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Genetic parameters in female reproductive traits of Nile tilapia (*Oreochromis niloticus*)

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ABSTRACT

Genetic parameters for reproductive traits in female Nile tilapia were estimated in this study using Bayesian inference method. The data set presented information from 451 Nile tilapia females that were evaluated at two different places in Maringá - Paraná - Brazil (hapas of 1 and 10 m^3) and at one location in Alfenas - Minas Gerais - Brazil. A spawning examination was conducted once a week from October 2012 to March 2013 for a total of 23 weeks of evaluation. Single-trait analyses for spawning success, multiple spawning, spawning frequency, and volume of eggs/female were performed by using the software MTGSAM Threshold. The heritability estimates were 0.14, 0.16, 0.53, and 0.08 for spawning success, multiple spawning, spawning frequency and volume of eggs/female, respectively, indicating it is possible to achieve a substantial genetic gain using these reproductive traits as selection criteria.

Key words: Bayesian Inference, heritability, *Oreochromis niloticus*, repeatability, spawning.

INTRODUCTION

The identification of growth traits related to the objective of selection is widely studied in aquaculture species (Quinton et al. 2005, Trọng et al. 2013a, Yoshida et al. 2013a). Harvest weight has been the main trait of interest in Nile tilapia with genetic gains ranging from 10% to 15% per generation (Ponzoni et al. 2011, Thodesen et al. 2011). In addition, several traits, including fillet yield (Rye et al. 2011, Turra et al. 2012), survival rate (Santos et al. 2011), resistance to low water temperatures (Charo-Karisa et al. 2005), and body shape (Trọng et al. 2013a, Oliveira et al. 2016), were studied as the objective of selection in the genetic improvement programs for this particular species.

In Nile tilapia, optimization of hatchery efficiency is significant if production is to be maximized and maintained. However, the reproduction of this species is characterized by early maturity, low fecundity, and the asynchronous nature of tilapia spawning cycles of individual broodstock. Moreover, for optimizing seed production under farm condition, hatchery operators have tended to increase the number of broodfish

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(Jalabert and Zohar 1982, Coward and Bromage 2000). Furthermore, large variation in reproductive performance (Hamzah et al. 2014), diversity of environmental conditions (Duponchelle et al. 2000, Yoshida et al. 2015), nested mating (Trọng et al. 2013b), sex ratio (Barman and Little 2006, Tsadik and Bart 2007), and unwanted correlated responses in reproduction when selecting for growth (Trọng et al. 2013b) might result in a prolonged period to produce the desired number of families (~50) to be used in tilapia breeding programs (Ponzoni et al. 2011, Bentsen et al. 2012). Given these hypotheses and taking into account the possibility of listing new traits as the selection criteria, some studies have been conducted to estimate genetic parameters for different reproductive traits (Trọng et al. 2013a, c, Hamzah et al. 2014).

In the Brazilian Nile tilapia breeding program established in Maringá, the objective of selection is growth rate, and the selection criterion used is daily weight (Yoshida et al. 2013b, Neto et al. 2014). However, given the possible negative impact on reproductive traits, the objective of the present study was to verify the extent of genetic variation in reproductive traits of Nile tilapia, which aimed to include them as the selection criteria in the existing breeding program.

MATERIALS AND METHODS

The data used in the present study were obtained from 451 female Nile tilapia representing 15, 27, and 19 families during the breeding seasons in 2009/10, 2010/11, and 2011/12, respectively. The breeding structure of the genetic improvement program for Nile tilapia consisted of 180 hapas, which allocated 120 for females and 60 for males. During the three breeding seasons, the animals were kept in individual hapas with a volume of 1 m^3 in an earthen pond of 360 m^2 and an average depth of 1.0 m, and stored in a greenhouse located at the Fish Culture Experiment Station of the Universidade Estadual de Maringá (UEM-CODAPAR) in the Floriano District, Maringá, Paraná, Brazil (23°31′25″ S, 52°03′12″ W). Nested mating was conducted in a 2 females:1 male ratio, and spawning was verified twice a week. When spawning was observed, the male was removed from the female hapa, and the larvae were kept with their mothers until the end of the breeding season (up to 3 months), thus creating a common nursery environmental effect.

