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Genotype × environment interaction for growth traits of Nile tilapia in biofloc technology, recirculating water and Cage systems

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ABSTRACT

An assessment was made on the genotype-environment interactions affecting growth traits of Nile tilapia (*Oreochromis niloticus*) reared in recirculating water (RAS), biofloc technology (BFT) and Cage systems. Weight data collected at 56 (W56) and 168 (W168) days of age came from a study designed with 86 full-sib families originating from 43 sires and 86 dams. All animals were raised in RAS until reaching approximately 56 days of age. After that, they were distributed among the three systems evaluated. Variance in W168 was higher in the RAS group, when compared to BFT and cage groups. Posterior means (highest posterior density interval with 95% of samples) of heritability in groups W56, W168 BFT, W168 RAS and W168 Cage were 0.84 (0.77; 0.91), 0.82 (0.73; 0.94), 0.62 (0.53; 0.72) and 0.78 (0.67; 0.88), respectively. Posterior means of genetic correlation (highest posterior density interval with 95% of samples) between W168BFT and W168 RAS, W168BFT and W168 Cage, and W168 RAS vs W168 Cage were 0.99 (0.98; 1.00), 0.83 (0.75; 0.89), and 0.88 (0.83; 0.93), respectively. Posterior means (highest posterior density interval with 95% of samples) of expected response concerning direct selection in groups W168 BFT, W168 RAS and W168 Cage were 87.14 (73.61; 102.64), 98.74 (82.12; 114.98) and 74.23 (60.95; 87.79) grams/generation, respectively. Expected response concerning indirect selection of W168 was similar to direct response. Heritability of W168 depends on farming system but is high; therefore it is safe to say that genetic progress is obtainable through selection. Variance in W168 is subject to the environment. It is unnecessary to develop environment-specific breeding programs aiming for higher weight at 168 days of age of Nile tilapia reared in recirculating water, biofloc and Cage systems.
Statement of relevance: Genetic parameters of BFT and G × E for Nile tilapia.

1. Introduction

Cage farming is utilized globally as one of the main production systems for Nile tilapia (*Oreochromis niloticus*) culture. The presence of large reservoirs associated with hydroelectric power in tropical countries, such as Brazil, has prompted growth of tilapia cage farms. However, in developed countries, many of which having temperate climate, it is common to see fish production systems, including tilapia farms, using water recirculating systems (RAS). Some of the reasons why that system has drawn global investment and had studies carried out internationally on its use for aquaculture systems are the rational use of space, low use of water, lower environmental impact, labor optimization, controlled conditions suitable for farming throughout the year, and also, the possible closeness between production and consuming centers. The biofloc farming system (BFT) has recently started to be studied in many countries, as it has under Brazilian on-farm conditions, and its characteristics suggest meaningful benefits for the production chain of Nile tilapia.

Fish production in biofloc systems developed from water recirculating systems, on which there are neither mechanical filters nor conventional biological ones. In BFT, organic waste produced is used as substrate for heterotrophic bacteria responsible for water treatment and production of a highly nutritional microbial biomass for filter-feeding species like Nile tilapia. Therefore, the possibility of producing in a controlled environment with minimal water expenditure, using feeds with smaller protein content and in lower amount, smaller power consumption due to the

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absence of recirculating water and the possibility of reducing environmental impacts are features that help justify the studies and investments made on that system.

Knowing production systems is highly important to establish and manage animal breeding programs, since differences in individual reactions to environment changes may result in genotype-environment interaction (Falconer and Mackay, 1996). When aiming to establish new farming systems for Nile tilapia, such as BFT, on a global scale, studies are necessary to obtain relevant genetic parameters and genetic resources suitable for farming under that system's conditions.

Genetic parameters for economically relevant traits in Nile tilapia reared in cage (Bentsen et al., 2012), ponds (Trong et al., 2013b; Thodesen et al., 2011, 2013; Santos et al., 2011) and RAS (Rutten et al., 2005; Turra et al., 2012a,b) endorse the practice of selection as a tool to alter the mean phenotype of relevant traits in the species. Nonetheless, estimates of genetic parameters for populations farmed in BFT were not found.

Studies on genotype-environment interaction (GE) have also been made for Nile tilapia farmed in cage or ponds (Santos et al., 2011; Bentsen et al., 2012). However, works aiming to estimate genetic covariance between any production-relevant traits concerning RAS, BFT and other farming systems are unknown to us.

On the presence of GE, the environment employed for breeder selection must be similar to the environment used to rear offspring, so that a decrease in progeny performance is avoided. The implementation and maintenance of breeding programs suitable for each of the production systems differently affected by GE brings an increase in production costs. Thus, the study aimed to estimate genetic parameters and examine the genotype-environment interactions for growth traits of Nile tilapia farmed in BFT, RAS and Cage.

2. Material and methods

2.1. The experiment

The experiment was held at the Aquaculture Laboratory (Laboratório de Aquacultura - LAQUA) of the Veterinary School, Federal University of Minas Gerais (Universidade Federal de Minas Gerais - UFMG), Brazil, where the RAS and BFT systems are located, and at the 2.5 ha reservoir at Helio Barbosa's Experimental Farm, a farming research center owned by UFMG. The pedigreed population used in the study was the laboratory's Chitralada strain of Nile tilapia, descendants of a seed stock acquired from a commercial hatchery in Minas Gerais State that conducts a breeding program based on weight.

