}{se},$$

where h^2 is the estimates of heritability, and se is the standard errors of heritability.

The selection differential for growth was estimated for each generation by comparing the mean estimated breeding value of the brooders that actually produced progeny and the mean of all of the fish before the brooders were selected. Estimated breeding values were calculated based on phenotype information available at the time of selection. The genetic gain in each generation was also calculated by comparing the mean estimated breeding value of the current and previous generation. The cumulative genetic gain after two selections was expressed as a percentage based on the following formula:

$$P_c = \prod_i^n (1 + P_i) - 1,$$

where P_c is the cumulative genetic gain (%), P_i is the genetic gain (%) for the ith generation, and i is the number of the selection generation (i=1, 2).

3 Results

3.1 *Descriptive statistics*

The main statistical results of data set are shown in Table 3 and Table 4. The least square means of harvest body weight in Rushan farm were larger than Haiyang in 2009 and 2011 and progenies in the other years were only cultured in one farm. In total, 508 full-sib turbot families were constructed from 2006 to 2014. There were no and very few mature female fish in 2008 and 2012, respectively, therefore, no families were produced in either year. Because the selected parent individuals develop at different rates, each generation contained families in either two or three years. The number of full-sib families for each year ranged from 54 to 97. Because some parent individuals were mated with more than one partner, there were also some maternal half-sib families and paternal half-sib families in each year. The data set consisted of 10 952 individuals in total. The average number of individuals in each full-sib family ranged from 12.63 to 31.14 in different years.

Table 3. The least square means of harvest body weight in two farms by each year

Year	Farm	Number of individuals	Least squares mean/g
2006	Haiyang	1 307	328.18
	Rushan	*	–
2007	Haiyang	1 775	274.27
	Rushan	*	–
2009	Haiyang	234	294.29
	Rushan	761	337.36
2010	Haiyang	*	–
	Rushan	682	323.52
2011	Haiyang	1 305	336.86
	Rushan	1 018	361.23
2013	Haiyang	1 946	332.42
	Rushan	*	–
2014	Haiyang	*	–
	Rushan	1 924	347.35

Note: The asterisk (*) indicates turbot were not cultured in the farm.

3.2 *Genetic analysis*

The variance components, heritability, and maternal and common environmental effects are listed in Table 5. Four heritability (h^2) estimators for the harvest body weight were obtained. Heritability within G0 (0.11±0.08) was lower than that within G1, G2, and across generations. The other estimates were very similar, 0.18±0.09 within G1, 0.17±0.07 within G2, and 0.19±0.04 across generations. The heritability estimate for body weight in G0 was not significantly different from zero and in G1 and G2 were significantly different from zero. The heritability estimate across generations was very significantly different from zero. Maternal and common environmental effects (c^2) within and across generations closely corresponded to heritability. The heritability and maternal and common environmental effects standard errors across generations were smaller than those within genera-

Table 4. Number of sire, dam, families, individuals, average number of individuals per family, and least squares mean in each year and generation

Generation	Year	Sire	Dam	Full-sib families	Sire half-sub families	Dam half-sub families	Number of individuals	Average number of individuals per family	Least squares mean/g
G0	2006	32	33	55	19	14	1 307	23.76	299.250 5
	2007	46	33	57	14	10	1 775	31.14	
G1	2009	46	37	71	17	18	995	14.01	347.070 6
	2010	44	26	54	9	12	682	12.63	
	2011	75	49	95	18	27	2 323	24.45	
G2	2013	53	35	79	17	17	1 946	24.63	338.891 4
	2014	80	52	97	13	29	1 924	19.84	
Total		376	265	508	107	127	10 952	21.56	

Table 5. Variance components, heritability, and maternal and common environmental effects on harvest body weight within and across generations

Generation	σ_p^2	σ_a^2	σ_c^2	σ_e^2	h^2±se	c^2±se
G0	21 725.00	2 442.73	2 171.65	17 100.90	0.11±0.08	0.10±0.04
G1	14 690.42	2 789.38	2 209.84	10 291.20	0.18±0.09*	0.14±0.04
G2	7 054.70	1 182.06	935.41	4 937.14	0.17±0.07*	0.13±0.03
Across-generation	17 156.17	3 289.37	2 099.40	11 767.40	0.19±0.04**	0.12±0.01

Note: The asterisk (*) indicates estimate is significantly different from zero (P<0.05) and the double-asterisk (**) estimate is very significantly different from zero (P<0.01).

Table 6. Average estimated breeding value, average estimated breeding value of brooders, selection differential, and genetic gain in each generation

Generation	Average estimated breeding value of all individuals/g	Average estimated breeding value of brooders/g	Selection differential/g	Genetic gain/g	Genetic gain/%
G0	–0.82	17.42	18.24	–	–
G1	21.24	42.43	21.19	22.06	6.36
G2	33.17	–	–	11.93	3.52

tions.

