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Estimating genetic parameters and genotype-by-environment interactions in body traits of turbot in two different rearing environments

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ABSTRACT

Estimates of heritability and genotype-by-environment (G × E) interactions for three common traits, such as harvest weight (HW), body length (BL), and condition factor (K) were estimated for harvest-size turbot in an industrial farming system (IFS) and a similar system maintained at a lower temperature (IFSLT). The only difference between the two environments was the variation in water temperature. The experimental population (69 families) was composed of 16 maternal half-sib family groups and 17 full-sib families generated by artificial mating. After 15-months of rearing, 2125 and 2925 individuals from the IFS and IFSLT environments were evaluated, respectively. The genetic analysis was based on an animal model with mean family weight at tagging as a covariate, test tank effect as a fixed effect, and an additive genetic effect plus an effect common to full-sib families as random effects using the restricted maximum likelihood method. Heritability estimates within the IFS environment were medium for HW and BL (0.34 ± 0.12 and 0.34 ± 0.10) but very low for K (0.009 ± 0.03). Heritability estimates within the IFSLT environment for HW, BL, and K were 0.16 ± 0.05, 0.17 ± 0.05, and 0.04 ± 0.04, respectively. The genetic correlations between HW and BL in both environments were very high (0.99) with small standard errors. However, the genetic correlations between K and other two traits (HW and BL) were both not significant. The genetic coefficients of variations for HW in the IFS and IFSLT environments were 20.16 and 9.62, and those for BL were 6.68 and 3.70. The genetic correlations for HW and BL between environments were 0.97 ± 0.15 and 0.90 ± 0.12, respectively. Our results suggest weak re-ranking of genotypes and heterogeneity of additive genetic variation across environments for HW and BL. The genetic correlation (0.78) for K was near the break-even point but with a high standard error (0.77). This is the first report on G × E interactions across environments for turbot growth traits, which will be of great value to optimize a turbot selective breeding program.

Statement of relevance: Our paper offers guideline to select breeding strategy.

1. Introduction

Turbot (*Scophthalmus maximus* L.) is a marine finfish with rapid growth rate and strong tolerance to cold temperature. Turbot is the most widely cultured commercial flatfish in the world, with the highest annual aquaculture production (60,000 t) in 2010 (Lei et al., 2012). Turbot is a native European species and was introduced to China in 1992 (Lei and Liu, 1995). After breakthroughs in artificial breeding by Lei et al. (2002), turbot became one of the most abundant marine species in the seas off the North China coast (Lei et al., 2012).

Growth is an important trait in commercial aquaculture. Faster growth rates reduce rearing cycle duration, leading to lower costs. Total phenotypic variation results from both genetic and environmental sources of variation as well as interactions between them (Falconer, 1990). Studies about turbot growth traits have focused on genetic evaluations of fish held in a single environment (Gjerde et al., 1997; Ma et al., 2009; Zhang et al., 2008a). However, when a strain is selected in different rearing systems or a selected strain is maintained in a different environment, knowledge of the genotype-by-environment (G × E) interactions is important because these interactions could reduce genetic gains (Mulder and Bijma, 2005). G × E interactions have different forms, such as re-ranking of genotypes across environments (re-ranking effect) and heterogeneity of genetic variances across environments (scaling effect) (Falconer and Mackay, 1996; Lynch and Walsh, 1998; Ponzoni et al., 2008).

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Turbot is farmed in intensive recirculating aquaculture systems, in on-shore tanks, and in sea cages in China (Lei et al., 2012). Lei et al. (2002) proposed an industrialized culture pattern for on-shore tanks called "greenhouse + deep-well seawater", which is popular on the north coast of China (mainly in Shandong and Liaoning provinces). This system uses on-shore tanks in greenhouses and controls water temperature by mixing natural seawater with deep-well water (Lei et al., 2002). However, water temperature in Liaoning province can only be adjusted to 7–8 °C during winter because of the high latitude, compared with 18–20 °C in Shandong province. The optimum temperature for turbot growth is 18–20 °C (Fang et al., 2001). A sea bass experiment was performed under two water temperatures by Saillant et al. (2006), and a significant G × E interaction was reported. Similar G × E interactions between different environments have been discovered in other aquaculture species (Evans and Langdon, 2006; Kvingedal et al., 2010; Sae-Lim et al., 2013; Trọng et al., 2013). Thus, a G × E interaction may occur in turbot when they are reared in different environments under different water temperatures. However, the G × E interaction for turbot reared in different environments has not been investigated. If the G × E interaction is significant, the selection strategy will be adjusted and will vary based on the environments (Mulder et al., 2006). Therefore, there is a need to investigate the G × E interactions in different environments, such as in Shandong and Liaoning provinces.

Most estimates of genetic parameters focus on harvest weight (HW) (Trọng et al., 2013). Because the commercial value of a fish depends directly on its HW, selecting for HW is fundamental during breeding. However, little research has been conducted about heritability and genetic correlations of turbot HW. Most previous studies concentrated on estimating the genetic parameters for juvenile turbot growth traits (Ma et al., 2008; Zhang et al., 2008a, 2008b). Therefore, studies on HW are urgently needed to implement a turbot breeding program.

