Aquaculture 513 (2019) 734429

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture

Genotype by environment interaction across time for Nile tilapia, from juvenile to finishing stages, reared in different production systems

Arthur F.A. Fernandes[a], Érika R. Alvarenga[b], Gabriel F.O. Alves[b], Ludson G. Manduca[b], Fábio L.B. Toral[b], Bruno D. Valente[c], Martinho A. Silva[b], Guilherme J.M. Rosa[a], Eduardo M. Turra[b,*]

[a] University of Wisconsin-Madison, 1675, Observatory Dr., Madison, WI 53706, USA
[b] Escola de Veterinária da Universidade Federal de Minas Gerais, Av. Antônio Carlos, no 6627, Caixa Postal 567, Campus da UFMG, CEP 30123-970. Belo Horizonte, MG, Brazil
[c] Genus PLC, 100 Bluegrass Commons Blvd., Ste. 2200, Hendersonville, TN 37075, USA

ARTICLE INFO

Keywords:
Random regression
Selection optimization
Breeding strategies
Biofloc technology
Oreochromis niloticus

ABSTRACT

Nile tilapia is one of the most important fish for aquaculture worldwide and it is produced under many different environmental and system conditions. Even though genotype by environment interaction (GEI) can arise due to many factors, most studies with Nile tilapia have focused more on the effects of water quality parameters and pound or cage systems. There is also lack of knowledge on GEI between fish at different ages, as before and after reaching sexual maturity. Therefore, the objective of the current work was to evaluate the magnitude of GEI on body weight in Nile tilapia raised in biofloc technology (BFT), cage and recirculation aquaculture systems (RAS) from 100 to 350 days of age. To evaluate the temporal trend of GEI a multi-trait random regression model (MTRRM) with age as random regression covariable was employed. Higher values of heritability estimates were found around 225 days, with a maximum of 0.4 for BW at RAS. Estimated genetic correlations between BFT and RAS were above 0.7 for almost any combination of ages evaluated. On the other hand, genetic correlations between Cage at ages below 150 days and either BFT or RAS at any other age were positive but lower than 0.6. Results for the estimated ratio of the indirect by direct response to selection were lower for selection performed at very younger ages whereas the desired response is for older ages. However, if the selection is performed around 225 days for either BTF or RAS this ratio is above 0.8 for most of the situations considered. In conclusion, MTRRM is shown to be a powerful statistical tool to assess changes across the time for genetic parameters of interest, such as covariance, correlations, and heritability. Also, the GEI across the three production systems considered was found to be dynamic across the ages evaluated, with stronger effects between Cage and both BFT and RAS if the selection is performed prior to 150 days of age.

1. Introduction

Nile tilapia is one of the most widely farmed fish worldwide, with a production of 3.67 million tons in 2014 (FAO, 2016). It is produced in more than 100 countries under many different environmental conditions ranging from tropical to temperate climates. Therefore, many different production systems are used for tilapia production, with the most common being pond and cage systems. These systems, are highly affected by changes in climate and quality of water source but tend to be the most cost-efficient.

Other systems of importance are recirculation aquaculture systems (RAS) and biofloc technology (BFT). RAS is known for its effective water reuse, control of water quality parameters, high biosecurity, and high stocking densities. Therefore, this technology is used worldwide in breeding programs, reproduction facilities or production of animals that have higher commercial value and higher requirements of water quality. Nonetheless, RAS has a high operation cost. Despite the economic restrictions, the interest in RAS has grown in recent years, due to the appeal of minimal environmental impact and system integration with other crops (Dalsgaard et al., 2013). BFT follows the same principle of a minimal environmental impact and higher control of water quality parameters and biosecurity as RAS but it has some advantages over the later. The BFT system is based on the mutual production of microbial community with the aquatic species of interest, without the

* Corresponding author.
E-mail address: eduardoturra@yahoo.com.br (E.M. Turra).

https://doi.org/10.1016/j.aquaculture.2019.734429
Received 15 April 2019; Received in revised form 9 August 2019
Available online 30 August 2019

need for an external water treatment unit (Avnimelech et al., 2015). The microbial community captures nitrogen compounds, such as ammonia, for growth. It can also serve as supplemental nutrition for the fish. In short, this system can provide improved cost efficiency compared to RAS. These desirable features of BFT were responsible for its expansion in shrimp production worldwide that occurred as a consequence of the spread of diseases, such as the white spot disease (Brito et al., 2014).

Genotype by environment interaction (GEI) can arise due to many factors in aquaculture such as nutrition, water quality and production system differences. Moreover, the GEI can change over time due to different gene activity as the fish grows. A strong GEI may compromise the performance of genetically improved fish lines, which is troublesome for breeding programs. Thus, since there are major differences between cage, RAS and BFT systems, a question that arises is if there is important genotype x environment interaction (GEI) between Nile tilapia raised on these systems. The identification of GEI that affects traits of interest under these different systems is of importance when devising breeding strategies. Mostly, the presence of GEI is determinant for the decision to develop different breeding programs focused on each system. However, most of the literature information on Nile Tilapia is restricted to pond and cage systems. To the best of our knowledge, only Turra et al. (2016) studied GEI for live body weight (BW) of Nile tilapia reared in BFT, cage, and RAS. In this previous study, negligible GEI was reported for BW at ages of 56 and 168 days post-hatching and average BW of 256 g. That age interval represents the period from tagging to the selection of fish that will be the broodstock of the next generation. However, in a commercial system, there is a need for fish to reach heavier weights, between 0.5 and 1 kg. This implies in longer rearing cycles, increasing the chances for GEI effects to accumulated and be expressed.

The literature has many examples of studies of GEI in fish, with a variety of modeled environmental factors, such as temperature and water salinity (Dinh Luan et al., 2008; Sae-Lim et al., 2014), and diets (Khaw et al., 2009), or complex combinations of factors such as different production locations and or rearing systems (Bangera et al., 2015; Bentsen et al., 2012; Santos et al., 2011). A recent review on GEI in aquaculture can be found in Sae-Lim et al. (2015). Various statistical approaches have been proposed to investigate GEI, such as accounting for the interaction term of genotype and environment, multi-trait analysis, or reaction norms (Falconer, 1990; Falconer and Mackay, 1996; Meyer, 2009). However, GEI is normally studied as a constant, assuming that there is no temporal change in the GEI. Even when there is interest in investigating potential temporal changes on GEI, quite often several analyses are conducted, one for each period of interest. This approach, however, may be cumbersome for the interpretation of the results.

A more interesting methodology to study temporal changes with longitudinal data while accounting for possible GEI is through random regression models (RRM). With RRM, not pointwise variance but the shape of the covariance surface can be modeled as a function of the random regression covariable (Henderson Jr, 1982; Schaeffer, 2016). In GEI studies RRM has been used as a way to model environmental sensitivity via reaction norms, in which, the environmental variable is modeled as the random regression covariable. Such an approach has been well explored in livestock genetics e.g. Calus et al. (2002), Kolmodin et al. (2002), Sae-Lim et al. (2014) and Mota et al. (2015). Also, RRM can be extended for multi-trait analysis by modeling the covariance structure of multiple traits. This multi-trait RRM (MTRRM) has been used before in aquaculture for estimation of heritability and genetic correlations between growth traits across time (He et al., 2017; Rutten et al., 2005a; Turra et al., 2018). However, to the best of our knowledge, there is no study that applied MTRRM in order to evaluate GEI. This approach is appealing for evaluating the GEI trend between longitudinal traits measured in different environmental conditions across time.

The main objective of the present work was to study the temporal trajectory of the genetic parameters and the effects of GEI for BW of Nile tilapia, from 100 to 350 days of age, produced under three different systems: BFT, cage, and RAS. For this purpose, a MTRRM approach was applied for the estimation of covariance components between BW measured in the different production systems. As such, the genetic correlation could be estimated for any combination of production system and time point within the studied range.