Eighty-six full-sib families were produced by mating 43 males and 86 females that were randomly sampled from 150 males and 400 females, each tagged with a unique passive integrated transponder device (pit tags). A male and two females previously identified as “ready to spawn” were maintained in a 1 m^3 fiberglass tank for one week. At the end of this period, the eggs from fertilized females were taken out from their mouths and transferred to individual stainless steel strainers with 8 cm diameter for a one-week incubation period. The strainers were kept floating in a 1 m^3 fiberglass tank using Styrofoam bars. Air bubbles from a blower and air diffusers inside the fiberglass tank helped provide adequate water flow for the eggs.

To obtain the necessary number of full-sib families, new females were randomly sampled from among “ready to spawn” females from the initial group to replace non-reproducing females. Males that did not produce a full-sib family during the two-week interval or that killed a female were also replaced.

Full-sib families were produced in an 8-week period from December 2013 to January 2014. During that time, the 1 m^3 tanks were maintained in a recirculating water system, with water quality control to provide welfare and promote reproductive success of fish. The males and females that were not chosen for reproduction stayed in 4 m^3 biofloc tanks separate by sex, inside a greenhouse.

Larvae from each dam were cultured in two separate 100 l hapas (nylon mesh net cages), each one containing 35 to 50 larvae (75 to 100 larvae per full-sib family, taking into account the two hapas). Twenty hapas were placed in each of the 4 m^3 tanks, which were maintained in a greenhouse. Good water quality was sustained by replacing 30% of the water per day and aeration came from side channel blowers and air diffusers. Nine tanks were used to allocate all hapas. Three different mesh sizes of hapas were used. In the first week, larvae stayed in 1 mm mesh size hapas, in the second week they were transferred to 3 mm mesh size hapas, and in the third week they were transferred to 5 mm mesh size hapas, and kept there until being tagged. After tagging, (pit tags) they were combined and placed in tanks using RAS, BFT and Cage systems.

Tilapia from the first 45 full-sib families produced (in the first four weeks of the reproduction period) were tagged and combined in a first group. When the fish from these families were tagged, their average age was 60 days (45 to 76 days of age post-hatching interval). The other 41 full sib-families were combined in a second group (produced in the last four weeks of the reproduction period). The fish from these last families also had the same average age and post-hatching interval when they were tagged. Sixteen males had progenies in the first group, fourteen males had progenies in the second one and almost a third of sires (13) had progenies in both groups, which ensured connectedness of data. Each group was reared in four tanks (4 m^3 capacity/tank) using BFT system, two tanks using RAS system (3 m^3 capacity/tank) and in one cage using Cage system (4 m^3 capacity/cage). Thus, eight BFT tanks, four RAS tanks and two cages were used in the experiment. The period of communal stock went from May to August 2014, for the first group, and from June to September 2014, for the second one.

All tanks and cages used for each group received members from each hapa from the respective group (two to three tilapias from each hapa). The RAS and BFT tanks received 275 tilapias each and cage tanks, 550 tilapias. Unidentified fish previously and randomly removed from the families were used to complete the stocking densities when the amount of tilapias from a family was not sufficient. The total amount of tagged tilapias in BFT system was: 1986 fish (1065 from group 1 and 921 from group 2); in RAS system, 988 (group 1 = 532, group 2 = 456) and in Cage system, 1002 (group 1 = 532, group 2 = 470); totalizing 3976 tilapias. The BFT tanks were inside a greenhouse adjacent to LAQUA, the RAS tanks were inside LAQUA (both at the Veterinary School of UFMG – 19°52′16″S; 43°58′15″W) and the cage tanks were placed in a reservoir at UFMG's farm (20°04′20″S; 44°20′51″W).

Feeding management was the same for all hapas before tagging, and remained constant among the three different farming systems. Fish were fed five times a day with commercial powder containing 50% crude protein at a rate of 8% body weight during the first four weeks, and micro pellets containing 42% crude protein at a rate of 5% body weight during the four other weeks. After being distributed to the three systems, fish were fed three times a day with commercial pellets containing 32% crude protein at a rate of 5% body weight.

2.2. Recordings

Each fish was individually weighed when tagged, and moved to one of the three different systems, which happened around 45 to 76 days of age post-hatching. They were weighed again around 100 days later, after which they had their sex determined. At the second weighing, their average age was 160 days post-hatching, with an interval of 142 to 176 days of age post-hatching. The electronic balance used to weight the tilapia for the first time had a 5000 g capacity, 0.1 g precision and accuracy for measures larger than 1 g.

