




Effects of genotype × environment interaction on the estimation of genetic parameters and gains in Nile tilapia

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Received: 3 April 2020 / Revised: 9 July 2020 / Accepted: 11 August 2020
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Abstract

Nile tilapia (*Oreochromis niloticus*) is the major fish species produced in Brazil, a country with a vast territory and great climate diversity. This study assessed the effects of the genotype × environment interaction on heritability estimates and selection responses in Nile tilapia (Tilamax strain) cultivated in earthen ponds and net cages. The weight at harvest, trunk length, and head percentage of 4400 individuals were determined. Trait heritabilities were higher in pond fish (0.27–0.52) than in caged fish (0.09–0.33). Genetic correlations between farming systems were lower than 0.5 for the three traits. The rank position of the top 10 families differed according to the environment, as did the response to direct and indirect selection. The results revealed significant genotype × environment effects on the heritability of Nile tilapia farmed under different systems.

Keywords *Oreochromis niloticus* · Morphometric trait · Genetic correlation · Heritability · Response to selection

Introduction

Nile tilapia (*Oreochromis niloticus*) is one of the most widely farmed fish in the world. In Brazil, it is the most cultivated fish

species, making the country the fourth-largest tilapia producer (PeixeBr 2020). Because Nile tilapia can adapt well to different environmental conditions, its production extends throughout the country. Farming systems range from subsistence to large-scale cage farms.

In Brazil, tilapia farming has been traditionally carried out in earthen ponds, but there has been a recent increase in the use of net cages. Cage farming allows cultivating fish at high densities, increasing profitability. Net cages can be set up in lakes, ponds, or reservoirs, an interesting feature, particularly in Brazil, where more than 5 million ha of reservoir waters is distributed in large hydrographic basins (Halwart et al. 2007; Bueno et al. 2008).

Since 2000, genetic improvement programs and scientific research have been conducted to improve the productive performance of Nile tilapia (Porto et al. 2015; Turra et al. 2016; Oliveira et al. 2017; Zardin et al. 2019). The variability in environmental conditions and farming systems, however, is a factor that must be considered in breeding programs (Eknath et al. 2007; Ponzoni et al. 2008; Khaw et al. 2009, 2012; Nguyen et al. 2017; Oliveira et al. 2017; Agha et al. 2018). The genotype × environment interaction may have important effects; programs are generally carried out under specific, controlled conditions, but genetically improved fish are sold to farms where they may grow under different conditions than those found in nurseries (Sae-Lim et al. 2010; Khaw et al. 2012).

Communicated by: Maciej Szydlowski

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Most breeding programs use fish ponds (Eknath et al. 2007; Ponzoni et al. 2008; Khaw et al. 2009, 2012; Nguyen et al. 2017). Therefore, there is a lack of information on the genetic parameters, selection response, and rank correlations of fish reared in cage systems. The genetic improvement program of the State University of Maringá, Brazil, is conducted in net cages (Oliveira et al. 2015, 2016; Porto et al. 2015; Zardin et al. 2019). This study aimed to assess the effects of genotype \times environment on the estimation of genetic parameters and selection response for important economic traits in Nile tilapia reared one under different farming system in Brazil.

Material and methods

Animal population

Data on 4400 Nile tilapia of the Tilamax strain grown in earthen ponds and net cages were obtained from the Nile Tilapia Genetic Improvement Program of the State University of Maringá. Animals were the 6th, 7th, and 8th generations of genetically improved fish. The base population was derived from GIFT tilapia from Malaysia through a partnership between the World Fish Center and the State University of Maringá in 2005. The genetic improvement program aimed to develop an improved variety that was well adapted to farming conditions in Brazil.

Since 2007, when the 1st generation was obtained, fish have been selected for growth rate in cage farms established on the Corvo River, Diamante do Norte, Paraná, Brazil, from April to October. Detailed information on family formation and fish nutrition can be found in Oliveira et al. (2016). The average cultivation period is 191 days in net cages and 198 days in ponds.

Trait measurements and data recording

The evaluated traits were weight at harvest, trunk length, and head percentage. Trunk length was calculated as the difference between standard length and head length, and the head

percentage was calculated as head length divided by standard length multiplied by 100 (Table 1).

A total of 3623–3645 animals from 162 families grown in net cages from 2013 to 2015 were evaluated. The mean number of representatives per family was 22.5. Net cages (6 m³) were stocked with 100 kg/m³ at the Demonstration Unit of the State University of Maringá, Corvo River, Diamante do Norte, Brazil.

In the 400-m² earthen pond system, 770 to 772 fish from 60 families were evaluated. The nursery had a stock density of 1 kg/m³, and animals were tested from April to October 2015. The pond was located at the Experimental Fish Farming Station of the State University of Maringá. In 2015, a mean of 16.1 representatives per family were assessed in both systems.