At the end of the reproduction period, 100 fingerlings from each family were divided into two equal groups, and they were transferred to a nursery structure and kept in 1 m^3 hapa in an earthen pond until reaching an average weight of 10 g. Thereafter, individual identification was performed for 50 animals of each family through passive integrated transponder tag. After one week, the animals were transferred into a cropping farm in fish rearing tanks located in Diamante do Norte, Paraná, Brazil (22°39′21″ S, 52°51′36″ W) and were evaluated for ~7 months. Two cages measuring 6 m^3 (2 × 2 × 1.5 m) remained, with the same density in both tanks, the number of animals/family was divided equally between each of the two tank networks. Measurements were carried out monthly to collect morphometric information and sex of animals.

The families were evaluated at the end of the growing season, and the best were then selected. Daily weight gain (weight/age) was used as the selection criteria consisting of a group of animals that were to be used for reproductive assessment. In the animal model, the random effects of the common hatchery and nursery environmental conditions, as well as the fixed effects of sex and the cages in which the animals were evaluated, were considered (Oliveira et al. 2016).

This process was conducted during the breeding seasons in 2009/10 and 2010/11, when 100% of broodstock was replaced (discrete generation), in 2011/12, the same broodstock was also used to generate the animals that were evaluated in the present study. Therefore, the offspring produced in 2009/10 comprised the group of the fourth generation, and the offspring produced in 2010/11 and 2011/12 corresponded to the animals of the fifth generation of the genetic improvement program of Nile tilapia.

Female reproductive performance was evaluated in three different environmental conditions.

Place 1: A total of 159 females and 53 males (3 females:1 male ratio) representing 11 and 9 families (8 females/family) were generated during the breeding seasons in 2010/11 and 2011/12, respectively. These animals were distributed in 5 polyethylene hapas with a volume of 10 m^3 (1 m of depth × 2 m of width × 5 m of length) and an open mesh of 1 mm^2, and maintained in an earthen pond of 360 m^2 and an average depth of 1 m.

Place 2: A total of 127 females and 127 males (1 female:1 male ratio) representing 23 and 18 families (3 females/family) were generated during the breeding seasons in 2010/11 and 2011/12, respectively. These animals were individually distributed in polyethylene hapas with a volume of 1 m^3 (1 m of depth × 1 m of width × 1 m of length) and an open mesh of 1 mm^2, and maintained in an earthen pond of 400 m^2 in an agricultural greenhouse and an average depth of 1 m. Both places 1 and 2 were located at the Fish Culture Experiment Station of UEM-CODAPAR.

Place 3: A total of 165 females and 64 males (2.6 females:1 male ratio) with females representing 15 and 9 families (7 females/family) were generated during the breeding seasons in 2009/10 and 2010/11, respectively. These animals were distributed in 4 polyethylene hapas, two with volumes of 28 m^3 (1 m of depth × 2 m of width × 14 m of length) and two hapas with volumes of 14 m^3 (1 m of depth × 2 m of width × 7 m of length), both had an open mesh of 1 mm^2 and were maintained in an earthen pond of 360 m^2 and an average depth of 1 m located in Alfenas, Minas Gerais, Brazil (37°25′19.1″ N and 122°05′06″ W).

The animals were fed in three locations with a specific commercial extruded feed for Nile tilapia breeding, the amount of feed corresponded to 1% of body weight and was given once daily in the morning immediately after the collection of samples. The fed diet comprised a minimum of 38% crude protein, 3,400 kcal/kg digestible energy, 10% ether extract, 1% phosphorus, 500 mg/kg vitamin C, and a maximum of 2% calcium. The average water temperatures were 29.60, 31.50, and 27.80 °C for places 1, 2, and 3, respectively.