The first weight was standardized to 56 days post-hatching (8 weeks), and the second one to 168 days post-hatching (24 weeks). These are selection criteria defined for the Nile tilapia breeding program of LAQUA. Heavier fish at 56 days of age post-hatching will allow for a

reduction in time until tagging in the future. Heavier fish at 168 days of age post-hatching (slightly less than half of a year) can enable the selection of two generations per year in the breeding programs. Besides, previous papers (Rutten et al., 2005; Turra et al., 2012a) have shown that the trait weight close to this age has high genetic correlation (>0.85) with weights at older ages, and so it is not necessary to prolong the growth of fish, reducing the cost of the breeding program. In addition, the heritability for this age is moderate to high, allowing significant genetic gains.

The first weight (W56) was standardized as:

$$W56 = \frac{Wtag}{Atag} \times 56,$$

where *W*56 is the weight standardized to 56 days post-hatching, *Wtag* is the weight when the tilapia was tagged, *Atag* is the age when the tilapia was tagged.

The second weight (*W*168) was standardized as:

$$W168 = \frac{W2nd - Wtag}{A2nd - Atag} \times (168 - A2nd) + W2nd,$$

where *W*168 is the weight standardized to 168 days post-hatching, *W*2*nd* is the second weight of the tilapia, *A*2*nd* is the age when the tilapia was weighed for the second time.

Despite being possible to use age as a covariable in the analysis, we do not think this would be the best option for this dataset. If we use age as a covariable, we assume that fish from all families have the same daily weight gain, reducing the additive genetic variance. Therefore, by correcting individually instead of using age as covariable, we account for the individual growth of each fish. This practice reduces the error in the estimated weight, since each fish has its weight adjusted by its own growth records and not by the average of its group.

The electronic balance used to weigh the tilapia at the second occasion had a 5000 g capacity, 0.1 g precision and accuracy for measures larger than 50 g. So, at that time, when tilapia weighed <50 g, they would not be not be included in the W168 data set, despite the fact that, if the fish could be sexed, its first weight would be included the W56 data set. Because of that, the total variance of the W168 data set is less than what it would be. And so, the data set for W56 contained all measures of tilapias weighed when tagged and sexed at the second weighing (3869 tilapias out of the 3976 initially tagged ones). The W168 data set contained weights of tilapia sexed and heavier than 50 g at the second weighing (3723 tilapias). In the current analysis, those animals that could not be weighed were treated as missing data in the W168 data set. Therefore, there is a small selection bias due to the inexistence of approximately 3.7% of the animals from W56 in W168. The descriptive statistics for growth traits are shown in Table 1.

Average standardized weight obtained at 56 days post hatching was 20 ± 9 g standard deviations and average standardized weight at 168 days post hatching was 235 ± 105 g standard deviations. On Table 1 all data is displayed according to fish sex and production system in which tilapia were stocked after being tagged. Throughout the entire 14-week period (approximately 100 days) in which animal were reared together in the different production systems, physical and chemical water quality parameters were constantly monitored and manipulated, when possible, so that they remained in suitable levels for tilapia. For this reason, at all three systems oxygen levels remained higher than 4 mg/l, ammonia always lower than 0.5 mg/l and pH between 7.0 and 7.5. Water temperature, however, went from 27 to 28 °C in the RAS tanks (groups 1 and 2); 24 to 29 °C and 23 to 28 °C in BFT tanks, groups 1 and 2, respectively; 19 to 21 °C and 18 to 20 °C, in cage tanks, groups 1 and 2, respectively.

Allocating fish from each hapa into every system ensured that average tagging ages and average standardized weight at 56 days of age were very similar among all systems, within each group. Nevertheless, such average weights were slightly inferior in group 2 when compared to group 1. This is explained by a minor decrease in water temperature during hapa farming stages in group 2 (23–27 °C), when compared to group 1 (24–28 °C), due to the beginning of the fall, with lower temperatures outside the greenhouse.

In both groups, at all farming systems, the number of fish weighed for the second time was smaller than what had been initially stocked, as a result of small mortality and a minor loss of pit tags (practically none). However, in group 2 the number of females reared in cages that could be sexed and weighed for a second time was even smaller than at other farming systems. In June, when fish from group 2 were distributed among systems, water temperature at the reservoir was already quite low due to the coming of winter. Temperature was lower than what had been in May, when fish from group 1 were stocked. A higher sum of fish in group 2, particularly females, could not reach weight superior to 50 g, and so were not weighed.

2.3. Statistical analysis

The components of variance were estimated by a four-trait Bayesian analysis. The assessed traits included the weight standardized to 56 days post-hatching (W56, the weight around the time fish were tagged) and the weights standardized to 168 days post-hatching at the three different production systems, W168 BFT, W168 RAS and W168 Cage.

The mixed animal model for the analysis of all traits included the fixed effect of sex and random effects for additive genetic merit and hapa (Table 2). Since the families were reared in two separated hapas until having gained enough weight to be tagged, this last effect is an attempt to account for non-additive genetic influences, additive maternal genetic effects and effects of a common environment (Martinez et al., 1999; Pante et al., 2002). Fixed effect of tank (the effect from different tanks, at the different systems where fish were stocked after tagging) was also included for traits of standardized weight at 168 days of age.

Table 1
Means ± standard deviation of standardized weight at 56 days of age of male and female Nile tilapia deriving out of 86 full-sib families, and of standardized weight at 168 days of age in three farming systems: biofloc (BFT), recirculating water (RAS) and cage tanks (Cage).

