



Meta-analysis of genetic parameters for productive traits in Nile tilapia (*Oreochromis niloticus*)

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Abstract: The advances in the production traits of *Oreochromis niloticus* are due to the development of genetically superior broodstock animals. Understanding the genetic variability of fish stocks is crucial to any animal breeding program. The aim of this study was to perform a meta-analysis of genetic parameters that considers the variability between studies for economically important traits in the Nile tilapia (*Oreochromis niloticus*) production. The final dataset from literature review contained 226 estimates of heritability and 53 estimates of genetic correlation across 37 peer-reviewed articles published between 2002 and 2022. Weighted genetic parameter estimates were obtained by fitting a random effect model for all traits studied. Heterogeneity across studies were assessed using the Q statistic and I^2 index. Heritability estimates ranged from low to moderate magnitude, indicating that a greater response to selection is expected for body length (0.37), body weight (0.29), body width (0.28), and daily weight gain (0.28), compared to the other traits, body height (0.25) and fillet yield (0.19). Genetic correlations ranged from moderate to high magnitude (0.47 to 0.94), which suggests that part of expression of traits is regulated by the same gene groups. The meta-analysis study provided reliable genetic parameter estimates and these findings may be served as the baseline reference for new Nile tilapia (*Oreochromis niloticus*) breeding programs.

Keywords: genetic correlation; fish production; heritability; heterogeneity

Aquaculture has been growing since the 1950s, driven by increased fish consumption. In 2020, global production of aquatic animal reached 178 million tonnes, with capture fisheries contributing 51% and aquaculture contributing 49%. Overall production of aquatic animals, over 157 million tonnes were for human consumption. Nile tilapia (*Oreochromis niloticus*) ranks third among fish species produced worldwide, with 4.4 million tonnes in 2020, repre-

senting 8.6% of farmed fish production (FAO 2022). Genetic improvements in production traits have led to advancements in Nile tilapia (*Oreochromis niloticus*) production, primarily focusing on body weight and daily weight gain as selection criteria for growth rate. Morphometric traits such as body length, width, and height are routinely recorded and evaluated within breeding programs, as they correlate with growth traits (Cardoso et al. 2021).

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Selection is an important tool for increasing productivity, and understanding genetic parameters is essential for defining selection criteria, especially in captive fish stocks. Genetic variability in captive fish is vital for breeding programs, as reduced variability has negative implications for economic valuable traits. To avoid loss of adaptive potential, increasing gene flow is recommended (Ferreira et al. 2019). Genetic parameter estimates, including heritability and genetic correlation, form the basis for the development of Nile tilapia (*Oreochromis niloticus*) breeding programs. According to Bentsen et al. (2012), the overall heritability estimates for harvest body weight in Nile tilapia (*Oreochromis niloticus*) did not differ significantly between sexes (0.20 for females and 0.16 for males) on the standardized scale. In addition, the between-sex genetic correlations for body weight at harvest were all high (0.78–0.97). However, heritability for body weight were lower in ponds than in cages for male animals. The growth performance is more likely to be affected in ponds than in cages by individual variation in age at sexual maturation and reproduction, which support the assumption that such effects may be even more pronounced in males than in females (Bentsen et al. 2012).

Many studies have provided estimates for these genetic parameters; however, they have been obtained using different methods, designs, and sample sizes. To address the variability between studies, a meta-analysis can be a practical and efficient solution by considering differences between studies. A meta-analysis combines and summarizes multiple scientific studies using statistical methods (Sutton et al. 2000) and provides combined estimates by considering factors as sample size, sample variance or standard error. In animal breeding programs, the application of meta-analysis helps to avoid unnecessary expenditure on data collection in the field and increases the efficiency of the selection process. Meta-analysis using a random effects model will provide reliable estimates of genetic parameters, as well as helping to understand the patterns formed by heterogeneity between studies (Ambike et al. 2022). No study using meta-analysis of economic traits in Nile tilapia (*Oreochromis niloticus*) has been reported. The aim of this study was to perform a meta-analysis of genetic parameters for economic importance traits in Nile tilapia (*Oreochromis niloticus*) based on random effects model.