The evaluation period lasted for 23 weeks and was conducted from October 2012 to March 2013. Reproductive data were collected weekly by restricting the broodstock to a small area in the hapa, then, the animals were captured and checked for individual spawning. All females were checked for the presence of eggs in the mouth, when eggs were detected, the mouth was washed to remove the eggs, and the number of the microchip corresponding to that female who spawned was recorded.

The following traits were investigated and measured at all three places: spawning success (presence or absence of spawning), multiple spawning (females with more than one spawning), and spawning frequency (number of spawning/female during the evaluation period).

In addition, data with regard to the volume of eggs were collected at places 1 and 2. When spawning was observed upon inspection, the mouth was washed, and the total volume of eggs produced by each female was measured with a 100-ml graduated cylinder and a precision scale.

Single-trait analyses were conducted for spawning success, multiple spawning, spawning frequency, and volume of eggs through Bayesian inference and via Gibbs sampling, which uses the Monte Carlo Markov chain method (Mora et al. 2008). Statistical analyses were performed using the MTGSAM Threshold (Multiple Trait Gibbs Sampler for Animal Models) software (Van Tassel et al. 1998). The model included age as linear covariable, sex, and location as fixed effect. The fixed and random effects are considered random in the Bayesian analysis. A noninformative flat prior was assumed for variance components.

Spawning success and multiple spawning were established as threshold traits, where 1 was used for success (spawning occurrence and multiple spawning occurrence) and 0 if otherwise. Spawning frequency and volume of eggs were considered as continuous traits, and in MTGSAM Threshold, they were considered as 0 (using linear model) for these traits.

For volume of eggs, the phenotypes of 183 females and information of 679 animals were used to estimate genetic parameters. The following animal model was used for the evaluation of the volume of eggs: $y = X\beta + Z_1 a + Z_2 c + e$, where the assumptions of the model were as follows: *y* is the vector of observations of the characteristic volume of eggs, $\boldsymbol{\beta}$ is the vector of the systematic environmental effects (age, spawning frequency, and place), *a*, *c*, and *e* are the vectors of the additive genetic effects, permanent environmental effects, and residual random effects, respectively. The matrices *X*, Z_1, and Z_2 are related to the incidence of the systematic environmental effects, additive genetic effects, and permanent environmental effects, respectively.

The assumptions for variance components were that $\sigma_a^2 \sim N(0, A\sigma_a^2)$, $\sigma_c^2 \sim N(0, I\sigma_c^2)$, and $\sigma_e^2 \sim N(0, R\sigma_e^2)$, where σ_a^2, σ_c^2, and σ_e^2 are the components of the additive genetic direct effects, permanent environmental effects, and residual effects, respectively, *A* is the pedigree relationship matrix, *I* is the identity matrix of order equal to the number of animals with observations, *R* is the residual covariance matrix.

For spawning success, multiple spawning, and spawning frequency, the data were obtained from 451 female Nile tilapia, and the permanent environmental effect was excluded from the animal model.

In the threshold model, it was assumed that the underlying continuous scale (liability) follows a normal distribution and is represented as: $U \mid \theta \sim N\left(W\theta, I\sigma_e^2\right)$, where U is the vector of the order r, $\theta = (b, a)$ is the vector of location parameters of order s by b (defined under the frequentist point of view as fixed effects) and a (as additive genetic direct random effect), W is the matrix of order r by s, I is the identity matrix order r by r, σ_e^2 is the residual variance.

For all traits studied, 100,000 samples were obtained from chains of 1,100,000 cycles, and the first 100,000 cycles were removed. For all chains, the thinning interval was 10 rounds. The convergence analysis of the generated chains was performed as the Heidelberger and Welch criterion as described by Cowles et al. (1995) using the CODA library (Convergence Diagnosis and Output Analysis) implemented in the R program (version 2.15.2). For genetic parameters, an estimated credibility interval of 95% was considered.

The estimated repeatability value was obtained from the samples *a posteriori* of the variance components, single-trait analyses of the characteristic volume of eggs were generated by using the following expression: $t = \left(\sigma_a^2 + \sigma_c^2\right) / \sigma_p^2$, where σ_a^2, σ_c^2 and σ_p^2 are the additive genetic, permanent environmental, and phenotypic variances, respectively.