Fish body shape is an important economic trait from a marketing perspective because of consumer preference for well-shaped fish (Blonk et al., 2010b; Kause et al., 2003). Condition factor (K) is the most common parameter used to express fish shape (Trọng et al., 2013). Condition factors have been reported in species, such as salmon (Gjøen and Bentsen, 1997) and rainbow trout (Gjerde and Schaeffer, 1989). Liu et al. (2011) reported a medium heritability estimate for the juvenile turbot K value. However, no estimates of genetic parameters for turbot K at harvest were provided in previous studies.

In this study, we estimated heritability of HW, body length (BL), and K, as well as estimated the genetic correlations between different traits for turbot maintained in two environments with different water temperatures. The G × E interaction between the two environments was also investigated for the first time.

2. Materials and methods

2.1. Experimental animals

The experimental population was established and raised in Haiyang, Shandong province, the People's Republic of China. The base turbot population (G_0) was introduced twice in 2006 and 2007 from France and Denmark. Two artificially induced reproductive cycles were conducted in 2009 and 2010, generating two populations (G_{1_1} and G_{1_2}) by selecting the breeders from G_0. The next generation (G_2) was produced in 2013 via artificial fertilization involving 45 sires and 33 dams from G_1 (i.e., 17 males and 4 females from G_{1_1}; 28 males and 29 females from G_{1_2}). Among the 33 dams, 16 were mated with a mean of 3.3 sires (range, 2–7), and 17 dams were mated with 1 sire. In total, 69 families were produced, containing 16 maternal half-sib family groups (52 maternal half-sib families) and 17 full-sib families over an 18-day period (May 6–23). Mature eggs were stripped from females and fertilized with sperm. The fertilized eggs were incubated until hatch in constant 14–16 °C flow-through water for 100 h and transferred to 0.5-m^3 fiberglass-reinforced plastic tanks after hatching. Dead eggs were removed twice daily. Finally, each family was reared in a separate tank (family tank), and the rearing environment of every family tank remained as similar as possible. A total of 1000 larvae juvenile fish per family were selected randomly at approximately 35 days post-hatch and reared in new family tanks (0.5 m^3). When larvae reached 70 days post-hatch, 400 juvenile fish were selected and transferred to new family tanks again. During the separate rearing of families, the water temperature was controlled at 18–20 °C. A total of 100 progeny from each family were also chosen randomly on day 100 post-hatch, tagged using a visible implant elastomer to distinguish individuals between families, and divided randomly into two equal subsets (i.e., 50 individuals per subset). Before the fish were tagged, body weight and length were measured and recorded. Finally, the two subsets per family were randomly transferred for rearing in the two different environments.

2.2. Test environments and data collection

The changes in water temperature in the IFS and IFSLT environments are shown in Fig. 1.

The IFS environment was established according to an industrialized culture pattern called "greenhouse + deep-well seawater", which was proposed by Lei et al. (2002). The culture facilities mainly consisted of greenhouses and deep wells. The deep-well seawater temperature was relatively stable during the year, so well seawater was mixed with natural seawater to attain 18–20 °C. The well seawater was pre-filtered and oxygenated before mixing (Lei et al., 2002). The fish were divided randomly into two 5 × 5 × 0.6-m (L × W × H) test tanks at a density of 69 fish/m^2, salinity of 28–30‰, and dissolved oxygen of 6–8 mg/l. The fish were reared in a greenhouse under a constant 12L:12D photoperiod and fed commercial dry pellets (Great Seven, Beijing, China) manually twice daily.

The IFSLT environment was similar to the IFS environment but was maintained at a lower temperature. Fish in the IFSLT environment were also divided randomly into two 5 × 6 × 1.2-m (L × W × H) indoor concrete test ponds at a stocking density of 57.5 fish/m^2. Salinity was 30–32.6‰. Dissolved oxygen, photoperiod, and feeding were the same as in the IFS environment. Water temperature was adjusted to about 8 °C with a blend of well seawater from December 2013 to April 2014. Moreover, water temperature was controlled at about 20 °C using well seawater from the end of June until the measurements were taken. Culture water was used only with natural seawater after pre-filtering, as described above, except during the two periods.

2.3. Data and statistical analyses

The total rearing period after tagging until the fish were measured was approximately 12 months. Body weight and length data were collected from 15-month-old fish at the beginning of August 2014 from 2125 and 2925 fish in the IFS and IFSLT environments, respectively. Condition factor was calculated as: $K = HW\ (g) \times 100\ /\ (BL\ (cm))^3$ (Gjerde and Schaeffer, 1989).

Analysis of variance (ANOVA) using the "nlme" package developed by Pinheiro and Bates (2000) in R ver. 3.0.2 (R Development Core Team, 2013) was applied to test the effect of environment on turbot growth as reflected by the phenotypic values of the three studied traits. Before the ANOVA, normality of distributions and homogeneity of residual error variances for the phenotypic data of the three traits in the two environments were tested using Shapiro–Wilk's test (Royston, 1982) and Levene's test (Levene, 1960) using R. The results showed that the distributions of phenotypic data for the three traits in the two environments were normal, and the residual error variances for the three traits were equal between the two environments, respectively. The phenotypic data of the three traits were modeled using a linear mixed model, where test environment was used as a fixed effect and the covariate was the mean phenotypic value of the family at tagging; test tank