MATERIAL AND METHODS

Literature search and traits

Initially, a literature review was performed to identify all references that reported estimates of genetic parameters (heritability and genetic correlation) for economic traits in male and female population of Nile tilapia (*Oreochromis niloticus*). The traits included in the study were: body length at harvest (BL), body width at harvest (BWI), body height at harvest (BHE), body weight at harvest (BWE), daily weight gain (DWG), and fillet yield (FY). The following steps were utilized to conduct the search and select relevant studies:

1. A search was conducted from 2002 to 2022 using the access platforms including Web of Science, PubMed, Google Scholar, and Scopus;
2. Specific search terms such as “genetic parameters”, “heritability”, “genetic correlation”, “Nile tilapia”, “body length”, “body width”, “body height”, “daily weight gain”, “fillet yield”, as well as alternative or combined words, were employed to extract articles; and
3. Only scientific articles published in indexed journals and/or providing informative descriptions for the estimates were included.

Studies in all formats and languages were considered based on the terms mentioned above.

Data recording and exploratory analysis

Data were collected and included publication year, journal name, number of records, phenotypic means, standard deviation, coefficient of variation, and model statistical. Genetic parameter estimates were derived from restricted maximum likelihood method or Bayesian inference using a mixed animal model. For some genetic parameter estimates, the standard error (SE) was not reported, and in these cases the approximate standard error was calculated using the pooled variance method, as described by Sutton et al. (2000):

$$SE_{ij} = \sqrt{\left(\sum_{k=1}^k s_{ik}^2 n_{ik}^2 / \sum_{k=1}^k n_{ik} \right) / n'_{ij}} \quad (1)$$

where:

SE_{ij} – estimated standard error for the published parameter estimate for the i th trait in the j th study, where the SE has not been reported;

s_{ik} – published *SE* for the parameter estimate for the i th trait in the k th study, where the *SE* has been reported;

n_{ik} – number of records used to predict the published parameter estimate for the i th trait in the k th study with reported *SE*;

n_{ij} – number of records used to predict the published parameter estimate for the i th trait in the j th study without reported *SE*.

The published genetic correlation estimates are not used in most meta-analysis studies in animal breeding because they do not follow a normal distribution (Oliveira et al. 2017).

Thus, the genetic correlation estimates published were first transformed to an approximate normal scale by using the Fisher's Z transformation as described in the equation below (Borenstein et al. 2009):

$$Z_{ij} = 0.5[\ln(1 + r_{g_{ij}}) - \ln(1 - r_{g_{ij}})] \quad (2)$$

where:

Z_{ij} – transformed genetic correlation;

$r_{g_{ij}}$ – published genetic correlation estimate for the i th trait in the j th study.

Furthermore, the genetic correlations and their confidence interval were converted back to their original scale (Borenstein et al. 2009) using the following equation:

$$r_{g_{ij}}^* = (e^{2Z_{ij}} - 1) / (e^{2Z_{ij}} + 1) \quad (3)$$

where:

$r_{g_{ij}}^*$ – re-transformed genetic correlation estimate for the i th trait in the j th study.

Data quality control

A box plot weighted by the number of records was used to identify possible outliers. To ensure the reliability and avoid biased estimates, a minimum number of scientific articles was determined for each trait based on the relative standard error (RSE), with a maximum RSE limit of 25%, as suggested by Oliveira et al. (2017).

The procedure for calculating the RSE is as follows (Zarkovich 1979):

$$RSE_i = \frac{\left(\frac{s_i}{\sqrt{n_i}} \right)}{\bar{x}_i} \times 100 \quad (4)$$

where:

RSE_i – relative standard error;

s_i – SD estimated from the published parameter estimates for the i th trait;

n_i – number of studies that have reported parameter estimates for the i th trait;

\bar{x}_i – average of parameter estimates for the i th trait.

The total number of records for each trait was determined by summing the number of records across all located studies. Means and standard deviations were computed, with sample sizes serving as weights. Moreover, the coefficient of variation (CV) was determined for each trait:

$$CV_i(\%) = \frac{S_i}{\bar{X}_i} \times 100 \quad (5)$$

where:

S_i – SD for the i th trait;

\bar{X}_i – trait mean.