Spearman correlation values between genetic values of all animals predicted in the single-trait analyses for the traits of spawning success, multiple spawning and spawning frequency were estimated using the PROC CORR of SAS system for Windows® (version 9.0). In addition, the coincidence percentage of the best ten families was calculated for all traits except for the volume of eggs. These analyses were conducted to identify whether the animals and their families would be selected as the best for two traits.

RESULTS

There was an indication of convergence for all chains generated. The reduced contribution of the additive genetic variance and the wide effect of the residual variance in the total variance were observed for spawning success and multiple spawning, which resulted in the heritability estimates of 0.142 and 0.165, respectively. An opposite behavior was observed for spawning frequency, wherein the additive genetic effects accounted for more than 50% of the animal's phenotype. The medians were very close to the means, which show symmetric values, indicating convergence of analysis and consistency of samples (Table I).

The volume of egg due to the additive genetic effects (3.30) was lower than the contribution of the permanent environmental effects (11.41), and the heritability estimate (0.08) was greater than the contribution of the systematic mean environmental effects (0.28). The magnitude of repeatability (0.36) indicates the need for a better recording system on this trait, which could reduce the phenotypic variation (Table II).

In places 1 and 3, most of the families that ranked as the best for spawning success were also the best for multiple spawning and spawning frequency, with an 80% coincidence percentage in both places (Table III). In place 2, a lower coincidence percentage, ranging from 40% to 70%, was observed between spawning success and multiple spawning, and between spawning success and spawning frequency, respectively.

TABLE I
Posterior statistics for variance components and heritability for spawning success, multiple spawning, and spawning frequency in Nile tilapia.

Traits	Parameters	Means	SD	Median	Credibility interval	
					2.5%	97.5%
Spawning success	σ_a^2	0.0324	0.0188	0.0288	0.007	0.08
	σ_e^2	0.1939	0.0193	0.1940	0.15	0.23
	σ_p^2	0.2263	0.0158	0.2254	0.20	0.26
	h^2	0.1416	0.077	0.1288	0.03	0.32
Multiple spawnings	σ_a^2	0.0392	0.0182	0.0366	0.01	0.08
	σ_e^2	0.1965	0.0190	0.1963	0.16	0.23
	σ_p^2	0.2358	0.0164	0.2349	0.21	0.27
	h^2	0.1651	0.0718	0.1570	0.05	0.33
Spawning frequency	σ_a^2	1.7925	0.5252	1.7527	0.88	2.91
	σ_e^2	1.5298	0.3288	1.5295	0,89	2.17
	σ_p^2	3.3224	0.2986	3.2993	2.80	3.97
	h^2	0.5324	0.1200	0.5335	0.29	0.76

Additive genetic variance(σ_a^2), residual (σ_e^2), phenotypic (σ_p^2), heritability (h^2), standard deviation (SD) and credibility interval (CI).

TABLE II
Posterior statistics for variance components and heritability for volume of eggs in Nile tilapia.

	σ_a^2	σ_c^2	σ_e^2	σ_p^2	h^2	c^2	t
Mean	3.3033	11.4067	26.2011	40.9111	0.0785	0.2774	0.3565
SD	3.1557	4.8031	3.1391	3.9909	0.0757	0.1068	0.0762
Median	2.64	11.37	25.97	40.91	0.06	0.28	0.36
CI (2.5 – 97.5%)	0.13 - 12.43	2.53 - 21.07	20.71 - 32.97	33.97 - 49.55	0.03 - 0.29	0.06 - 0.47	0.21 - 0.50

Additive genetic variance (σ_a^2), nonsystematic environmental variance (σ_c^2), residual (σ_e^2),phenotypic (σ_p^2), heritability (h^2), permanent environmental effect (c^2), repeatability (t), standard deviation (SD) and credibility interval (CI).