3.3 *Response to selection*

The average estimated breeding value of all individuals and brooders in each generation are listed in Table 6. The growth selection differential was 18.24 g in G0 and 21.19 g in G1 corresponding to an average of 19.72 g per generation. The genetic gains were also obtained, they were 22.06 g in G1 and 11.93 g in G2, corresponding to 6.36% and 3.52% body weight. The cumulative genetic gain after two generations was 10.10% body weight.

4 Discussion

4.1 *Genetic analysis*

In this study, sex was not included in the mixed effect model analysis, because it is difficult to determine turbot gender morphologically at 15 months old and, moreover, dissecting to observe the gonad inevitably results in the death of the individual. Furthermore, Lyu et al. (2016) reported that variance analysis revealed no significant fixed effects of sex on harvest body weight. Wang et al. (2014) also obtained similar results, although female turbot had a growth advantage compared with males the difference was not significant in the early stage.

Heritability estimates for body weight within and across generations were all low to medium in 15 month-old turbot, based on the following categorization: low (0.05–0.15), medium (0.20–0.40), high (0.45–0.60), and very high (>0.65) (Cardellino and Rovira, 1987). There is a limited number of publications regarding the genetic parameters for body weight traits in turbot. Most previous estimates for body weight of adult turbot were medium to high (Gjerde et al., 1997; Ma et al., 2008; Lyu et al., 2016). Although genetic parameter estimates are only applicable to specific populations and environments, different populations, environmental conditions, and statistical models all result in different estimators (Gall et al., 1993); the heritability estimated in this study was lower than previous reports, which suggests that our heritability values may be underestimates. The most likely reason is that the sum of fixed environment effects was underestimated and phenotypic variance was overestimated because some possible subsistent fixed effect of pond was ignored. Furthermore, selecting individuals 3 months post-hatching may have resulted in a slight bias in the heritability estimate, because it might increase resemblance in family members. The heritability values for harvest body weight remained stable across generations, which suggested the potential for continued genetic improvement through selective turbot breeding in China.

A set of relatively large maternal and common environmental effects was estimated in this study. They were 0.10±0.04, 0.14±0.04, and 0.13±0.03 in G0, G1, and G2, respectively, and 0.12±0.01 across generations, which were similar to the heritability estimate values. Several studies have shown that maternal effects are high during early growth but have no obvious effect on adult fish (Liu et al., 2011; Furutsuka-Uozumi and Tabata, 1999; Shimada et al., 2007); therefore, these relatively large maternal and common environmental effects were likely the result of rearing full-sib families separately before they had reached a suitable size for tagging. Although the number of fish in each fiberglass-reinforced plastic tank was homogenized twice, at 35 and 70 days after hatching, the large variation in death rate in different families was associated with a large variation in breeding density, which resulted in a pronounced environmental effect. These results suggested better synchronized breeding and standardized family production is required.

Notably, the standard error of heritability across generations were much smaller than those within generations and the heritability estimate for body weight in G0 was not significantly different from zero. These indicate that a larger dataset (larger numbers of individuals, families, as well as generations) is necessary to accurately estimate genetic parameters.

4.2 *Response to selection*

In this study, we found a substantial selection response for growth. The selection differential calculated was 18.24 and 21.19 in G0 and G1, respectively. As a consequence of selection differential, the genetic gains were 22.06 and 11.93, corresponding to 6.36% and 3.52% body weight in subsequent generations. The small difference between selection differential and genetic gain may have been because the parents selected produced different amounts of progeny. Moreover random genetic drift was also a possible reason (Falconer and Mackay, 1996). The least squares mean of harvest body weight of G1 was 347.07 g, much larger than that of G0 (299.25 g). The above results indicate that the selection of G0 was successful. However, the actual phenotypic changes in G2 seemed incompatible with average breeding value changes. The most likely explanation was that the environment in G1 was far better than in G2. The changes in the phenotypic value might have been the result of a combined effect of selection differential and environmental changes. Therefore, the actual phenotypic change should only correspond to the expected response to selection when the environmental effects on the parental and progeny generations are identical (Gall et al., 1993).

After two generation selection, both average estimated breeding and phenotypic values were improved, which indicated that the BLUP selective breeding program for the body weight trait in turbot was successful. Nonetheless, the average genetic gains in this study were relatively small (<10% in one generation), compared with earlier reports on other aquatic species (Charo-Karisa et al., 2006; Liu et al., 2014; Luan et al., 2012; Maluwa and Gjerde, 2007; Rezk et al., 2009; Thodesen et al., 2012). Gjedrem (2000) also reported that genetic gain in growth per generation for aquatic animal species ranged from 10% to 20%. The main reason for low genetic gain in this study is that the proportion of turbot with well-developed gonads was low, which resulted in a low selection intensity.

In this study, the number of full-sib families for each year had a large variation, ranging from 54 to 97, and also there were significant difference among least square means of harvest body weight by each year. These results suggested aquaculture environment and management situations were far from the best condition, especially in gonad development process. Number of cultivated families was restricted by a low proportion of turbot with well-developed gonads (especially in female). A sufficient number of full-sib families form the basis of increasing selection intensity and avoiding inbreeding, which results in phenotypic depression (Thodesen et al., 2005).

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