Group	System	N[a]	Sex	N[b]	Weight at 56 days of age (g)	N[c]	Weight at 168 days of age (g)
1	RAS	532	M	293	24 ± 9	293	388 ± 69
			F	223	22 ± 9	223	303 ± 62
	BFT	1065	M	560	23 ± 9	560	247 ± 64
			F	482	21 ± 13	482	205 ± 53
	Cage	532	M	366	23 ± 10	347	148 ± 56
			F	159	25 ± 9	159	131 ± 40
	Sum	2129		2083		2064	
	Mean				23 ± 9		
2	RAS	456	M	228	17 ± 9	225	400 ± 110
			F	213	15 ± 7	213	315 ± 72
	BFT	921	M	493	17 ± 8	489	226 ± 75
			F	402	15 ± 7	399	190 ± 61
	Cage	470	M	352	15 ± 7	236	126 ± 52
			F	98	21 ± 6	97	117 ± 33
	Sum	1847		1786		1659	
	Mean				16 ± 9		
Total		3976		3869		3723	
Mean					20 ± 9		235 ± 105

[a] Number of fish tagged at the time of distribution among the systems.
[b] Number of fish weighed when tagged and sexed at the second weighing.
[c] Number of fish weighed when tagged, and also sexed and weighed on a second occasion.

Table 2
Fixed and random effects included in the statistical models of standardized weight at 56 days of age (W56), standardized weight at 168 days of age in biofloc (W168 BFT), recirculating water (W168 RAS), and cage tanks (W168 Cage).

Trait	Fixed effects[a]		Random effects	
	Sex	Tank	Hapa (family)	Animal
W56	X		X	X
W168 BFT	X	X	X	X
W168 RAS	X	X	X	X
W168 Cage	X	X	X	X

[a] Fixed effects that were considered of significance based on an analysis of variance ($p < 0.01$), through the PROC GLM procedure from the SAS statistical package.

The four-trait model is described in matrix notation as:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix} = \begin{bmatrix} X_1 & \phi & \phi & \phi \\ \phi & X_2 & \phi & \phi \\ \phi & \phi & X_3 & \phi \\ \phi & \phi & \phi & X_4 \end{bmatrix} \cdot \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} + \begin{bmatrix} Z_1 & \phi & \phi & \phi \\ \phi & Z_2 & \phi & \phi \\ \phi & \phi & Z_3 & \phi \\ \phi & \phi & \phi & Z_4 \end{bmatrix} \cdot \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{bmatrix} + \begin{bmatrix} W_1 & \phi & \phi & \phi \\ \phi & W_2 & \phi & \phi \\ \phi & \phi & W_3 & \phi \\ \phi & \phi & \phi & W_4 \end{bmatrix} \cdot \begin{bmatrix} f_1 \\ f_2 \\ f_3 \\ f_4 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix}$$

where y_i is the vector of observations for trait i, b_i is a fixed effect vector (sex and tank); u_i, f_i and e_i are vectors of additive genetic, hapa and residual random effects, respectively; X_i, Z_i and W_i and are design matrices related to vectors b_i, u_i and f_i, respectively; and ϕ is a null matrix.

Flat prior distributions were assumed for the fixed effects ($\begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$), and normal distributions were assumed for the random effects ($\begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{bmatrix} | G$, $\begin{bmatrix} f_1 \\ f_2 \\ f_3 \\ f_4 \end{bmatrix} | F$ and $\begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix} | R$), whereas an inverted Wishart distribution was assumed for (co)variance matrices ($G_0 | v_u, S_u$, $F_0 | v_f, S_f$ and $R | v_e, S_e$),

where $G = G_0 \otimes A$ represents the genetic (co)variance matrix; $G_0 = \begin{bmatrix} \sigma^2_{u_1} & \sigma_{u_1u_2} & \sigma_{u_1u_3} & \sigma_{u_1u_4} \\ \sigma_{u_1u_2} & \sigma^2_{u_2} & \sigma_{u_2u_3} & \sigma_{u_2u_4} \\ \sigma_{u_1u_3} & \sigma_{u_2u_3} & \sigma^2_{u_3} & \sigma_{u_3u_4} \\ \sigma_{u_1u_4} & \sigma_{u_2u_4} & \sigma_{u_3u_4} & \sigma^2_{u_4} \end{bmatrix}$ represents the matrix of genetic (co)variance between four traits; ${\sigma_{u_i}}^2$ represents the additive genetic variance of trait i; $\sigma_{u_iu_{i'}}$ represents the additive genetic covariance between traits i and i'; $F = F_0 \otimes I$ represents the hapa matrix; $F_0 = \begin{bmatrix} \sigma^2_{f_1} & \sigma_{f_1f_2} & \sigma_{f_1f_3} & \sigma_{f_1f_4} \\ \sigma_{f_1f_2} & \sigma^2_{f_2} & \sigma_{f_2f_3} & \sigma_{f_2f_4} \\ \sigma_{f_1f_3} & \sigma_{f_2f_3} & \sigma^2_{f_3} & \sigma_{f_3f_4} \\ \sigma_{f_1f_4} & \sigma_{f_2f_4} & \sigma_{f_3f_4} & \sigma^2_{f_4} \end{bmatrix}$ represents the matrix of hapa (co)variance between traits; ${\sigma_{f_i}}^2$ represents the hapa variance of trait i; $\sigma_{f_if_{i'}}$ represents the hapa covariance between traits i and i'; $R = R_0 \otimes I$ represents the residual (co)variance matrix; $R_0 = \begin{bmatrix} \sigma^2_{e_1} & \sigma_{e_1e_2} & \sigma_{e_1e_3} & \sigma_{e_1e_4} \\ \sigma_{e_1e_2} & \sigma^2_{e_2} & 0 & 0 \\ \sigma_{e_1e_3} & 0 & \sigma^2_{e_3} & 0 \\ \sigma_{e_1e_4} & 0 & 0 & \sigma^2_{e_4} \end{bmatrix}$, represents the matrix of residual variance of traits; ${\sigma_{e_i}}^2$ represents the residual variance of trait i; $\sigma_{e_ie_{i'}}$ represents the residual covariance between traits i and i'; v_a, v_f and v_e (degrees of freedom of the inverted Wishart distributions) and S_a, S_f and S_e (4×4 matrices with the prior "guess" for the variance components) represent the hyper-parameters of the inverted Wishart distributions of genetic, hapa and residual (co)variances; and the other terms are the same as those described above. The complete conditional posterior distributions are available in Sorensen and Gianola (2002).