TABLE III
Spearman correlation (above the diagonal) and percentage of coincidence of the top ten families (below the diagonal) between the genetic values of the traits spawning success (SS), multiple spawning (MS) and spawning frequency (SF) of Nile tilapia in three different places in the evaluation.

	Place 1			Place 2			Place 3		
	SS	MS	SF	SS	MS	SF	SS	MS	SF
SS	-	0.774	0.817	-	0.595	0.822	-	0.819	0.813
MS	80	-	0.815	40	-	0.710	80	-	0.850
SF	80	80	-	70	50	-	80	80	-

Overall, there was a strong association of genetic values between reproductive traits, with Spearman correlation values greater than 0.71, with an exception for the correlation between spawning success and multiple spawning in place 2, which presented a correlation of 0.60. This result might be due to the greater number of families used, so the greatest genetic variability might have caused changes to family classification for the traits studied.

DISCUSSION

With regard to genetic improvement of aquaculture species, only a few studies have estimated the genetic effects for reproductive traits, with a limited number of studies evaluating Nile tilapia. In general, some studies have found a moderate heritability estimate for reproductive traits. In studies with Pacific salmon (*Oncorhynchus kisutch*), Gall and Neira (2004) found the heritability estimates ranging from 0.24 to 0.33 for the interval of spawning between breeding and salmon length at spawning, respectively. In a study with rainbow trout (*Oncorhynchus mykiss*) performed by Su et al. (1997), the heritability estimate for weight at spawning was low (0.09).

In the present study, the heritability estimates for spawning success and multiple spawning ranged from 0.14 to 0.16, respectively. Those values were close to the heritability traits already used in the selection criteria, such as body weight and harvest weight (Santos et al. 2011, Trọng et al. 2013a, Yoshida et al. 2013b). The heritability estimates of 0.18 and 0.57 were obtained for gonad weight (Charo-Karisa et al. 2007) and sexual maturity stage (Kronert et al. 1989, Oldorf et al. 1989), respectively.

Studying the hypothesis of selection for growth, result in a prolonged period needed to obtain families for the genetic improvement program of Nile tilapia, Trọng et al. (2013b) obtained the heritability estimates for spawning success ranging from 0.02 to 0.14 for 12 and 20 days of evaluation, respectively, thus coinciding with the heritability estimate of 0.14 that was observed in the present study.

Phenotypes for spawning and multiple spawning were not good indicators of the genetic merit of female Nile tilapia. Moderate heritability estimates indicate large variation due to the environmental effects. However, the heritability estimate for spawning frequency was 0.53, which implied that the phenotype was a good indicator of the individual's genotype and allowed the use of this trait as a selection criterion. The identification of the groups of females with the highest number of spawning can be a practical alternative to improve female reproductive performance by keeping only these animals with a higher spawning frequency. Another alternative would be the indirect selection for reproductive traits using the growth traits, taking into account that some studies have shown a positive genetic correlation between the harvest weight with traits such as spawning success (0.52) and egg numbers (0.51) (Trọng et al. 2013a, c).

In this dataset specifically, the effects of the common hatchery (housing animals with their mothers from spawning until the end of the breeding season) and nursery environmental conditions (distribution of family representatives in hapas in different places in the tanks) were neglected, because preliminary analyses indicated a low participation of such effects, mainly due to the effect of distancing itself from the measurement of traits. Rutten et al. (2005), Charo-Karisa et al. (2006), and Yoshida et al. (2013b) suggested that the common family environmental conditions tend to decrease with advancing age.

In the present study, the heritability estimate to volume of eggs was 0.08, which was lower than 0.30 reported by Gall and Huang (1988) in rainbow trout. When considering estimates using the REML procedure, Su et al. (1997) observed that 55% of the variation in the volume of eggs was due the genetic effects in rainbow trout. The discrepancy in the results might be explained by the fact that rainbow trout are characterized by synchronous spawning, in other words, rainbow trout have an annual spawning period during which all oocytes are released at once. This differs from Nile tilapia, which is characterized by asynchronous spawning. Spawning in tilapia might occur in intervals of less than 21 days (Ridha 2010), and according to Tsadik (2008), an increased frequency in spawning resulted in a reduction of the number of eggs/spawning, which makes the spawning frequency a source of variation for the volume of eggs produced.