Meta-analysis of genetic parameters

Weighted genetic parameter were obtained by fitting a random effect model. Estimates were assumed to be independent and normally distributed, using the Box-Pierce and Shapiro-Wilk tests, respectively, using statistical software R (R Core Team 2021). The meta-analysis was performed considering the following random effects model for each trait:

$$\hat{\theta}_j = \bar{\theta} + u_j + e_j \quad (6)$$

where:

$\hat{\theta}_j$ – published parameter estimate in the j th study;

$\bar{\theta}$ – weighted population parameter mean;

u_j – among-study component of the deviation from the mean;

e_j – within-study component due to sampling error in the parameter estimate in the j th study.

The u_j and e_j were assumed to follow normal distributions, with $u_j \sim N(0, \tau^2)$ and $e_j \sim N(0, \sigma_e^2)$, respectively, where τ^2 is the variance representing the amount of heterogeneity among studies and

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σ_e^2 is the within-study variance. The meta-analysis was conducted using the *metaphor* package (Viechtbauer 2010) available in R software (R Core Team 2021).

Heterogeneity and publication bias

To quantify the degree of heterogeneity (τ^2) between studies, the I^2 index was used (Higgins et al. 2003), described as:

$$I^2 = \frac{Q - df}{Q} \times 100 \quad (7)$$

where:

Q – statistic (Cochran 1954) given by:

$$Q = \sum_{j=1}^J w_j (\hat{\theta}_j - \bar{\theta})^2 \quad (8)$$

where:

- w_j – weight of the parameter estimate, assumed as the inverse of published sampling variance for the parameter, $(1/s_j^2)$ in the j th study;
- $\hat{\theta}_j$ – parameter estimate published in the j th study
- $\bar{\theta}$ – weighted mean estimate of the population parameter, both were defined previously in the random-effects model.

The df denotes the degrees of freedom ($J - 1$, where J is the number of used studies) of a Chi-squared distribution assumed for the expected Q value under the assumption that $\tau^2 = 0$.

Variations between studies were assessed using the Q statistic at a significance level of 0.01, as it has limited power with few studies (Huedo-Medina et al. 2006). The I^2 index was also used to measure the degree of heterogeneity. In addition, the 95% confidence intervals were considered, and the lower and upper limits will be calculated by:

$$LL_{\bar{\theta}} = \bar{\theta} - 1.96 \times SE_{\bar{\theta}} \quad (9)$$

$$UL_{\bar{\theta}} = \bar{\theta} + 1.96 \times SE_{\bar{\theta}} \quad (10)$$

where:

$SE_{\bar{\theta}}$ – predicted standard error for the estimated parameter $\bar{\theta}$, i.e.:

$$SE_{\bar{\theta}} = \sqrt{1 / \sum_{j=1}^J w_j} \quad (11)$$

where:

- $\bar{\theta}$ – predicted standard error for the estimated parameter;
- w_j – weight of the parameter estimate, assumed as the inverse of published sampling variance for the parameter, $(1/s_j^2)$ in the j th study;

Egger's linear regression asymmetry was used to examine the presence of publication bias and a P -value of 0.05 was set. If heterogeneity (Q statistic P -value < 0.05) was present, testing for publication bias is inappropriate since it may lead to positive missing results (Hossein-Zadeh 2021).

RESULTS

Summary statistic

The descriptive statistics and number of articles and records for evaluated traits in Nile tilapia (*Oreochromis niloticus*) mixed sex population are shown in Table 1. Outliers were removed during quality control. The dataset contained 226 estimates of heritability and 53 estimates of genetic correlation from 37 peer-reviewed scientific articles published between 2002 and 2022 [Electronic Supplementary Material (ESM) Table S1]. The weighted coefficients of variation for most traits were high and ranged from 12.5% (for FY) to 57.1% (for BWI) (Table 1).

Heritability

The number of contributing estimates (N), the weighted heritability estimates (h^2), the relative standard error (RSE) and the heterogeneity of the estimates (based on Q and I^2 statistics) for the studied traits obtained from the random effects model of the meta-analysis are shown in Table 2.