Gibbs chains of 410,000 iterations were generated for each parameter, with a burn-in period of 10,000 iterations and a sampling interval of 200 iterations in GIBBS1F90 program (Misztal et al., 2014). Convergence diagnostics were performed following Geweke's (1992) and Heidelberger and Welch's (1983) techniques, and visual analysis of trace plots was performed using the Bayesian Output Analysis (BOA, Smith, 2005) program in R software 2.9.0 (R Development Core Team, 2015). The Geweke test (Geweke, 1992) compares the means from the early and late parts of the Markov chain to detect failure of convergence in such a way that the null hypothesis tested confirms convergence because probabilities smaller than 0.05 provide evidence against convergence of the chain. In the Heidelberger and Welch (1983) diagnostic test, the null hypothesis is that sample values come from a stationary process. If there is evidence of nonstationarity, the test is repeated after discarding the first 10% of the iterations. This process continues until 50% of the iterations have been discarded or until the chain analyzed passes the test. The Heidelberger and Welch (1983) test uses the Cramer-von-Mises statistic. Visual inspection consists of observation of the plots generated, and convergence of the chains is evaluated by the tendency and areas of density of distribution of the chains.

Samples of the posterior distributions of the genetic correlations were used to determine the genotype-environment interaction according to Falconer (1952).

The genetic (r_g), hapa (family and common environment) effect (r_f) and residual (r_e) correlations between any pair of traits were estimated in the following way:

$$r_{g_{i,i'}} = \frac{\sigma_{g_ig_{i'}}}{\sqrt{\sigma^2_{g_i} * \sigma^2_{g_{i'}}}}, \quad r_{f_{i,i'}} = \frac{\sigma_{f_if_{i'}}}{\sqrt{\sigma^2_{f_i} * \sigma^2_{f_{i'}}}}, \quad r_{e_{i,i'}} = \frac{\sigma_{e_ie_{i'}}}{\sqrt{\sigma^2_{e_i} * \sigma^2_{e_{i'}}}}.$$

Samples of the posterior distributions of the direct and indirect responses to selection were obtained with the samples of the (co)variance components, and selection of 5% of the males with phenotypic data (selection intensity = 2.06) and 10% of females (selection intensity = 1.76), thus the average selection intensity used in the calculations of responses was 1.91. The expected responses to direct mass selection per generation were calculated using the following equation:

$$\Delta G_i = i_i h_i^2 \sigma_{p_i},$$

where ΔG_i represents the expected genetic gain per generation; i_i represents the selection intensity; h_i^2 represents the heritability; and σ_{p_i} represents the phenotypic standard deviation corresponding to trait i.

The expected correlated responses per generation were calculated using the following equation:

$$\Delta G_{yx} = r_{a_ya_x} h_y h_x i_x \sigma_{p_y},$$

where ΔG_{yx} represents the expected correlated response per generation relative to a given trait in environment Y by selecting for the same trait in environment X; $r_{a_ya_x}$ represents the genetic correlation of a trait measured in environment X and environment Y obtained in two trait analysis; h_y represents the square root of the heritability for trait in environment Y; h_x represents the square root of the heritability for trait in environment X; i_x represents the selection intensity in environment X; and σ_{p_y} represents the phenotypic standard deviation in environment Y.

3. Results

Posterior means of heritability for W56 and W168, in the three systems evaluated, showed great magnitude. Posterior mean of heritability for W168 was smaller despite posterior means of additive and residual genetic variance being higher for animals reared in RAS when compared to animals farmed in BFT or Cage (Table 3). For animals reared in BFT or Cage there was an overlapping of highest posterior density intervals with 95% of samples (HPD95%) for additive genetic and residual variance, as well as heritability. Thus, it was not possible to point out any differences between parameters obtained in BFT or Cage.