Estimates of genetic parameters for fertility traits in Nile tilapia were obtained by Trọng et al. (2013c), and the heritability estimates ranged between 0.05 and 0.08, similar to the values found for the volume of eggs in the present study. The higher variation could be results of environmental factors and the reduced amount of data collected for the volume of eggs, justify the low heritability estimate in our study. Hamzah et al. (2014) found that the heritability estimate for the number of eggs in Nile tilapia was equal to 0.20, which indicated that although the measurement of this trait might be costly, its use could promote great genetic progress.

To our knowledge, only few studies have assessed the repeatability of traits related to fish reproduction. Trọng et al. (2013a) observed a low repeatability value (0.04 to 0.17) for spawning success in Nile tilapia. For fertility traits, Trọng et al. (2013c) found a maximum repeatability value of 0.17. The repeatability expresses the proportion of variation due to the permanent environmental effects and genetic differences between individuals, it also establishes the upper limit of the heritability estimate for the volume of eggs (Falconer and Mackay 1996). Thus, the heritability estimate of 0.08 and the repeatability value of 0.36 for the volume of eggs indicate that an increase in data from the same individual for this parameter will reduce the variance of the systematic environmental effects. The consequent reduction of the phenotypic variance will increase accuracy, which gives a maximum heritability estimate of 0.36 (Pereira 2008).

The Spearman correlation values indicated a small change in the rank among spawning success, multiple spawning, and spawning frequency, which demonstrate that there might be a correlated response when using one of these traits as the selection criteria. The greater change of rank was observed in place 2 for spawning success and multiple spawning (0.60). This result might be a consequence of the low number of females that presented multiple spawning. The high coincidence percentage among the top ten families can be significant in practice, because they would facilitate the selection of families to be transferred for the productive sector, taking into account that families will have good answers to the three characteristics that were selected.

The large genetic variation for reproductives traits in Nile tilapia is an indicative of the potential genetic improvement for these traits. Despite the fact that reproductive traits are determined by multiple genes (Puppin et al. 1991), the results obtained in the present study suggested that the additive genetic effects can be exploited by selecting the best individuals.

REFERENCES

BARMAN BK AND LITTLE DC. 2006. Nile tilapia (*Oreochromis niloticus*) seed production in irrigated rice-fields in Northwest Bangladesh—an approach appropriate for poorer farmers? Aquaculture 261: 72-79.

BENTSEN HB ET AL. 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.

CHARO-KARISA H, BOVENHUIS H, REZK MA, PONZONI RW, VAN ARENDONK JA AND KOMEN H. 2007. Phenotypic and genetic parameters for body measurements, reproductive traits and gut length of Nile tilapia (*Oreochromis niloticus*) selected for growth in low-input earthen ponds. Aquaculture 273: 15-23.

CHARO-KARISA H, KOMEN H, REYNOLDS S, REZK MA, PONZONI RW AND BOVENHUIS H. 2006. Genetic and environmental factors affecting growth of Nile tilapia (*Oreochromis niloticus*) juveniles: Modelling spatial correlations between hapas. Aquaculture 255: 586-596.

CHARO-KARISA H, REZK MA, BOVENHUIS H AND KOMEN H. 2005. Heritability of cold tolerance in Nile tilapia, *Oreochromis niloticus*, juveniles. Aquaculture 249: 115-123.

COWARD K AND BROMAGE NR. 2000. Reproductive physiology of female tilapia broodstock. Rev Fish Biol Fisher 10(1): 1-25.

COWLES MK, BEST N AND VINES K. 1995. Convergence diagnostics and output analysis. MRC Biostatistics Unit, UK. Version 0.40.

DUPONCHELLE F, CECCHI P, CORBIN D, NUÑEZ J AND LEGENDRE M. 2000. Variations in fecundity and egg size of female Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Côte d'Ivoire. Environ Biol Fish 57(2): 155-170.