The mating of 39 sires and 58 dams produced the 60 families evaluated in 2015. In both farming systems, 35 sires and 58 dams had progenies. The family size average was 22.81 and 13.71 in cages and earthen ponds.

Fish were fed according to their growth requirements. Commercial feed providing 32% crude protein, 9% carbohydrates, 16% crude fat, and 13% ash was supplied at 1 to 2% biomass.

Statistical analysis

Data were assessed for consistency, and variance components and heritabilities for each trait were estimated by single-trait models, considering the information from each farming system separately.

The genetic correlations between the farming system, for each trait, were estimated using two-trait models, considering the observations of the same trait as different traits according to the system. Analyses were conducted using Multiple Trait Gibbs Sampling for Animal Models (Van Tassell and Van Vleck 1996). Statistical models considered the within-year effects for net cages, sex, and age as co-variables. Linear, quadratic, additive genetic, and common family effects were estimated. Necessary to account for common family effects because families were reared separately until tagging (Campos et al. 2020).

Table 1 Descriptive statistics of weight at harvest, head percentage, and trunk length of Nile tilapia

Trait	Group	<i>n</i>	Male (<i>n</i>)	Female (<i>n</i>)	Mean \pm SD	Min	Max
Weight (g)	EP	772	359	413	251.5 \pm 102.5b	36	584
	NC	3645	1929	1716	653.6 \pm 281a	54	1755
Head percentage (%)	EP	770	357	413	32 \pm 2a	22	43
	NC	3623	1915	1708	30 \pm 2b	12	42
Trunk length (cm)	EP	770	357	413	12.97 \pm 2.1b	6.5	18.8
	NC	3627	1918	1709	16.84 \pm 2.3a	7	29.9

Means followed by different letters differ significantly at $p < 0.05$ by Tukey's test

EP earthen pond, NC net cage, SD standard deviation

About 3200 caged individuals, distributed in four net cages (about 800 individuals per cage), were analyzed in 2013, 2014, and 2015. Therefore, it was necessary to assess within-year effects for net cage farming. Pond fish, however, were evaluated only in 2015, precluding the need to consider within-year effects for pond farming.

For single-trait analyses, 10,000 samples were generated from a Markov chain with 600,000 iterations, a burn-in period of 100,000 iterations, and a sampling interval of 50 iterations. For bi-trait analyses, 10,000 samples were generated from 1,200,000 iterations with a burn-in period of 200,000 iterations and a sampling interval of 100 iterations. Chain convergence was tested using the criterion of Heidelberger and Welch (1983) in the coda package of the R statistical software.

Coincidence percentage was determined by ranking the top 10 families in both farming systems and determining how many families were ranked at the same position in both environments. Rank correlations between genetic values of families in each environment were estimated using Spearman's rank correlation test.

We determined the genetic gains according to the response to three different selection methods: direct response to selection based on the traits of animals reared in ponds, correlated response to selection based on the traits of animals reared in cages, and response to selection of caged fish based on traits of siblings reared in ponds (sib-family). For direct and correlated responses, the considered traits were exclusive to the farming system. We selected the highest expected breeding value for weight and trunk length and the lowest for head percentage.

Results

The weight and trunk length of caged fish were higher ($p < 0.05$) than those of pond fish (Table 2). The head percentage, in contrast, was higher ($p < 0.05$) in pond fish.

We observed higher genetic ($p < 0.10$) and phenotypic ($p < 0.05$) variances in weight in caged fish than in pond fish (Table 2). However, the variances in trunk length and head percentage were slightly higher in pond fish (Table 2). Overall, the heritability estimates of studied traits were higher in pond fish. The greatest difference in heritability estimates between farming systems was observed for head percentage, although credible intervals overlapped (Table 2).

Genetic and phenotypic correlations between farming systems were low, ranging from 0.47 to 0.48 and 0.07 to 0.20, respectively. For trunk length, there was a probability that genetic and phenotypic correlations were zero (Table 3).

Forty to 60% of families ranked among the top 10 in one farming system had the same rank in the other system. The coincidence percentage was lowest for head percentage (Table 4). The within-family correlation was highest for head percentage (0.74) and lowest for weight (0.49) (Table 4).

Traits also differed in direct responses (−3.5 to 35.6%), correlated responses (−0.2 to 12.4%), and responses based on family data (−1.2 to 9.1%) (Table 5).

The results showed that weight had the highest selection response and head percentage the lowest, regardless of the selection method. The highest genetic gains could be obtained through direct selection. Genetic gains ranged from 9.1 to 35.6% for weight, 5.6 to 10.6% for trunk length, and −3.5 to −0.2% for head percentage (Table 5).