2. Material and methods

2.1. Fish production and data collection

The experiment was conducted following rigorous animal handling procedures that are in compliance with federal and institutional regulations regarding proper animal care practices (CONCEA, 2016). Full-sib families were produced in an 8-week period from December 2013 to January 2014. In order to produce the fish for this experiment, 43 males and 86 females were randomly selected from the broodstock of Chitralada Nile tilapia line of the Aquaculture Laboratory (LAQUA) of the Veterinary School, Federal University of Minas Gerais (UFMG). Each male was matted to 2 females in a 1 m^3 fiberglass tank on a RAS with water quality parameters monitored and controlled, thus, producing a total of 43 half-sib families (86 full-sib families). After a one-week period, the females were checked for fertilized eggs in their mouths and removed from the reproduction tanks. The eggs from each fertilized female were collected and artificially incubated. After one week of incubation, larvae from each female were transferred to two separated 100 L hapas (35 to 50 larvae) and reared to approximated 60 days post-hatching. The hapas were maintained into 4 m^3 tanks inside a greenhouse. Hapas of 3 different mesh size were used (1, 3 and 5 mm), changed accordingly to fish growth. After the end of this period, fish from families closer in age were tagged and distributed to experimental units at the 3 systems. The systems were composed of 8 tanks of BFT, 4 tanks of RAS and 2 cages. At allocation time, fish from each family were proportionally distributed, so that every family had a suitable number of individuals in all 3 systems, ensuring data connectivity. In the end, each half-sib family had at least 10 fish in each system and each rearing tank had at least 172 fish (Supplementary Tables S1 and S2). The RAS and BFT complex was located at LAQUA (Latitude: −19.871198, Longitude: −43.970573), while cages were allocated on the water reservoir of the Experimental farm (Latitude: −20.071751, Longitude: −44.347748), of the Veterinary School of UFMG. The feed strategy was the same for all fish, before and after tagging, following common practices of tilapia feeding. Each fish was individually weighed up to 3 times during its life: the first at tagging, with approximately 60 days post-hatching; the second at approximately 160 days, mimicking the selection age at a breeding program; the last weighing was approximately at one of 3 ages 220, 280 and 340 days post-hatching. At this final weighing, fish were randomly selected and slaughtered. This process was performed in order to increase the range of studied ages and to have an appropriate number of individuals weighed across the studied period.

2.2. Statistical analysis

RRM has been used to model longitudinal data in many areas of application. Specifically, in GEI studies, RRM has been used mostly in reaction norms, where the environmental variable of interest is modeled as a covariance function. This approach is interesting if the environmental variable has a continuum or at least ordered behavior. In these cases, the GEI can be assessed for a gradient of the environmental variable, with the phenotype expressed by a regression of the genotype described as a function of the environment (Falconer and Mackay, 1996). However, in the present study, there is no clear order or gradient of the environmental variable (production systems). Hence, BW was

modeled as a different trait for each environment, with time (age post-hatching) as the regression covariable. A MTRRM was adopted, which, for a given point of the random regression covariable, can be described as:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{Wpe} + \boldsymbol{Cce} + \boldsymbol{e},$$

or in expanded form:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 & 0 \\ 0 & \mathbf{X}_2 & 0 \\ 0 & 0 & \mathbf{X}_3 \end{bmatrix} \times \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 & 0 \\ 0 & \mathbf{Z}_2 & 0 \\ 0 & 0 & \mathbf{Z}_3 \end{bmatrix} \times \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & 0 & 0 \\ 0 & \mathbf{W}_2 & 0 \\ 0 & 0 & \mathbf{W}_3 \end{bmatrix} \times \begin{bmatrix} \mathbf{pe}_1 \\ \mathbf{pe}_2 \\ \mathbf{pe}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{C}_1 & 0 & 0 \\ 0 & \mathbf{C}_2 & 0 \\ 0 & 0 & \mathbf{C}_3 \end{bmatrix} \times \begin{bmatrix} \mathbf{ce}_1 \\ \mathbf{ce}_2 \\ \mathbf{ce}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix},$$

where $\boldsymbol{y}' = [\,\boldsymbol{y}'_1\,\boldsymbol{y}'_2\,\boldsymbol{y}'_3]$ is the vector of observations for the 3 traits (i.e. weight measured at each different system). The vector $\boldsymbol{b}$ contains the fixed effects of sex, tank and growth trajectory as covariables. The vectors $\boldsymbol{a}$, $\boldsymbol{pe}$, and $\boldsymbol{ce}$ contain the random regression coefficients assigned to each level of additive genetic, permanent environment and common family environment respectively, and $\boldsymbol{e}$ is the vector of residuals.

Longitudinal covariables (as time in this case) can be modeled via covariance functions (Kirkpatrick et al., 1990). In addition, it is interesting to use orthogonal polynomials instead of the actual covariable since the orthogonal polynomials are less correlated to each other than the actual covariable (Schaeffer, 2016). One of such orthogonal polynomials is the Legendre polynomials, which are often used due to their easier formulation. In order to transform a longitudinal covariable into the correspondent orthogonal polynomials, one must first rescale the m studied time values of interest to a range from -1 to 1 by the formula:

$$q_i = -1 + 2\left(\frac{t_i - t_{min}}{t_{max} - t_{min}}\right),$$

where q_i's are the rescaled values and t_i's the values on the original scale. Thus, the normalized series of Legendre polynomials $\varphi_n(q_i)$, where n is the order of the polynomial, can be defined as:

$$\varphi_n(q_i) = \left(\frac{2n+1}{2}\right)^{0.5} L_n(q_i).$$

The Legendre polynomials $L_n(q_i)$ are $L_0(q_i) = 1$, $L_1(q_i) = q_i$ and for the general case:

$$L_{n+1}(q_i) = \left(\frac{1}{n+1}\right)[(2n+1)q_i L_n(q_i) - nL_{n-1}(q_i)].$$

Finally, the covariance structure of the random variable of interest can be recovered, for any combination of time points by $\mathbf{G}_{ij} = \mathbf{\Phi}_i\mathbf{K}_a\mathbf{\Phi}_j'$, $\mathbf{P}_{ij} = \mathbf{\Phi}_i\mathbf{K}_{pe}\mathbf{\Phi}_j'$ and $\mathbf{F}_{ij} = \mathbf{\Phi}_i\mathbf{K}_{ce}\mathbf{\Phi}_j'$. $\mathbf{G}_{ij}$, $\mathbf{P}_{ij}$, and $\mathbf{F}_{ij}$ are the covariance matrices (between time points i and j) of the additive genetic, permanent environment and common family environment random variables respectively. $\mathbf{\Phi}_i$ is the matrix containing the normalized polynomials for time point i. The order of $\mathbf{\Phi}$ is m * $(n + 1)$, for m time points and n the order of the Legendre polynomials. The matrices $\mathbf{K}_a$, $\mathbf{K}_{pe}$, $\mathbf{K}_{ce}$ are the correlation matrix of the Legendre polynomials for additive genetic, permanent environment and common family effects, respectively. In this study, we assumed Legendre polynomials of quadratic order for all random effects. Also, the correlation matrix of the polynomials, for each random effect can be expressed as:

$$\mathbf{K}_a = \begin{bmatrix} \mathbf{M}_{a11} & \mathbf{M}_{a12} & \mathbf{M}_{a13} \\ \mathbf{M}_{a12} & \mathbf{M}_{a22} & \mathbf{M}_{a23} \\ \mathbf{M}_{a13} & \mathbf{M}_{a23} & \mathbf{M}_{a33} \end{bmatrix}, \quad \mathbf{K}_{pe} = \begin{bmatrix} \mathbf{M}_{pe11} & 0 & 0 \\ 0 & \mathbf{M}_{pe22} & 0 \\ 0 & 0 & \mathbf{M}_{pe33} \end{bmatrix}, \mathbf{K}_{ce} = \begin{bmatrix} \mathbf{M}_{ce11} & 0 & 0 \\ 0 & \mathbf{M}_{ce22} & 0 \\ 0 & 0 & \mathbf{M}_{ce33} \end{bmatrix} \quad \text{and} \quad \boldsymbol{M}_{ijk} = \begin{bmatrix} \sigma_{ijk11} & \sigma_{ijk21} & \sigma_{ijk31} \\ \sigma_{ijk12} & \sigma_{ijk22} & \sigma_{ijk32} \\ \sigma_{ijk13} & \sigma_{ijk23} & \sigma_{ijk33} \end{bmatrix},$$

where, $\mathbf{M}_{ijk}$ are the covariance matrices of the i^{th} random variable within traits ($j = k$) and between traits ($j \neq k$). The σ_{ijkl} are the covariance terms of $n + 1$ order of the polynomial covariables. The residual variances σ_e^2 were assumed to be heterogeneous with 5 classes distributed across the studied period and uncorrelated between traits. The modeling choice of using Legendre polynomials of quadratic order, heterogeneous residual variance with 5 classes and no common environmental covariance between the 3 systems was made based on results from preliminary analysis using the bayesian information criteria (BIC) for model selection (Supplementary Table S3).

In order to estimate the $\mathbf{K}_i$ matrices, and then the full covariance structures of the random variables across ages, a Bayesian approach was used with the following assumptions: $\boldsymbol{y} \mid \boldsymbol{b,a,pe,ce,e} \sim \mathbf{NMV}(\mathbf{Xb} + \mathbf{Za} + \mathbf{Wpe} + \mathbf{Cce}, \mathbf{\Sigma}_e)$ where *NMV* stands for the normal multivariate distribution and $\mathbf{\Sigma}_e$ is the residual covariance matrix such that, $\mathbf{\Sigma}_e \mid \nu_e, \mathbf{S}_e^{-1} \sim \mathbf{W}^{-1}(\nu_e, \mathbf{S}_e^{-1})$, where ν_e represent the degree of freedom and $\mathbf{S}_e^{-1}$ the scale matrix of the Inverse-Wishart distribution $\mathbf{W}^{-1}$; a flat prior on $\boldsymbol{b} \propto constant$; $\boldsymbol{a} \mid \mathbf{K}_a \sim \mathbf{NMV}(0, \mathbf{G})$ with the covariance matrix $\mathbf{G} = \mathbf{A} \otimes (\mathbf{\Phi}\mathbf{K}_a\mathbf{\Phi}')$, where $\mathbf{A}$ is the numerator relationship matrix, $\otimes$ the Kronecker product, and $\mathbf{K}_a \mid \nu_a, \mathbf{S}_a^{-1} \sim \mathbf{W}^{-1}(\nu_a, \mathbf{S}_a^{-1})$; $\boldsymbol{pe} \mid \mathbf{K}_{pe} \sim \mathbf{NMV}(0, \mathbf{P})$ with $\mathbf{P} = \mathbf{I} \otimes (\mathbf{\Phi}\mathbf{K}_{pe}\mathbf{\Phi}')$, and $\mathbf{K}_{pe} \mid \nu_{pe}, \mathbf{S}_{pe}^{-1} \sim \mathbf{W}^{-1}(\nu_{pe}, \mathbf{S}_{pe}^{-1})$; $\boldsymbol{ce} \mid \mathbf{K}_{ce} \sim \mathbf{NMV}(0, \mathbf{F})$ with $\mathbf{F} = \mathbf{I} \otimes (\mathbf{\Phi}\mathbf{K}_{ce}\mathbf{\Phi}')$, and $\mathbf{K}_{ce} \mid \nu_{ce}, \mathbf{S}_{ce}^{-1} \sim \mathbf{W}^{-1}(\nu_{ce}, \mathbf{S}_{ce}^{-1})$; where $\mathbf{I}$ is an identity matrix, $\boldsymbol{\nu_a}$, $\boldsymbol{\nu_{pe}}$ and ν_{ce}, represent the degrees of freedom and $\mathbf{S}_a^{-1}$, $\mathbf{S}_{pe}^{-1}$ and $\mathbf{S}_{ce}^{-1}$ the scale matrices of the Inverse-Wishart distributions of additive genetic, permanent environment and common family environment, respectively.

The GEI can be evaluated via the additive genetic correlations between BW across the three production systems. As a rule, lower additive genetic correlations are indicative of strong GEI. On a MTRRM the covariance matrix for any given combination of two data points i and j can be estimated from the additive genetic covariance function. Therefore, a full correlation structure can be inferred, and the genetic correlations (ρ_g) between any two traits can be obtained for any combination of age i and j. For example, given that $\mathbf{G}_{ij} = \begin{bmatrix} \sigma_{g1}^2 & \sigma_{g12} & \sigma_{g13} \\ \sigma_{g12} & \sigma_{g2}^2 & \sigma_{g23} \\ \sigma_{g13} & \sigma_{g23} & \sigma_{g3}^2 \end{bmatrix}$, which can be obtained as previously described, the ρ_g between traits 1 and 2 can be evaluated as $\rho_{g12} = \frac{\sigma_{g12}}{\sqrt{\sigma_{g1}^2 \times \sigma_{g2}^2}}$.

It is also interesting to evaluate the GEI in terms of selection response. Even with a high additive genetic correlation the covariance estimates can be different between the environmental levels leading to different heritability estimates. Thus, if the selection is performed in an environmental condition different from the one used in the grow-out farms, it is interesting to have another measure of GEI that accounts also for the differences in heritability estimates.

Recall the direct selection response for trait 1 is $\Delta g_1 = i_1 \times h_1 \times \sigma_{g1}$, where i is the selection intensity, h is the square root of the heritability, and σ_g is the additive genetic SD. Also, the correlated selection response for trait 1 given the selection was performed for trait 2 is $\Delta g_{1|2} = i_2 \times h_2 \times \rho_{12} \times \sigma_{g1}$. Thus, the loss (or gain) of selecting at one system with the fish been produced at another system can be accessed by the ratio of $\Delta g_{1|2}/\Delta g_1$ that can be reduced to $(h_2 \times \rho_{12})/h_1$, assuming same selection intensity ($i_1 = i_2$).

The analyses were implemented using the program GIBBS3F90 (Misztal et al., 2015) which generates Markov chain samples from the posterior distribution via Gibbs sampler. Three independent chains were run, each with a total of 500,000 iterations, with a burn-in of 100,000 and thinning interval of 50 samples. Convergence was evaluated using visual inspection and the BOA package (Smith, 2007) of the R language (R Core Team, 2017) and the POSTGIBBSF90 program (Misztal et al., 2015). For each sample from the converged portion of the Markov chains, the random regression (co)variances matrices were constructed. From those matrices, the posterior means for the parameters of interest and their 95% highest posterior density interval (HPD) were obtained and plots were generated using the ggplot2

(Wickham, 2009) and plotly (Sievert, 2018) R libraries.