FALCONER DS AND MACKAY TFC. 1996. Introduction to Quantitative Genetics. Longman, Harlow-GB.

GALL GAE AND HUANG N. 1988. Heritability and selection schemes for rainbow trout: female reproductive performance. Aquaculture 73: 57-66.

GALL GAE AND NEIRA R. 2004. Genetic analysis of female reproduction traits of farmed coho salmon (*Oncorhyncus kisutch*). Aquaculture 234: 143-154.

HAMZAH A, NGUYEN NH, MEKKAWY W, KHAW HL, YEE HY, BAKAR A, PONZONI RW AND AZIZAH S. 2014. Genetic parameters and correlated responses in female reproductive traits in the GIFT strain. Aquacul Res 47(5): 1488-1498.

JALABERT B AND ZOHAR Y. 1982. Reproductive physiology in cichlid fishes, with particular reference to *Tilapia* and *Sarotherodon*. In: Pullin RSV and Lowe-McConnell RH (Eds), The Biology and Culture of Tilapias (ICLARM conference proceedings 7). International Center for Living Aquatic Resources Management, Manila, Philippines, p. 129-140.

KRONERT U, HÖRSTGEN-SCHWARK G AND LANGHOLZ HJ. 1989. Prospects of selecting for late maturity in tilapia (*Oreochromis niloticus*): I. Family studies under laboratory conditions. Aquaculture 77: 113-121.

MORA F, GONÇALVES-VIDIGAL MC AND SANTOS AI. 2008. Bayesian analysis of the genetic control of survival in F3 families of common bean. Chil J Agr Res 68: 334-341.

NETO RVR, OLIVEIRA CAL, RIBEIRO RP, FREITAS RTF, ALLAMAN IB AND OLIVEIRA SND. 2014. Genetic parameters and trends of morphometric traits of GIFT tilapia under selection for weight gain. Sci Agr 71(4): 259-265.

OLDORF W, KRONERT U, BALARIN J, HALLER R, HÖRSTGEN-SCHWARK G AND LANGHOLZ HJ. 1989. Prospects of selecting for late maturity in tilapia (*Oreochromis niloticus*): II. Strain comparisons under laboratory and field conditions. Aquaculture 77: 123-133.

OLIVEIRA CAL, RIBEIRO RP, YOSHIDA GM, KUNITA NM, RIZZATO GS, OLIVEIRA SN, SANTOS AI AND NGUYEN NH. 2016. Correlated changes in body shape after five generations of selection to improve growth rate in a breeding program for Nile tilapia *Oreochromis niloticus* in Brazil. J Appl Genet 1: 1-7.

PEREIRA JCC. 2008. Melhoramento genético aplicado à produção animal. FEPMVZ Editora, Belo Horizonte-MG.

PONZONI RW, NGUYEN NH, KHAW HL, HAMZAH A, BAKAR KRA AND YEE HY. 2011. Genetic improvement of Nile tilapia (*Oreochromis niloticus*) with special reference to the work conducted by the WorldFish Center with the GIFT strain. Aquaculture 3: 27-41.

PUPPIN RSV, EKNATH AE, GJERDEM B, TAYAMEN MM, MACARANAS JM AND ABELLA TA. 1991. The genetic improvement of farmed tilapias GIFT project: the story so far. NAGA, the ICLARM Quarterly, April, 3-6.

QUINTON CD, MCMILLAN I AND GLEBE BD. 2005. Development of an Atlantic salmon (*Salmo salar*) genetic improvement program: Genetic parameters of harvest body weight and carcass quality traits estimated with animal models. Aquaculture 247: 211-217.

RIDHA MT. 2010. Spawning performance and seed production from hybridization between *Oreochromis spilurus* and the GIFT strain of the Nile tilapia *Oreochromis niloticus*. Aquac Res 41: e723-e729.