Heritability estimates for all traits analysed in this study assumed independence and normal distribution. Additional information of heritability estimates for evaluated traits obtained from published papers are shown in the Forest plot available in ESM Figures S1–6.

Weighted heritability estimates ranged from 0.19 to 0.37. All these estimates had low standard errors and were significant (P -value < 0.01) (Table 2). The relative standard error for the weighted param-

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Table 1. Number of articles (NA), number of phenotypic records (NR), mean, standard deviation (SD) and coefficient of variation (CV%) for each trait evaluated in mixed sex population of Nile tilapia (*Oreochromis niloticus*)

Traits	Abbreviation	Unit	NA	NR	Mean	SD	CV (%)
Body length	BL	cm	14	263 495	14.7	4.00	27.1
Body width	BWI	cm	7	70 850	3.03	1.73	57.1
Body height	BHE	mm	5	20 054	58.2	12.1	20.7
Body weight	BWE	g	28	633 494	307	105	34.4
Daily weight gain	DWG	g/day	11	117 270	1.80	0.74	40.9
Fillet yield	FY	%	9	141 104	37.3	4.70	12.5

BHE = body height; BL = body length; BWE = body weight; BWI = body width; DWG = daily weight gain; FY = fillet yield

Table 2. Number of estimates (N), heritability (h^2), standard error (SE), 95% confidence interval (95% CI), significance of the random effect model (P -value), Q statistic (Q) and their significance (P -value), relative standard error (RSE %), and heterogeneity index (I^2 %) estimated through meta-analysis based on random-effects models for each trait evaluated in Nile tilapia (*Oreochromis niloticus*)

Traits	N	h^2	SE	95% CI	P -value	Q	P -value	RSE %	I^2 %
BL	51	0.37	0.02	0.31–0.41	0.000 1	187	0.000 1	10.3	73.2
BWI	16	0.28	0.03	0.22–0.34	0.000 1	45.2	0.000 1	15.2	69.1
BHE	15	0.25	0.02	0.22–0.29	0.000 1	20.5	0.114 2	14.9	33.1
BWE	93	0.29	0.02	0.26–0.33	0.001 0	1 647	0.000 1	10.5	90.4
DWG	23	0.28	0.02	0.24–0.32	0.000 1	113	0.000 1	7.78	73.3
FY	28	0.19	0.01	0.17–0.22	0.000 1	34.7	0.144 8	11.6	27.9

BHE = body height; BL = body length; BWE = body weight; BWI = body width; DWG = daily weight gain; FY = fillet yield

Table 3. Number of estimates (N), genetic correlation (r_g), standard error (SE), 95% confidence interval (95% CI), Q statistic (Q), relative standard error (RSE %), and heterogeneity index (I^2 %) estimated through meta-analysis based on random-effects models for each trait evaluated in Nile tilapia (*Oreochromis niloticus*)

Traits	N	r_g	SE	95% CI	P -value	Q	P -value	RSE %	I^2 %
BL – BHE	7	0.79	0.14	0.71–0.88	0.000 1	239	0.000 1	7.22	97.7
BL – DWG	4	0.65	0.12	0.50–0.80	0.000 1	9.65	0.021 7	12.3	70.6
BL – BWI	5	0.57	0.20	0.27–0.86	0.000 3	292	0.000 1	23.9	97.0
BL – FY	2	0.47	0.16	0.18–0.75	0.001 0	1.21	0.271 3	24.0	17.3
BWE – BHE	5	0.90	0.15	0.80–0.99	0.000 1	388	0.000 1	4.62	99.1
BWE – BL	9	0.92	0.13	0.88–0.96	0.000 1	1 512	0.000 1	2.34	99.0
BWE – DWG	6	0.94	0.24	0.90–0.99	0.000 1	2 961	0.000 1	3.71	99.9
BWE – BWI	8	0.82	0.15	0.72–0.92	0.000 1	276	0.000 1	7.74	97.7
BWE – FY	3	0.59	0.15	0.36–0.81	0.000 1	3.50	0.173 7	15.5	43.6
DWG – BHE	4	0.77	0.07	0.67–0.87	0.000 1	4.50	0.211 8	3.75	36.2