Discussion

Productive performance

The higher weight (400 g) and trunk length (3.9 cm) of animals grown in net cages were probably associated with environmental conditions. The constant flow of water through the cages is responsible for the oxygenation and removal of metabolic residues and leftover feed, and with that, the level of

Table 2 Variance components and genetic parameters of weight at harvest (g), trunk length (cm), and head percentage (%) determined by single-trait analysis of Nile tilapia

Parameter	Group	Weight	Trunk length	Head percentage
σ^2_a	EP	3484 ± 1095 (1686–5958)	1.13 ± 0.39 (0.51–2.07)	9.1e−05 ± 3.0e−05 (4.2e−05–1.7e−04)
	NC	10,009 ± 2617 (5280–15,620)	0.83 ± 0.21 (0.44–1.27)	3.0e−05 ± 9.0e−06 (2.0e−05–5.0e−05)
σ^2_p	EP	6541 ± 580 (5579–7845)	2.62 ± 0.22 (2.27–3.12)	3.4.e−04 ± 2.2e−05 (3.0e−04–3.9e−04)
	NC	29,650 ± 1379 (27160–32,590)	2.60 ± 0.11 (2.40–2.84)	3.7e−04 ± 9.3e−06 (3.6e−04–3.9e−04)
h^2	EP	0.52 ± 0.12 (0.29–0.77)	0.43 ± 0.12 (0.22–0.68)	0.27 ± 0.08 (0.13–0.46)
	NC	0.33 ± 0.08 (0.19–0.49)	0.32 ± 0.07 (0.17–0.46)	0.09 ± 0.02 (0.05–0.14)
c^2	EP	0.03 ± 0.02 (0.007–0.080)	0.05 ± 0.03 (0.016–0.120)	0.01 ± 0.01 (0.003–0.030)
	NC	0.15 ± 0.03 (0.09–0.22)	0.10 ± 0.02 (0.06–0.16)	0.007 ± 0.003 (0.003–0.016)

Data are presented as mean ± standard deviation (95% credible interval)

EP earthen pond, NC net cage, σ^2_a additive genetic variance, σ^2_p phenotypic variance, h^2 heritability, c^2 common family effect

Table 3 Genetic and phenotypic associations between traits of Nile tilapia grown in earthen pond (EP) and net cages (NC)

Parameter	r_A	r_P
Weight at harvest (g)	0.47 ± 0.18 (0.07–0.79)	0.20 ± 0.09 (0.03–0.38)
Trunk length (cm)	0.47 ± 0.22 ns (– 0.02–0.82)	0.19 ± 0.10 ns (– 0.006–0.040)
Head percentage (%)	0.48 ± 0.20 (0.03–0.79)	0.07 ± 0.03 (0.005–0.14)

Data are presented as mean ± standard deviation (95% credible interval)

r_A genetic correlation, r_P phenotypic correlation, ns not significant at the 95% credibility level

oxygen dissolved is maintained, and there is no accumulation of nitrogenous molecules such as ammonia and nitrite that are harmful to fish development (Tidwell 2012). The cages in the present study were fixed in a site that has good water quality indexes, which can be confirmed by studies carried out by Braccini et al. (2008) and Andreto et al. (2015).

The genetic improvement program of the State University of Maringá uses net cages to rear and select fish since 2007 because of the various benefits of cage farming. The cultivation period of 6 months may also have influenced the differences in weight and trunk length between pond and caged fish, as the time to reach commercial weight is longer in pond systems. In this system, the water is retained in a limited space, and the exchange is carried out mainly to replace losses through evaporation and infiltration, and this way, there is no constant water flow or waste removal, and this reduces the environmental quality and, consequently, the fish growth (Tidwell 2012).

The strong genetic correlation between trunk length and weight in caged fish (> 0.85, data not shown) indicates that selection for weight can lead to gains in length. This is another evidence of the benefits of cage farming compared with pond farming.

Heterogeneity of variance

Differences in phenotypic and additive genetic variances greater than 4.5-fold (6541 and 29,650) and 2.8-fold (3484 and 10,009), respectively, are suggestive of heterogeneous variances in data. The non-overlap of the 10% and 5% credible intervals (for genetic and phenotypic variances, respectively) corroborate this observation (Table 2). However, the differences in weight at harvest indicate that the heterogeneity of variance can be associated with differences in the magnitude of

weight measurements between farming systems. These results agree with those of Sae-Lim et al. (2013, 2015), Oliveira et al. (2017), and Agha et al. (2018), who reported heterogeneity of variance between different farming systems.

In previous studies, estimates of genetic variance in weight at harvest of GIFT tilapia were found to vary from 783 to 2778 g (Rutten et al. 2005; Charo-Karisa et al. 2007), values higher than those observed in the current study (1686 to 5989 in EP and 5280 to 15,620 in NC according to Table 2). The differences in variances may be related to the differences in mean weights between studies.