3. Results and discussion

3.1. Family production and descriptive statistics

A total of 3875 fish were tagged from the full-sib families produced, from those 740 (265 males and 475 females) were removed for breeding purposes, 132 did not have BW measured all 3 times, 22 died, escaped or lost the tag, and 2977 had their BW measured 3 times and were used in the present study. The distribution of the fish used in the study across families and production systems can be found in the Supplementary Table S1 and S2. The short period of families' production (8 weeks), plus the minimal differences in rearing pre-tagging are important for a tilapia breeding program for several reasons. At tagging, the fish had an average age of 59d (SD 9d), 59d (SD 9d), and 61d (SD 8d), and an average BW of 20 g (SD 12 g), 21 g (SD 12 g), and 24 g (SD 12 g) for BFT, RAS, and cage respectively. First, the short period directly influences group homogeneity, so that fish in the same tank are closer in age and the initial sizes are less variable. Secondly, the confounding between common family environmental effect and additive genetic effect is reduced. Previous studies with tilapia including common family effect showed the importance of a reduced pre-tagging period and the control of the differences between hapas/family environment for a better prediction of the additive genetic effect (Bentsen et al., 2012; Khaw et al., 2009).

The scatter plot of fish BW along the experimental period (Fig. 1) shows differences in the average growth curves between fish reared in the different systems. Even though the three curves present different trajectories, fish in RAS and BFT showed more linear growth curves, while for cage the growth curve was more quadratic and steep at the end of the evaluated period. We suspect that this difference in the growth curve for Cage is mostly due to temperature variation across the rearing period. At the beginning of the growth period, the water temperature at the reservoir with the cages was lower than for the other systems (BFT and RAS). However, after 150 days post-hatching (fish with BW around 300, 175 and 100 g for RAS, BFT and cage respectively) there was an increase in the water temperature at the reservoir, which may have contributed to a compensatory growth of the fish.

3.2. Estimated (co)variances and heritability

The posterior means of the correlation matrices between the Legendre polynomials used to generate the covariance parameters are presented in the Supplementary Tables S4 to S6. The estimated variances show a trend of increase with age, with a more accentuated increment after 250 days (Fig. 2). Also, the same behavior can be observed at the genetic covariance surfaces between traits (Supplementary Fig. S1). This behavior was expected since fish had an average BW increase of almost 40-fold, from approximately 20 g at the tagging age to approximately 750 g after 300 days post-hatching. Also, the data was more disperse towards the end of the period for all three systems (Fig. 1), and so, an increase in the estimated variances is observed as the fish grows (Fig. 2). Even though the covariance presented similar trends for all three environments evaluated, there are clear differences in scale between the estimated trends. As shown in Fig. 2, the posterior means of additive genetic and permanent environmental effects for BW at RAS were higher in comparison to the other systems. In addition, Cage presented an overall higher common environment and residual variances. This higher residual variance for the cage system was expected due to the intrinsic nature of this system to have less controlled temperature and water quality in comparison to the other 2 systems.

Heritability estimates were moderate to high and within the literature range (Rutten et al., 2005b; Turra et al., 2012) for most of the studied period, with an increasing trend until 250 days of age in all 3 systems (Fig. 3). The lowest estimate was of 0.075 at 100 days of age for Cage, and the highest estimate was of 0.395 near 250 days for RAS. It is worth noticing that the heritability estimates for BFT and RAS were always higher than that for Cage, with RAS achieving highest values overall. This is in agreement with the fact that estimated residual and common family environment variances for Cage were higher in general. The posterior means of genetic correlation between BW at the three

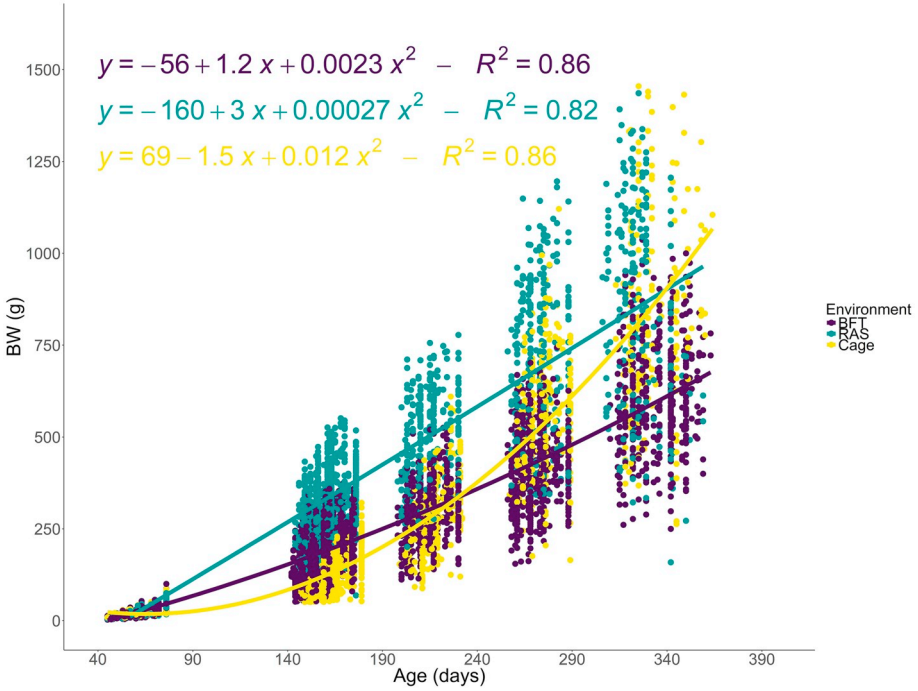

Fig. 1. Fish body weight (BW) in grams (g) by age (days) in biofloc (BFT), Cage and recirculation aquaculture (RAS) systems and corresponding average growth curves.