BHE = body height; BL = body length; BWE = body weight; BWI = body width; DWG = daily weight gain; FY = fillet yield

eters were lower than 15.2%, for all traits analysed. In general, the test for heterogeneity of the weighted heritability estimates using the Q statistic (Table 2) showed significant heterogeneity (P -value < 0.05). The I^2 index showed values ranging from 27.9%

to 90.4% for the heritability estimates, indicating low to high heterogeneity between the studies (Table 2). These results highlight the need to use meta-analysis based on random effects models for most of the traits analysed. Egger's test was ap-

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plied to the heritability estimates for BHE and FY, indicating that there was no publication bias (ESM Table S2).

Genetic correlation

The mean estimates of genetic correlation for analysed traits are shown in Table 3. Some genetic correlations were not available and are limited in the literature. In addition, there were genetic correlations had to be eliminated from the study because their RSE values were greater than 25% (Table 3). The estimates of genetic correlations used in the meta-analysis study also assumed normal distribution and independence. Additional results of genetic correlation estimate among evaluated traits obtained from published articles are shown in the Forest plot available in ESM Figures S7–16.

Weighted genetic correlation estimates among traits ranged from moderate to high (0.47 to 0.94). The relative standard error estimates were lower than 24.0% (Table 3). Most estimates had high heterogeneity (P -value of Q statistic < 0.01 and $I^2 > 70.6\%$). Egger's test not indicated significant publication bias (P -value > 0.05) for BWE and FY, and DWG and BHE genetic correlations (ESM Table S2).

DISCUSSION

A higher number of scientific studies have been conducted on the heritability of BWE, BL, and DWG, as indicated in Table 1. This demonstrating the economic importance of these traits in Nile tilapia (*Oreochromis niloticus*) production. However, the limited number of studies on BH and BWI suggests a need for further investigation into the impact of these traits within breeding programs. The low amount of information could be associated with a limitation in data collection procedures due to associated costs, with a focus on prioritizing body length as the main morphometric trait in production system. Body weight provides the industry with a direct assessment of an animal performance and potential farm productivity (Hasan et al. 2020). In addition, this trait is an important determining factor of price paid for stock at the farm gate. Furthermore, estimates of genetic parameters for FY have been reported less frequently in lit-

erature, despite being influential in the consumers market of the fish production system. The substantially lower representation of FY in this analysis can be attributed to the measurement difficulty found in the structure of most breeding programs and facilities.

The high coefficient of heterogeneity for most traits could be explained by the different farming environments of Nile tilapia (*Oreochromis niloticus*) production. Furthermore, most of fish are raised in the diverse water environments characterized by highly variable aquatic parameters among different ponds or production units, including variation in temperature, salinity, pH, and level of oxygen. In addition, the published studies are based on information from animals raised in different generations (Hasan et al. 2020). These environmental factors can impact on heritability estimates of economically important traits. Generally, the genotype by environment interaction is evidenced in fish farming (Araujo et al. 2020), increasing genetic distance and variability, especially in species such as Nile tilapia (*Oreochromis niloticus*), which survive in challenging environments (Miao and Wang 2020).

In summary, the heritability estimates for the traits were of low to moderate magnitude, indicating that a greater response to selection is expected for BL (0.37), BWE (0.29), BWI (0.28), and DWG (0.28), compared to the other traits, BHE (0.25) and FY (0.19). Nile tilapia accounts for 8.3% of global fish production, and the industry aims to increase sustainable production while maintaining quality (FAO 2022). It is important to highlight that daily weight gain depends on factors such as genetic and nutrition. In this context, it is known that a portion of the variation in the economic traits of Nile tilapia (*Oreochromis niloticus*) is determined by additive genetic effects, and these can contribute to the response to selection (Marjanovic et al. 2016; Khaw et al. 2009).