Genetic, phenotypic, and rank correlations

There were low genetic correlations (< 0.5) between farming systems for single traits (Table 3). Genetic correlations lower than 0.7–0.8 suggest significant genotype × environment interaction effects (Robertson 1959). Logarithmic transformation of weight data was performed to normalize variance; nevertheless, the genetic and phenotypic correlations between farming systems were weak (0.36 and 0.16, respectively).

The low rank correlations (0.49–0.74) and percentages of coincidence of families ranked among the top 10 (40–60%) indicate that families were reclassified according to the farming system. In other words, families with the best performances in net cages did not necessarily hold the same rank position in the pond system (Table 4). Similar results were reported for Nile tilapia in previous studies (Oliveira et al. 2017; Agha et al. 2018).

Heritability and direct and indirect responses to selection

The estimated heritabilities for weight at harvest (0.52 for pond fish and 0.33 for caged fish) are in agreement with literature data (0.19–0.40 for pond fish and 0.23–0.34 for caged fish) (Khaw et al. 2012; Trong et al. 2013; Sae-Lim et al. 2015; Nguyen et al. 2017).

The moderate heritability estimates and weak genetic correlations between environments support the low correlated responses compared with direct responses (Table 5). Therefore, genetic gains will likely be higher

Table 4 Coincidence percentage (CP) of the top 10 families and Spearman correlation coefficient (r_{FAM}) between families ranked by genetic value

Parameter	Weight	Head percentage	Trunk length
CP (%)	50%	40%	60%
r_{FAM}	0.49	0.74	0.68

Table 5 Responses to selection for growth traits and genetic gains in Nile tilapia

Trait	DR	GDR (%)	CR	GCR (%)	RF	GRF (%)
Weight	89.50	35.59	31.10	12.37	22.92	9.13
Trunk length	1.38	10.64	0.73	5.63	0.81	6.25
Head percentage	-0.01	-3.47	-0.001	-0.19	-0.01	-1.19

DR direct response, *GDR* gain in DR, *CR* correlated response, *GCR* gain in CR, *RF* response to selection based on family data, *GRF* gain in RF

if animals are tested and selected under similar conditions to those of commercial farming system. The correlated (> 12%) and family gains (9%) in weight show that positive selection results may be obtained even under different conditions for which they were selected (Table 5). Similar results were reported by Khaw et al. (2009, 2012); Nguyen et al. (2017); and Oliveira et al. (2017).

Evidence of the genotype \times environment interaction in aquaculture species was also found by Khaw et al. (2009), Sae-Lim et al. (2013), Oliveira et al. (2017), and Agha et al. (2018), in agreement with the results of the current study. Trong et al. (2013), Turra et al. (2016), and Nguyen et al. (2017), in contrast, did not find such evidence for Nile tilapia. The high mortality (> 70%) of caged fish observed in the study of Trong et al. (2013) might have reduced family representation and, therefore, biased the estimates of correlations between farming systems, as suggested by Sae-Lim et al. (2010). According to Khaw et al. (2012), the degree of genotype \times environment interactions in fish communities may vary between studies because of differences in test environments and experimental designs.

Breeding programs may benefit from using different farming systems, as shown by the high gains through direct selection. Therefore, the cost–benefit ratio of implementing breeding programs in different farming environments must be evaluated. Our results indicated that responses to direct selection for weight were at least 2.87 times higher than indirect responses. On the other hand, responses to indirect selection for weight were higher than 9% and could be used as an alternative to implementing breeding programs under different farming conditions.

The family information would be an option where the genotype \times environment interaction is significant, and when the direct selection is not possible to carry out by economic issues. Thus, the selection could be done in the nucleus, considering the breeding values estimated using the information of relatives from different farming systems (Khaw et al. 2009; Khaw et al. 2012; Nguyen et al. 2017).

Our results indicated the occurrence of significant genotype \times environment interaction effects on traits according to the farming system. We observed weak

genetic correlations, heterogeneity of variances, and differences in animal performance, family ranks, and heritability estimates between animals farmed in net cages and those farmed in earthen ponds.

Acknowledgments PeixeGen Research Group at State University of Maringá.

Graduate Program in Animal Science at State University of Maringá for granting an Academic Excellence Program (PROEX) scholarship to the authors.

Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES).

Code availability Not applicable.

Author's contributions All the authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Carlos Antonio Lopes de Oliveira, Ricardo Pereira Ribeiro, Humberto Todesco, Grazyella Massako Yoshida, and Nguyen Hong Nguyen. The first draft of the manuscript was written by Filipe Chagas Teodózio de Araújo, Eric Costa Campos, and Vanessa Lewandowski, and all the authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding information This research was financed in part by the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES).

Data availability Not applicable.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent informed Consent was obtained from all individual participants included in the study.

Ethical approval Not applicable.

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