Posterior mean of variance on account of hapa effect was smaller in W168BFT than in W168RAS and Cage (Table 3). However, posterior means for the proportion of phenotypic variance due to hapa variance (f^2) were similar among all environments, with overlapping of HPD95% (Table 3). Coefficients of phenotypic, residual, hapa and genetic variation for Cage systems (Table 4) were higher than in the other traits.

Genetic correlations between W56 and W168 were positive, regardless of rearing environment, with the highest correlation observed between W56 and W168 Cage (Table 5). Also, the genetic correlations between environments for W168 were positive, with the highest between W168 RAS and BFT. Posterior means of correlations among hapa (family and common environment) effects between W56 and W168 Cage and between W168 BFT and W168 Cage were positive (Table 6). HPD95% for hapa correlation among the other pairs of traits was wide and included zero. Residual correlation between W56 and W168 acquired in RAS and Cage was positive, but HPD95% for residual correlation between W56 and W168 BFT included zero, indicating there was no environment association between those two traits (Table 6).

Direct selection for W56 is more efficient than indirect selection through W168 in BFT, RAS or Cage (Table 7). It is possible to increase W168 BFT through direct selection, or indirect selection for W168 RAS or W168 Cage, due to the overlapping of HPD95% of indirect and direct responses in W168 BFT. Similar genetic gain in W168 RAS and W168 Cage can be obtained through direct or indirect selection. In fact, selection to increase W56 implies indirect genetic changes in W168 Cage similar to the ones obtained through direct selection for that last trait. Comparable genetic changes can be obtained in W168 in the three farming systems considered in this study, since there was overlapping of HPD95% for direct and indirect responses of W168 in the three farming systems.

Table 4
Coefficients of phenotypic (CV_p), residual (CV_e), hapa (CV_f) and genetic (CV_a) variation for weight at 56 days of age (W56) and at 168 days of age of Nile tilapias in biofloc technology (W168 BFT), recirculating water (W168 RAS) and cage systems (W168 Cage).

Parameters	W56	W168		
		BFT	RAS	Cage
CV_a	37.37	23.11	19.01	33.92
CV_f	11.03	3.26	5.33	10.75
CV_e	12.08	10.10	13.72	14.29
CV_P	40.79	25.71	22.52	39.67

4. Discussion

When we assume that the world's largest producers of Nile tilapia (China and Southeast Asia) heavily exploit the production in ponds, one could probably infer that the biggest part of the production of this species occurs in this system. The Nile tilapia production statistics in Brazil are not clear enough to identify what production system is the most important. The results of the last census (IBGE, 2014) indicated that domestic production held in ponds and cages possibly had similar amounts, showing how the existence of large reservoirs of inland waters for electricity generation in the country contributed to the activity. This information reinforces the importance of maintaining, especially in Brazil, a breeding program that includes the improvement of the Nile tilapia weight at Cage systems.

From the point of view of production intensification, the cage is an efficient production system. However, concerns about environmental impacts strengthen the importance of studies of production systems that generate sustainable intensification (Garnett et al., 2013). RAS and BFT systems are undeniable options for the generation of much of the Nile tilapia production in the near future (Avnimelech, 2009; Stockstad, 2010), complying with the concepts of intensification that use fewer natural resources and result in less environmental impact, justifying genetic studies of the species in them.

The market weight of Nile tilapia for demanding and better remunerative markets, such as the US and European (Rutten et al., 2005), is >700 g. At the age of 168 days post-hatching, the fish from our genetic improvement program have not yet reached the weight required for more demanding markets. However, Nile tilapia takes much more time to reach heavier weights. Generally it takes at least 300 days of age post-hatching to reach 700 g or above (Rutten et al., 2005), almost twice the time we adjusted the fish weights for our breeding program. Besides, the tilapia were reared at high stocking density in BFT (>60 fish·m^{-3}) and in low temperature averages in cages. These probably affected their growth. But the age of 168 days post-hatching continues to be a good choice for selection criteria as we explained before. The breeding program becomes cheaper and fish farmers, benefited by using these improved animals, may produce fish with the necessary weights for demanding markets in the near future, producing two harvests per year, thus increasing profitability.

Posterior means of heritability for W56, W168 BFT, RAS and Cage were high (Table 3), indicating that selection can alter the mean values of those traits throughout generations. Such results corroborate the ones obtained by Trong et al. (2013b), Khaw et al. (2012) and Bentsen et al. (2012) for heritability of body weight of Nile tilapia reared in cages, those being 0.55 ± 0.12, 0.34 ± 0.06 and 0.42 ± 0.17,

Table 3
Posterior means (highest posterior density interval with 95% of samples) of genetic parameters for weight at 56 days of age (W56) and at 168 days of age of Nile tilapias in biofloc technology (W168 BFT), recirculating water (W168 RAS) and cage systems (W168 Cage).