Based on previous estimates, Nile tilapia (*Oreochromis niloticus*) breeding programs may benefit through direct selection for body length. In addition, morphometric traits as body width, and height are routinely recorded and used in breeding programs to select for body shape, as these parameters tend to be highly correlated with growth-related traits (Cardoso et al. 2021). In fish farming, body weight and daily weight gain are commonly adopted as the main selection criteria, increasing fish size, and in turn, larger fish are processed

for the fillet market. Body weight is important as it provides industry with a direct assessment of an animal's performance and its farm productivity (Hasan et al. 2020). Therefore, using BWE, DWG, and BL as selection criteria can improve fish yield and genetic quality of Nile tilapia (*Oreochromis niloticus*) culture stock.

Notably, the strongest genetic correlations were found between BWE and DWG (0.94), BWE and BL (0.92), and BWE and BHE (0.90), suggesting shared genetic regulation. Thus, selection of one trait will lead to a change in others. BL showed genetic correlation of 0.79 with BHE, 0.65 with DWG, 0.57 with BWI, and 0.47 with FY. Moderate genetic correlations were observed between BWE with BWI (0.82), and with FY (0.59), and between DWG and BHE (0.77). This implies that indirect genetic gains for economic traits in Nile tilapia (*Oreochromis niloticus*) can be expected.

In Nile tilapia breeding programs focused on traits as body weight and fillet yield, direct selection is favorable due to their high genetic variability. Alternatively, correlated traits can be used as selection criteria, but this method is effective only when the selected trait has high heritability and a strong genetic correlation with the target traits (Turra et al. 2018). In this case, favorable genetic correlations exist among morphometric, performance, and carcass traits, allowing for indirect gains when selecting any of them. Selection for growth could also impact in body shape, as reported by Oliveira et al. (2016), which can be relevant where Nile tilapia is consumed whole and fresh (Cardoso et al. 2021).

In addition, there is a growing interest from the industry to improve other traits of economic importance, such as fillet yield (Garcia et al. 2017). In some countries, the payment system has changed from whole-body weight to fillet weight (Nguyen et al. 2010). However, improving fillet yield is not simple because it requires slaughtering many animals, increasing costs, and reducing the number of candidates for selection. As an alternative, using indirect selection through studies of genetic correlations with body measurements (Garcia et al. 2017).

On the market, tilapias are sold as either whole fish or as fresh or frozen fillets (Gjerde et al. 2012) and direct selection for increased fillet yield is beneficial only if this result in faster genetic gain compared to indirect method. If traits that can be recorded on live broodstock candidates are

strongly correlated with fillet weight and yield, both the selection intensity and accuracy of selection can be increased, resulting in a higher genetic gain compared to sib selection. The close genetic correlation between fillet yield and body weight indicates that to improvement of fillet yield would be expected based on selection for body weight alone.

In breeding programs focused on all-male farming systems, where the commercial fish usually is a mixture of genetic males and phenotypically sex-reversed females, the selection based on grow performance in mixed sex pond culture is expected to result in a desired selection pressure for increased age at sexual maturation in both sexes if the target is pond culture systems (Bentsen et al. 2012).

Nevertheless, differences in growth between males and females in mixed sex populations versus monosex populations have been observed (Bentsen et al. 2012). Omasaki et al. (2016) found limited evidence for genotype by environment interaction for daily growth rate between mixed sex nucleus and male monosex groups. For this reason, the authors recommended that a breeding programme aiming to provide genetically improved Nile tilapia (*Oreochromis niloticus*) broodstock to hatcheries providing monosex fry to smallholder pond farmers should consider genetic parameters for both monosex and mixed sex populations.

CONCLUSION

The heritability estimates found in this meta-analysis indicate that there is moderate genetic variability for economically important traits in the Nile tilapia (*Oreochromis niloticus*). Thus, genetic progress can be achieved by including morphometric traits, weight, and fillet yield as selection criteria. The high estimates of genetic correlation found among these traits suggest that indirect selection could be a good strategy to improve all of them or can be simultaneously improved using index selection. These findings found in this meta-analysis study will serve as the baseline reference for new Nile tilapia (*Oreochromis niloticus*) breeding programs.

Conflict of interest

The authors declare no conflicts of interest.

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