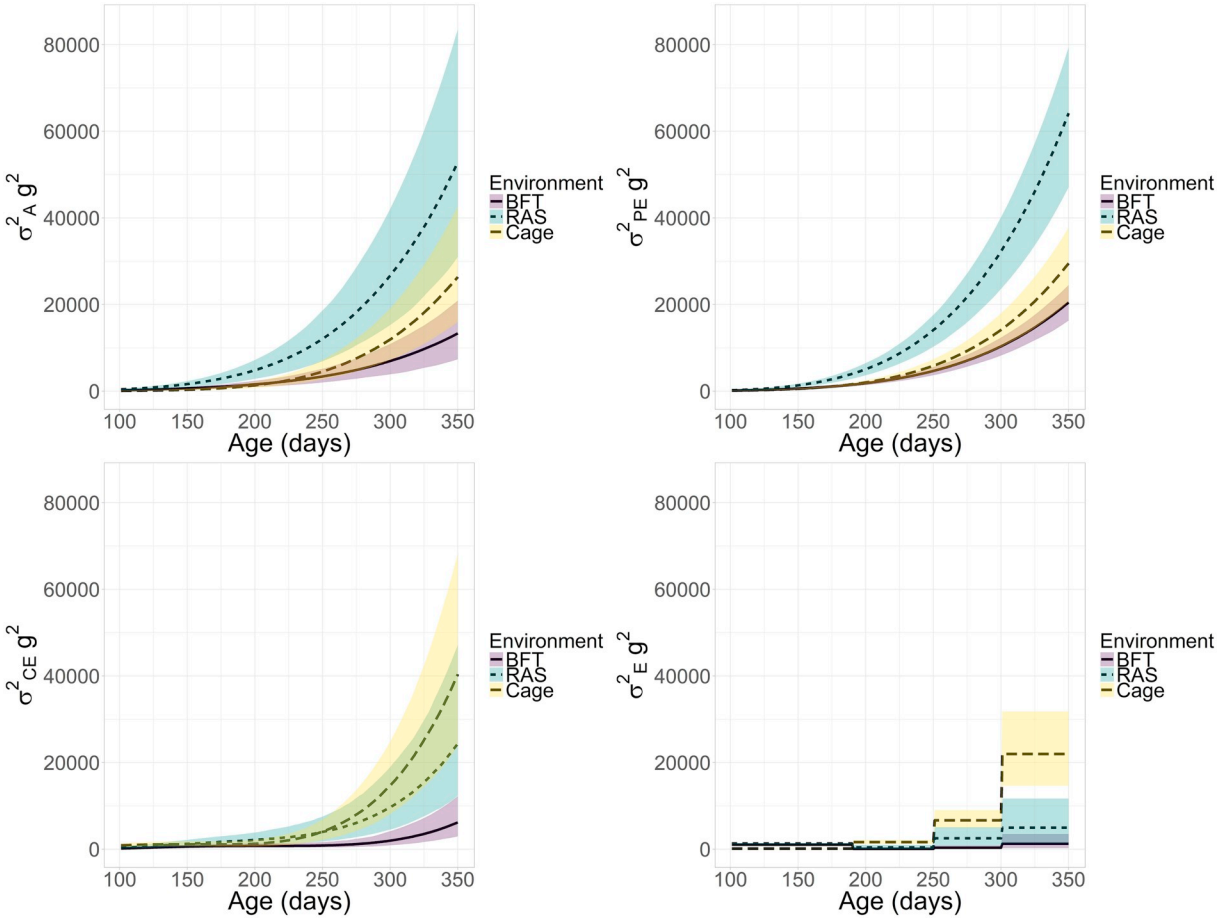

Fig. 2. Posterior means (lines) and 95% HPD interval (shadowed areas) for additive genetic (σ2A), permanent environment (σ2PE), family common environment (σ2CE) and residual (σ2E) variances in squared grams (g2) of BW of Nile tilapia in biofloc (BFT), recirculating aquaculture (RAS) and Cage systems for the range of studied ages (days).

systems ranged from approximately 0.05 to 0.85 (Fig. 3) and maximum values were found around 150 days between BFT vs RAS (0.85), around 220 days for BFT vs Cage (0.72), and around 225 days for RAS vs Cage (0.67). The lowest values were at the initial ages, with the 95% HPD covering negative values for the correlations between Cage and the other two systems. To the best of our knowledge, there is only one other work in the literature that evaluated GEI, for Nile tilapia, between the three systems evaluated here (Turra et al., 2016). Although, in this previous work, the fish were evaluated only at an age of 168 days and the average estimated genetic correlations were higher than the ones presented here, ranging from 0.83 for BFT vs Cage to 0.99 for BFT vs RAS. Therefore, the best time point for selection for BW in the Nile tilapia strain seems to be within 175 and 225 days post-hatching. Also, the posterior mean genetic correlations show a slightly decreasing trend with time after 225 days. It is worth noticing the oscillation on the ratio of the common family variance over the phenotypic variance (CE/Phe) with a slight increase after approximately 200 days for Cage and after 250 days for BFT and RAS (Fig. 3). Interestingly, CE is a variable that combines several effects that are common to animals in the same family. Part of these effects refers to differences previous to fish tagging, such as maternal effects and rearing conditions (pre tagging tank) effect. Thus, it was expected the CE/Phe ratio to decrease over time. However, there was an initial decay followed by an increase, which was more pronounced for Cage. A hypothesis for this slight increase is probably due to the fact that CE is capturing social effects that are related to kin. The authors' hypothesis is that the serial harvest of fish in different ages in the present study could have induced the development of new social interactions in the growing tanks with the reorganization of the fish hierarchy. This could promote detrimental social interactions, such as fights, in which more aggressive families would be favored, ultimately resulting in the increase observed on CE variance. Previous works with chickens have shown that detrimental social interactions can cause individual selection to be suboptimal, suggesting that group selection could reduce cannibalism and increase egg production (Muir, 1996). In another study, Muir et al. (2013) presented that the partition of the total variance into direct genetic effects, indirect genetic effects, and their covariance components, can be useful in multilevel selection, reducing mortality in quails while incorporating the detrimental social interaction as an indirect genetic effect in the model. However, the higher CE (Fig. 2), and the higher CE/Phe ratio (Fig. 3) for the cages in comparison to the other systems, mainly BFT, is not explained. A hypothesis is that this difference in CE can be correlated to the differences in luminosity, water transparency, water quality and temperature across systems. For instance, it is expected that the fish in BFT to be less aggressive due to the constant presence of food from the biofloc and lower water transparency in comparison to the other systems. This can explain the overall reduction of total variance and CE in the BFT system. However, to the best of the authors' knowledge there is no study that elucidates the question of differences in Nile tilapia behavior across these systems neither that evaluated the genetic differences or GEI for Nile tilapia behavior, and why there may be a difference in CE, and probably behavior between Nile tilapia in these systems. Such questions are pertinent for future studies on genetic parameters for Nile tilapia behavior and or GEI regarding differences in luminosity and water turbidity.

GEI studies often try to identify an environmental variable of major

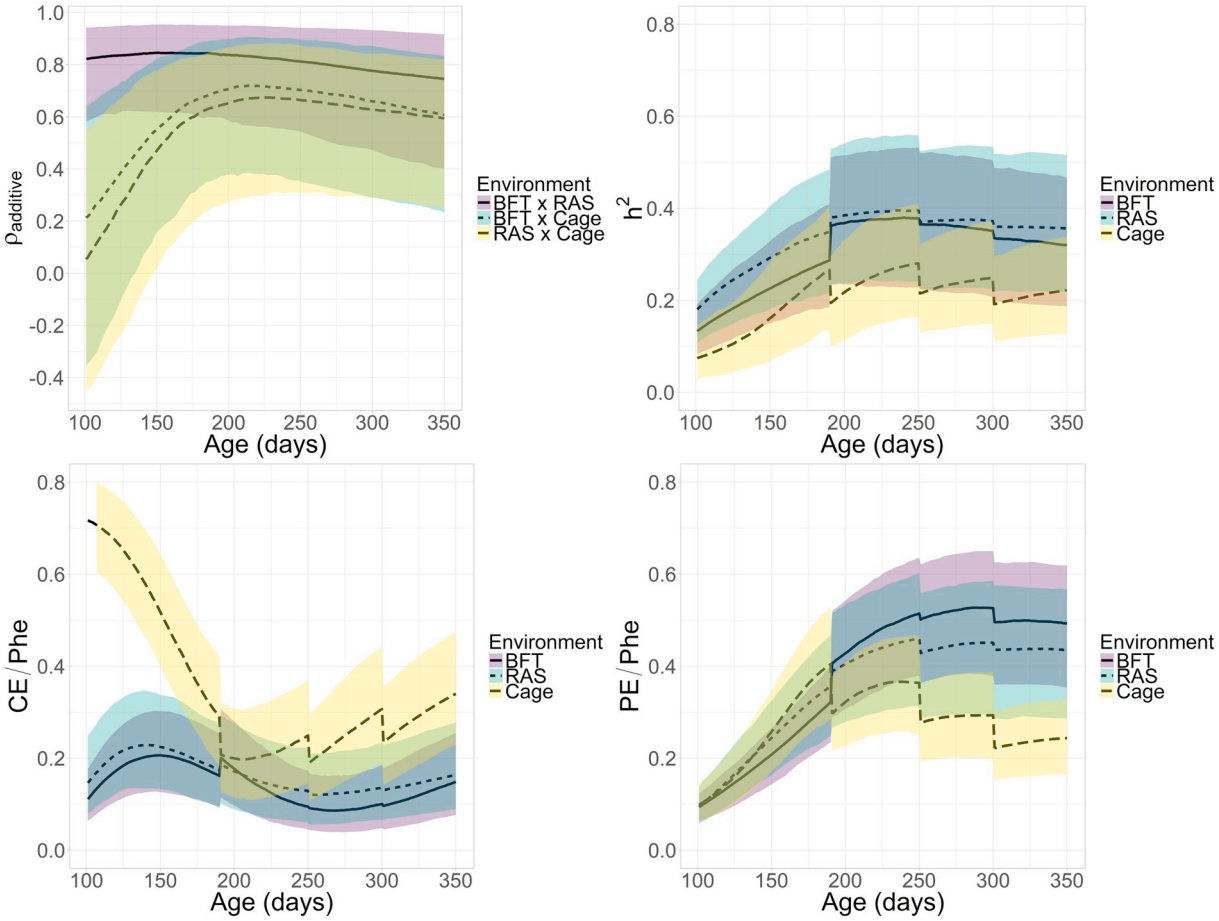

Fig. 3. Posterior means (lines) and 95% HPD interval (shadowed areas) for genetic correlations (ρ), heritability (h^2), permanent environment (PE/Phe) and common family environment (CE/Phe) variances over phenotypic variance of BW of Nile tilapia in biofloc (BFT), recirculating aquaculture (RAS) and cage systems for the range of studied ages (days).