Parameters[a]	W56	W168		
		BFT	RAS	Cage
σ_a^2	55.87 (49.63; 62.10)	2571.18 (2066.00; 3139.00)	4498.71 (3755.00; 5370.00)	2097.71 (1668.00; 2540.00)
CV_a	37.37 (35.22; 39.40)	23.11 (20.71; 25.53)	19.01 (17.37; 20.78)	33.92 (30.25; 37.33)
σ_f^2	4.87 (2.37; 7.60)	51.10 (9.60; 105.80)	353.99 (149.00; 579.50)	210.46 (105.30; 341.40)
CV_f	11.03 (7.69; 13.78)	3.26 (1.41; 4.69)	5.33 (3.46; 6.82)	10.75 (7.60; 13.68)
σ_e^2	5.84 (3.02; 8.99)	491.47 (192.00; 744.90)	2340.34 (1648.00; 2888.00)	372.11 (147.30; 601.00)
CV_e	12.08 (8.69; 14.99)	10.10 (6.31; 12.44)	13.72 (11.51; 15.24)	14.29 (8.99; 18.16)
h^2	0.84 (0.77; 0.91)	0.82 (0.73; 0.94)	0.62 (0.53; 0.72)	0.78 (0.67; 0.88)
f^2	0.07 (0.02;0.11)	0.02 (0.00; 0.03)	0.05 (0.00; 0.08)	0.08 (0.00; 0.13)

[a] σ_a^2 = additive genetic variance, σ_f^2 = hapa (family common environment) variance, σ_e^2 = residual variance, h^2 = heritability and f^2 = proportion of phenotypic variance on account of hapa variance.

Table 5
Posterior means (highest posterior density interval with 95% of samples) of the genetic correlation for weight at 56 days of age (W56) and at 168 days of age of Nile tilapias in biofloc technology (W168 BFT), recirculating water (W168 RAS) and cage systems (W168 Cage).

	W56	W168 BFT	W168 RAS	W168 Cage
W56	–	0.59 (0.51; 0.67)	0.68 (0.61; 0.75)	0.85 (0.80; 0.90)
W168 BFT	–	–	0.99 (0.98; 1.00)	0.83 (0.75; 0.89)
W168 RAS	–	–	–	0.88 (0.83; 0.93)

respectively. These higher posterior means of heritability presented here for all environments may be due to differences between the strains of tilapia studied and the smaller importance of the hapa (family common environment) effect. Highest posterior mean for additive genetic, hapa and residual variances of W168 from animals reared in RAS might be related to higher average weight observed in that system, when compared to BFT or Cage. This hypothesis is endorsed by the smaller phenotypic CV's obtained in RAS system (Table 4). From the higher phenotypic CV's and CV_e (Table 4) from Cage system, it is possible to infer that this was a more competitive environment when compared to RAS and BFT. Nevertheless, from the higher CV_a (Table 4) shown by the Cage system it is possible to infer that these environment effects (ex.: temperature range) were constant challenges for fish and stimulated the expression of cryptic genetic variation (Paaby and Rockman, 2014; Gibson and Dworkin, 2004).

Hapa (family and common environment) effect is mainly an outcome of having to rear the fish from each family separately for a while, around 60 days post hatching, since they are born extremely light and their identification is impossible. At the end of that period, once they reach weight superior to 4 g it is possible to tag and establish communal rearing of individuals from different families. As a result, including that effect on genetic analysis models enables higher accuracy in predictions. Turra et al. (2012a) noticed that, until reaching 220 days of age, family effect was superior to the direct additive genetic effect in Nile tilapia reared in RAS. Long periods of time until communally stocking the different families may bring differences between families and similarities within families. That brings confusion when dimensioning direct additive genetic effect and family effect (Bentsen et al., 2012). Similar results were obtained by Thodesen et al. (2011) and Santos et al. (2011). It is necessary to draw attention to how the short time to produce these families was important in improving the estimates. Trong et al. (2013a) reinforced the importance of reducing the time to produce the families and their results in improvement of the variance partitioning, allowing higher heritability results. Our time for producing families (8 weeks) was lower than several others reported in the literature (Rutten et al., 2005; Turra et al., 2012a; Trong et al., 2013b). Nonetheless, in this study only a small fraction of phenotypic variance is explained by hapa variance. This may have been a result of crucial management plans carried out, such as: well designed experiment, short period of time for reproduction, rearing the families split between two hapas, sustained use of the same feeding plan and water quality among hapas, and, after identifying families, distributing fish from every hapa into all units (of each group) from the three farming systems (Table 3). That allowed for a better understanding of variances obtained, and helped identify genetically superior animals within and between families, and so enabled access to more precise and accurate values for genetic parameters.