RUTTEN MJ, KOMEN H AND BOVENHUIS H. 2005. Longitudinal genetic analysis of Nile tilapia (*Oreochromis niloticus* L.) body weight using a random regression model. Aquaculture 246: 101-113.

RYE M, WANG YX, YANG KX, BENTSEN HB AND GJEDREM T. 2011. Genetic improvement of tilapias in China: Genetic parameters and selection responses in growth of Nile tilapia (*Oreochromis niloticus*) after six generations of multi-trait selection for growth and fillet yield. Aquaculture 322: 51-64.

SANTOS AI, RIBEIRO RP, VARGAS L, MORA F, ALEXANDRE FILHO L, FORNARI DC AND OLIVEIRA SND. 2011. Bayesian genetic parameters for body weight and survival of Nile tilapia farmed in Brazil. Pesqui Agropecu Bras 46: 33-43.

SU GS, LILJEDAHL LE AND GALL GAE. 1997. Genetic and environmental variation of female reproductive traits in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 154: 115-124.

THODESEN J, RYE M, WANG YX, YANG KS, BENTSEN HB AND GJEDREM T. 2011. Genetic improvement of tilapias in China: genetic parameters and selection responses in growth of Nile tilapia (*Oreochromis niloticus*) after six generations of multi-trait selection for growth and fillet yield. Aquaculture 322: 51-64.

TRỌNG TQ, ARENDONK JAM AND KOMEN K. 2013b. Genetic parameters for reproductive traits in female Nile tilapia (*Oreochromis niloticus*): I. Spawning success and time to spawn. Aquaculture 416-417: 57-64.

TRỌNG TQ, ARENDONK JAM AND KOMEN K. 2013c. Genetic parameters for reproductive traits in female Nile tilapia (*Oreochromis niloticus*): II. Fecundity and fertility. Aquaculture 416-417: 72-77.

TRỌNG TQ, MULDER HA, VAN ARENDONK JA AND KOMEN H. 2013a. Heritability and genotype by environment interaction estimates for harvest weight, growth rate, and shape of Nile tilapia (*Oreochromis niloticus*) grown in river cage and VAC in Vietnam. Aquaculture 384: 119-127.

TSADIK GG. 2008. Effects of maternal age on fecundity, spawning interval, and egg quality of Nile tilapia, *Oreochromis niloticus* (L.). J World Aquacult Soc 39(5): 671-677.

TSADIK GG AND BART AN. 2007. Characterization and comparison of variations in reproductive performance of Chitralada strain Nile tilapia, *Oreochromis niloticus* (L.). Aquacul Res 38(10): 1066-1073.

TURRA EM, APARECIDA DAO, DOURADO BV, ALENCAR ET, ASSIS SP, RAMOS EA AND ALMEIDA MS. 2012. Longitudinal genetic analyses of fillet traits in Nile tilapia *Oreochromis niloticus*. Aquaculture 356: 381-390.

VAN TASSELL CP, VAN VLECK LD AND GREGORY KE. 1998. Bayesian analysis of twinning and ovulation rates using a multiple-trait threshold model and Gibbs sampling. J Anim Sci 76(8): 2048-2061.

YOSHIDA GM, OLIVEIRA CAL, KUNITA NM, OLIVEIRA SN, FILHO LA, RESENDE EK, LOPERA-BARRERO NM AND RIBEIRO RP. 2013a. Resposta a seleção de características de desempenho e morfométricas de tilápias-do-nilo ao longo do período de cultivo. Arq Bras Med Vet Zoo 65: 1815-1822.

YOSHIDA GM, OLIVEIRA CAL, KUNITA NM, RIZZATO GS AND RIBEIRO RP. 2015. Reproduction performance of female Nile tilapia under different environments and age classes. Acta Sci Anim Sci 37(3): 221-226.

YOSHIDA GM, OLIVEIRA CAL, OLIVEIRA SN, KUNITA NM, RESENDE EK, FILHO LA AND RIBEIRO RP. 2013b. Associação entre características de desempenho de tilápia-do-nilo ao longo do período de cultivo. Pesqui Agropecu Bras 48: 816-824.