importance. Environmental variables such as water temperature, photoperiod, and salinity among others have already been identified as influential in GEI to some extent for several fish species (Sae-Lim et al., 2015). However, it is possible that more than one environmental variable is acting at the same time. In this situation, there is increased complexity in the system, with the possibility of interaction between environmental variables. However, from a production/breeding point of view, it is more advantageous to simply identify the presence (or absence) of GEI as a whole, mainly between nucleus farm and growth farms. In other words, it is important to identify if there is GEI affecting the trait of interest instead of the identification of the specific underlying environmental variables. Therefore, the genetic correlation between traits measured in different environments can be interpreted as a sensitive parameter of importance. One way to evaluate if the GEI can be ignored or not is by using a break-even genetic correlation value (Mulder and Bijma, 2005). The break-even genetic correlation can be interpreted as the threshold value, so that if the estimated genetic correlation is higher than this value it is unnecessary to consider GEI. On the other hand, if the estimated genetic correlation is below this threshold, it becomes important to account for GEI and thus multiple breeding programs became a viable option. As a general rule, a break-even genetic correlation around 0.7 has been used in aquaculture (Sae-Lim et al., 2015). Thus, the genetic correlations estimated between cage with both BFT and RAS in the present work point out to low GEI, across the studied period (Fig. 3). Moreover this GEI is higher before 150 days of age, as the genetic correlations are lower (below 0.6). But, after 150 days of age the estimated genetic correlations between Cage and both BFT and RAS were above 0.6 and reach 0.7. Moreover, the lower estimates were for the ages below 150 days, which is of minor concern since selection is commonly performed on older fishes.

In previous work with Nile tilapia in which the genetic correlations for BW were evaluated at different ages, it was found that the genetic correlation between different ages have a trend to decrease as the differences between ages increase (He et al., 2017; Rutten et al., 2005b; Turra et al., 2012). However, in all of these works GEI was not considered, and so only one environment was evaluated, more specifically RAS in the first two or pond for the latter. With MTRRM, it is analytically possible to estimate covariance functions that define the structure of the genetic correlation between two traits over time. Thus, a low genetic correlation between a trait measured in different environments at different ages does not necessarily means GEI, since the genetic correlations for different ages within a system can also be lower. Nonetheless, differences in the genetic correlation structure between environments across time in regard to the within environment structure are indicative of GEI. The full correlation matrix between BFT, RAS, and Cage (Fig. 4) show that the correlations between BFT and RAS are in general more similar to the correlations within BFT or RAS, showing the same trend of lower correlations for ages that are more distant. On the other hand, the genetic correlations between Cage with RAS or BFT show a fairly flat surface, with values near 0.5 to 0.6 for most of the time points and values lower than 0.3 for Cage at the ages lower than 125 days with RAS or BFT at any age in the interval. However, one could be interested in the selection of animals at younger ages, before they reach market size. As Nile tilapia reach reproductive maturity before they reach market size, this practice can reduce the generation interval. Also, it would be advantageous for a Nile tilapia production

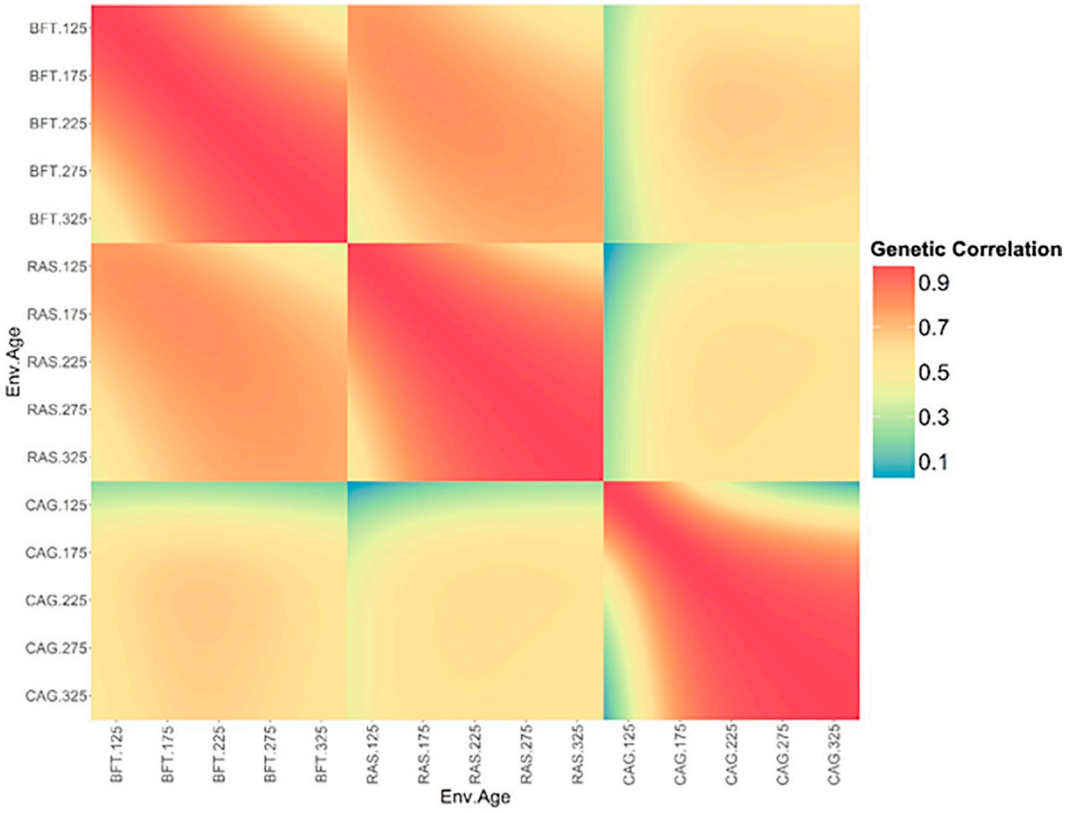

Fig. 4. Genetic correlations surface between biofloc (BFT), recirculation (RAS) and cage (CAG) systems over time from 100 to 350 days of age.

chain if the broodstock was reared and managed at a more controlled production system, such as BFT or RAS. That is because, in a more controlled system there will be lower risks of predators, spread of disease, and the possibility for increased fingerling production per area. Also, for subtropical regions, where the water temperature can drop to conditions inadequate for breeding, BFT and RAS could be used for reproduction at cold seasons, thus increasing the number of generations produced per year. However, if the nucleus environment is different from the growth farm environment, a grow-out test of relatives may be necessary. In order to rule out the need for grow-out tests, GEI should be negligible with the correlated response to selection high enough for indirect selection to be a good alternative. Thus, a more practical approach would be to use the ratio between correlated over the direct response to selection ($\Delta g_{2|1}/\Delta g_2$) to assess the effects of GEI at the selection of animals for different environments across different ages.