Selecting for W168 in Cages through selection at 56 days of age apparently brings no damage to genetic gain per generation, since there was great overlapping of HPD95% for response to direct and indirect selection of those traits. Still, it is important to highlight that the lower temperatures of the water in the reservoir (18 a 21 °C) kept tilapia from properly developing. As a result, it is possible that differences between individual weights at tagging occasion may have lasted until the end of rearing period in cages, what is worsened by the fact that fish weighing <50 g were not considered. That scenario may have contributed to increase genetic covariance between W56 and W168 Cage (Table 5) and, consequently, response correlated with selection. Selection based on W56 can reduce the costs of maintaining animals for longer periods before selection, reduce generation intervals and increase selection intensity based on W56, since it is easier to farm a bigger number of animals until reaching 20 g than 230 G. However, it is still not possible to sex tilapia at 56 days of age. That implies in extending farming periods until an intermediate age between 56 and 168 days, reducing the advantages from indirect selection for W168 Cage through W56. In the cases of W168 in BFT and RAS, direct selection was more efficient than indirect selection through W56 (Table 7). Higher water temperature in BFT tanks (greenhouse) and RAS (constant electric heating) allowed better development of tilapia, enabling the weight differences in animals when tagged to be altered, thus reducing genetic association between W56 and W168 BFT and W168 RAS (Table 5). Since we cannot select males and females at 56 days of age, one strategy that may be interesting in this case is to use two-stage selection (Martinez et al., 2005; Sae-Lim et al., 2012). With two-stage selection one can reduce the costs and increase genetic gains, since the selection can be done in a larger initial group of fish. In a two stage selection frame-work, fish can be selected first for weight at tagging age (56 days in this case) without accounting for different selection intensity for males and females. Later on, at approximately 168 days, sex can be easily determined and a second selection can be applied, this time with different selection intensities between males and females.

When genetic correlation between the same trait measured in different environments is smaller than 1.0 (Falconer, 1952) or 0.8 (Robertson, 1959), existence of genotype-environment interaction is observed. Furthermore, James (1961) and Mulder et al. (2006) stated that, when finding genetic correlations inferior to 0.70 and 0.61, respectively, it is desired that breeder's selection occurs in an environment similar to the one used to farm progeny. In a recent and wide review about GE, Sae-Lim et al. (2015) showed that that re-ranking appears to be moderate (average genetic correlation = 0.72) for growth in a quantitative review across 38 aquaculture species.

The genetic correlation between W168 measured at the different systems was higher than the limit set by James (1961); Mulder et al. (2006) and, many of the paper reviewed by Sae-Lim et al. (2015). For that reason, it is not necessary to develop specific animal breeding programs for the improvement of the Nile tilapia weight at this age post-hatching, for each of the three systems evaluated (Table 5). Moreover, HPD95% for direct and indirect response of W168 greatly overlapped among the three farming systems tested, indicating that selection in a single system does not cause losses in genetic gain per generation for the other systems (Table 7). For that reason, animals of higher genetic value for W168 in BFT system can be used as breeders in RAS or Cage systems, without harming progeny performance at this age. Accordingly, breeders of higher genetic value in RAS or Cage can be used in BFT systems.

Table 6
Posterior means (highest posterior density interval with 95% of samples) of the family correlation (above diagonal) and residual correlation (below diagonal) for weight at 56 days of age (W56) and at 168 days of age of Nile tilapias in biofloc technology (W168 BFT), recirculating (W168 RAS) and cage systems (W168 Cage).

	W56	W168 BFT	W168 RAS	W168 Cage
W56	–	0.37 (−0.17; 0.79)	−0.53 (−0.86; −0.16)	0.86 (0.71; 0.97)
W168 BFT	−0.32 (−0.65; 0.01)	–	−0.06 (−0.56; 0.52)	0.69 (0.37; 0.97)
W168 RAS	0.70 (0.55; 0.84)	–	–	−0.19 (−0.66; 0.26)
W168 Cage	0.50 (0.22; 0.72)	–	–	–

Table 7
Posterior means (highest posterior density interval with 95% of samples) of direct (diagonal) and indirect-selection responses (off-diagonal, and in columns[a]) for weight at 56 days of age (W56) and at 168 days of age of Nile tilapias in biofloc technology (W168 BFT), recirculating water (W168 RAS) and cage systems (W168 Cage).

	W56	W168 BFT	W168 RAS	W168 Cage
W56	12.59 (11.28; 13.96)	7.29 (6.25; 8.39)	7.43 (6.44; 8.34)	10.32 (8.87; 11.62)
W168 BFT	51.36 (44.28; 59.14)	87.14 (73.61; 102.64)	75.27 (62.34; 88.95)	69.99 (57.83; 81.25)
W168 RAS	78.19 (69.16; 86.95)	112.39 (97.04; 132.01)	98.74 (82.12; 114.98)	97.30 (82.10; 111.14)
W168 Cage	65.32 (56.83; 75.80)	62.86 (51.92; 73.88)	58.49 (48.32; 67.72)	74.23 (60.95; 87.79)

[a] Traits in columns are the selection criteria and traits in lines are the selection goal. For example: 51.36 g, the number in the first column and in the second line, is the posterior mean of indirect selection response for W168 BFT, using W56 as selection criteria.

5. Conclusions

Heritabilities for weight at 56 and 168 days of age in Nile tilapia, in biofloc technology, recirculating water and Cage systems are high and selection should bring genetic changes in those traits. Genetic correlations for weight of tilapia at 168 days of age in biofloc technology, recirculating water or Cage systems are high and indirect responses are similar to direct responses, regardless of system considered. At first, it is not necessary to develop environment-specific animal breeding programs for higher weight at 168 days of age of Nile tilapia reared in biofloc technology, recirculating water and Cage systems.

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