The estimated $\Delta g_{2|1}/\Delta g_2$ ratios (Fig. 5) show interesting results overall; as expected the ratio increases for ages closer to the target age. Moreover, if selection were performed between 175 and 225 days of age at BFT or RAS, the estimated ratio would be above 0.7 for most of the target environments and ages evaluated. The only exception is the estimated ratios for final BW in Cage at 275 days as target trait (fish BW of 500 g), for which the ratio is below 0.5 for almost every evaluated selection environment and age combination. Particularly interesting is the estimated ratios for final BW in Cage at 325 days as target trait (fish BW of 700 g), for which the ratio is above 0.8 for RAS BFT and RAS at 175 to 275 days. Moreover, the ratios for BFT and RAS are higher than for cage at younger ages indicating that it can be possible to have the nucleus farm on a more controlled system and achieve similar to better results if selecting fish at younger ages.

The approach used in the present work is applicable for any breeding program when defining selection strategies. In the present study, it was shown that it may be interesting for a Nile tilapia breeding program to have a nucleus farm on a more controlled system, such as RAS or BFT, and selecting animals for broodstock around 225 days of age (fish BW around 300–350 g). In this situation, if the target market age is around 325 days with average final BW of 700 g, the ratio $\Delta g_{2|1}/\Delta g_2$ is expected to be approximately around 1 for BFT and around 0.8 for either RAS or Cage. It is worth noting that for a target market age of 325 days for Cage (fish BW of 700 g), the indirect response to selection on RAS or BFT at 225 days of age would be higher than the response to selection on Cage at the same age (Fig. 5). Nonetheless, these results are not necessarily valid for other Nile tilapia breeding programs. Moreover, in order for a breeding program to decide to adopt any strategy the costs of production in each different environment need to be taken into account as well.

4. Conclusion

In the present study, was shown that MTRRM is an interesting tool to assess changes across time for (co)variances, correlations, and heritability. These changes can be used to evaluate the presence and impact of GEI in breeding programs. The genetic correlations between BFT and RAS were, in general, higher than those between Cage and both BFT and RAS. Also, the overall genetic correlation trajectories within and between BFT and RAS were more similar. These results indicate that GEI was stronger between Cage and both BFT and RAS. Moreover, additive genetic correlations of both BFT and RAS with Cage were high and positive for any age combination after 150 days of age with posterior means ranging from 0.5 at 150 days to 0.7 at 225 days (Fig. 4 and Fig. 5). These correlations, and the results of response to selection ratios $\Delta g_{2|1}/\Delta g_2$ (Fig. 5), are strong evidence that GEI may not be a concern for Nile tilapia, unless if selection is performed at ages lower than 150 days of age (fish BW of 200 g). Moreover, the results for response to selection reveal a better gain for target age around 325 days (average BW of 700 g) if selection is conducted at the more controlled production systems, such as BFT and RAS. Nonetheless, it is worth noting that our results may not apply to a different strain of Nile tilapia, or different environmental conditions between systems than the ones evaluated.

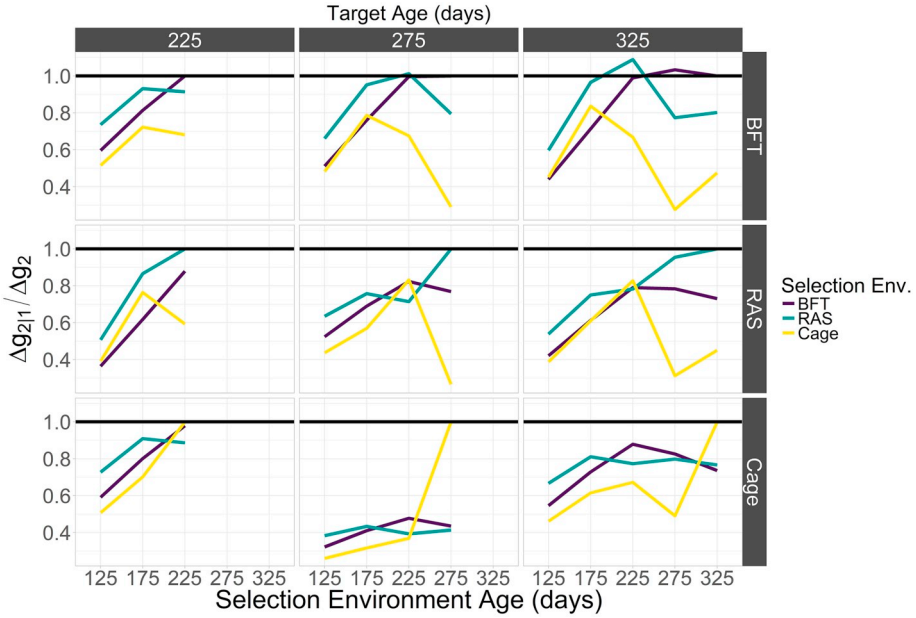

Fig. 5. Posterior mean ratios of Correlated response to selection over the direct response to selection ($\Delta g_{2|1}/\Delta g_2$), assuming similar selection intensities for biofloc (BFT), recirculating aquaculture (RAS) and Cage systems for body weight at 225, 275 or 325 days of age as target age.

Declaration of Competing Interest

The authors declare no conflict of interest.

Acknowledgements

This research received support from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Science without borders and the National Council for Scientific and Technological Development (CNPq), Brazil - 472081/2012-8 and 472149/2012-1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2019.734429.

References

Avnimelech, Y., De-Schryver, P., World Aquaculture Society, 2015. Biofloc technology : A practical guide book. In: World Aquaculture Society, 3rd ed. .

Bangera, R., Drangsholt, T., Nielsen, H., Sae-Lim, P., Ødegård, J., Puvanendran, V., Hansen, Ø., Mortensen, A., 2015. Genotype by environment interaction for growth in Atlantic cod (*Gadus morhua* L.) in four farms of Norway. J. Mar. Sci. Eng. 3, 412. https://doi.org/10.3390/jmse3020412.

Bentsen, H.B., Gjerde, B., Nguyen, N.H., Rye, M., Ponzoni, R.W., Palada de Vera, M.S., Bolivar, H.L., Velasco, R.R., Danting, J.C., Dionisio, E.E., Longalong, F.M., Reyes, R.A., Abella, T.A., Tayamen, M.M., Eknath, A.E., 2012. Genetic improvement of farmed tilapias: genetic parameters for body weight at harvest in nile tilapia (*Oreochromis niloticus*) during five generations of testing in multiple environments. Aquaculture 338, 56–65. https://doi.org/10.1016/j.aquaculture.2012.01.027.

Brito, L.O., Arana, L.A.V., Soares, R.B., Severi, W., Miranda, R.H., da Silva, S.M.B.C., Coimbra, M.R.M., Gálvez, A.O., 2014. Water quality, phytoplankton composition and growth of *Litopenaeus vannamei* (Boone) in an integrated biofloc system with *Gracilaria birdiae* (Greville) and *Gracilaria domingensis* (Kützing). Aquac. Int. 22, 1649–1664. https://doi.org/10.1007/s10499-014-9771-9.

Calus, M.P.L., Groen, A.F., de Jong, G., 2002. Genotype x environment interaction for protein yield in dutch dairy cattle as quantified by different models. J. Dairy Sci. Sci. 85, 3115–3123. https://doi.org/10.3168/jds.S0022-0302(02)74399-3.

CONCEA, 2016. Normativas do CONCEA para produção, manutenção ou utilização de animais em atividades de ensino ou pesquisa científica, 3rd ed. Conselho Nacional de Controle de Experimentação Animal, Brasília, Brazil.

Dalsgaard, J., Lund, I., Thorarinsdottir, R., Drengstig, A., Arvonen, K., Pedersen, B., 2013. Farming different species in RAS in Nordic countries: current status and future perspectives. Aquac. Eng. 53, 2–13. https://doi.org/10.1016/j.aquaeng.2012.11.008.

Dinh Luan, T., Olesen, I., Ødegård, J., Kolstad, K., Cong Dan, N., 2008. Genotype by environment interaction for harvest body weight and survival of Nile Tilapia (*Oreochromis niloticus*) in brackish and fresh water ponds. In: 8th International Symposium on Tilapia in Aquaculture. Cairo,Egypt, pp. 231–239.

Falconer, D.S., 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. Genet. Res. 56, 57. https://doi.org/10.1017/S0016672300028883.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, 4th ed. Longman.

FAO, 2016. Fisheries and Aquaculture Software. FishStatJ - Software for Fishery Statistical Time Series. [WWW Document]. URL. http://www.fao.org/fishery/statistics/software/fishstatj/en, Accessed date: 10 March 2019.

He, J., Zhao, Y., Zhao, J., Gao, J., Han, D., Xu, P., Yang, R., 2017. Multivariate random regression analysis for body weight and main morphological traits in genetically improved farmed tilapia (*Oreochromis niloticus*). Genet. Sel. Evol. 49, 80. https://doi.org/10.1186/s12711-017-0357-7.

Henderson Jr., C.R., 1982. Analysis of covariance in the mixed model: higher-level, nonhomogeneous, and random. Biometrics 38, 623–640. https://doi.org/10.2307/2530044.

Khaw, H.L., Bovenhuis, H., Ponzoni, R.W., Rezk, M.A., Charo-Karisa, H., Komen, H., 2009. Genetic analysis of Nile tilapia (*Oreochromis niloticus*) selection line reared in two input environments. Aquaculture 294, 37–42. https://doi.org/10.1016/j.aquaculture.2009.05.025.

Kirkpatrick, M., Lofsvold, D., Bulmer, M., 1990. Analysis of the inheritance, selection and evolution of growth trajectories. Genetics 124, 979–993.

Kolmodin, R., Strandberg, E., Madsen, P., Jensen, J., Jorjani, H., 2002. Genotype by environment interaction in nordic dairy cattle studied using reaction norms. Acta Agric. Scand. Sect. A Anim. Sci. 52, 11–24. https://doi.org/10.1080/09064700252806380.

Meyer, K., 2009. Factor-analytic models for genotype × environment type problems and structured covariance matrices. Genet. Sel. Evol. 41, 21. https://doi.org/10.1186/1297-9686-41-21.

Misztal, I., Tsuruta, S., Lourenco, D., Aguilar, I., Legarra, A., Vitezica, Z., 2015. Manual for BLUPF90 Family of Programs. [WWW Document]. URL. http://nce.ads.uga.edu/wiki/lib/exe/fetch.php?media=blupf90_all2.pdf, Accessed date: 14 February 2019.

Mota, L.F.M., Abreu, L.R.A., Silva, M.A., Pires, A.V., Lima, H.J.D., Bonafé, C.M., Costa, L.S., Souza, K.A.R., Martins, P.G.M.A., 2015. Genotype x dietary (methionine + cystine): lysine ratio interaction for body weight of meat-type quails using reaction norm models. Livest. Sci. 182, 137–144. https://doi.org/10.1016/j.livsci.2015.11.006.

Muir, W.M., 1996. Group selection for adaptation to multiple-hen cages: Selection program and direct responses. Poult. Sci. 75, 11.

Muir, W.M., Bijma, P., Schinckel, A., 2013. Multilevel selection with kin and non-kin groups, experimental results with Japanese quail (*Coturnix japonica*). Evolution (N. Y) 67, 1598–1606. https://doi.org/10.1111/evo.12062.

Mulder, H.A., Bijma, P., 2005. Effects of genotype × environment interaction on genetic gain in breeding programs1. J. Anim. Sci. 83, 49–61. https://doi.org/10.2527/2005.83149x.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rutten, M.J.M., Bovenhuis, H., Komen, H., 2005a. Genetic parameters for fillet traits and body measurements in Nile tilapia (*Oreochromis niloticus L.*). Aquaculture 246, 125–132. https://doi.org/10.1016/j.aquaculture.2005.01.006.

Rutten, M.J.M., Komen, H., Bovenhuis, H., 2005b. Longitudinal genetic analysis of Nile tilapia (*Oreochromis niloticus L.*) body weight using a random regression model. Aquaculture 246, 101–113. https://doi.org/10.1016/j.aquaculture.2004.12.020.

Sae-Lim, P., Komen, H., Kause, A., Mulder, H.A., 2014. Identifying environmental variables explaining genotype-by-environment interaction for body weight of rainbow trout (*Onchorynchus mykiss*): reaction norm and factor analytic models. Genet. Sel. Evol. 46, 16. https://doi.org/10.1186/1297-9686-46-16.

Sae-Lim, P., Gjerde, B., Nielsen, H.M., Mulder, H., Kause, A., 2015. A review of genotype-by-environment interaction and micro-environmental sensitivity in aquaculture species. Rev. Aquac. 1–25. https://doi.org/10.1111/raq.12098.

Santos, A.I., Ribeiro, R.P., Vargas, L., Mora, F., Filho, L.A., Fornari, D.C., Nogueira de Oliveira, S., 2011. Bayesian genetic parameters for body weight and survival of Nile tilapia farmed in Brazil. Pesqui. Agropecu. brasieleira 46, 33–43.

Schaeffer, L.R., 2016. Random Regression Models. [WWW Document]. URL. http://animalbiosciences.uoguelph.ca/~lrs/BOOKS/rrmbook.pdf, Accessed date: 27 March 2019.

Sievert, C., 2018. Plotly for R. [WWW Document]. URL. https://plotly-book.cpsievert.me, Accessed date: 27 March 2019.

Smith, B.J., 2007. Boa : an R package for MCMC output convergence assessment and posterior inference. J. Stat. Softw. 21, 1–37. https://doi.org/10.18637/jss.v021.i11.

Turra, E.M., Oliveira, D.A.A., Valente, B.D., Teixeira, E.A., Prado, S.A., Melo, D.C., Fernandes, A.F.A., Alvarenga, E.R., Silva, M.A., 2012. Estimation of genetic parameters for body weights of Nile tilapia *Oreochromis niloticus* using random regression models. Aquaculture 354, 31–37. https://doi.org/10.1016/j.aquaculture.2012.04.035.

Turra, E.M., Toral, F.L.B., Alvarenga, E.R., Raidan, F.S.S., Fernandes, A.F.A., Alves, G.F.O., Sales, S.C.M., Teixeira, E.A., Manduca, L.G., Brito, T.S., Silva, Marcos Antônio, S., Júnior, A.F., Almeida, L.F.C., Santos, C.R., Silva, Martinho, Almeida, 2016. Genotype × environment interaction for growth traits of nile tilapia in biofloc technology, recirculating water and cage systems. Aquaculture 460, 98–104. https://doi.org/10.1016/j.aquaculture.2016.04.020.

Turra, E.M., Fernandes, A.F.A., de Alvarenga, E.R., Teixeira, E.A., Alves, G.F.O., Manduca, L.G., Murphy, T.W., Silva, M.A., 2018. Longitudinal analyses of correlated response efficiencies of fillet traits in Nile tilapia. Animal 12, 445–453. https://doi.org/10.1017/S1751731117001768.

Wickham, H., 2009. ggplot2 Elegant Graphics for Data Analysis. Springer, New York, NY. https://doi.org/10.1007/978-0-387-98141-3.