

Original research article

Evaluating the genetic diversity in farmed populations of Nile tilapia (*Oreochromis niloticus*) from Brazil using SNP markers

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ABSTRACT

The Nile tilapia (*Oreochromis niloticus*) plays a significant role in global aquaculture, with Brazil ranking among the top producers worldwide. However, a considerable gap remains in the exploration of genetic diversity within Brazilian Nile tilapia stocks. To address this, we analyzed the genetic diversity of nine distinct farmed populations of Nile tilapia in Brazil, comprising a total of 600 individuals, using single-nucleotide polymorphisms (SNPs). Our objective was to provide essential genetic insights to establish the foundation for a new breeding nucleus. The pre-breeding populations exhibited high genetic diversity. Among them, Pop1 had the lowest diversity, characterized by the smallest proportion of polymorphic SNPs ($N_p = 92.3\%$), the lowest mean minor allele frequency ($MAF = 0.24$), and the lowest heterozygosity ($H_E = 0.32$). In contrast, Pop5 and Pop9 displayed the highest genetic diversity ($MAF = 0.30$; $H_E = H_0 0.39$), with nearly all loci in Hardy-Weinberg equilibrium ($HWE = 99.4\%$). Additionally, reduced effective population sizes (N_e) were observed in Pop1 ($N_e = 6.8$) and Pop4 ($N_e = 15.4$), with approximately 40 % of individuals classified as half-of full siblings, suggesting risks of inbreeding. These characteristics led to the genetic structuring of Pop1 and Pop4 in relation to the other populations, while Pop5 and Pop9 also formed a distinct cluster due to their higher genetic diversity. Despite the overall high genetic diversity observed across the analyzed populations, some populations exhibited parameters that may indicate potential future issues related to genetic diversity loss if not properly managed. Therefore, the findings presented here will help ensure the implementation of effective strategies during the pre-breeding phase of a new tilapia genetic improvement nucleus, supporting the long-term maintenance of genetic diversity in the breeding stock.

1. Introduction

Nile tilapia (*Oreochromis niloticus*) has become one of the most important species in global aquaculture (FAO, 2024). Its annual production has reached approximately 5.3 million tons, accounting for 9% of the total global production of freshwater fish (FAO, 2024). The white

flesh with a firm texture and delicate flavor makes it highly popular among consumers. Additionally, Nile tilapia is well-suited for aquaculture due to its fast growth and adaptability to diverse farming conditions (Freitas et al., 2012). The species is cultivated by both small-scale farmers and large-scale producers supplying international markets (Fitzsimmons et al., 2011, pp. 9–18).

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The production of Nile tilapia in Latin America has been rapidly expanding, primarily driven by the export of fillets to the United States (FAO, 2023a). Brazil is one of the leading global producers, with an average annual production growth of around 12% since 2000 (FAO, 2023b). In 2022, the Brazilian production reached 410 thousand tons, accounting for 66% of the total fish production in the country (IBGE 2023). The Southeast region is considered one of the most significant and structured hubs for Nile tilapia production in Brazil, and along with the South region, it represents 70% of the total annual tilapia production (Ribeiro et al., 2024).

The boost in tilapia production in Brazil began in 2005 with the importation of commercially valuable lines, such as the Genetically Improved Farmed Tilapia (GIFT). The GIFT tilapia genetic improvement program was launched in the 1980s in the Philippines by what is now known as the WorldFish Center. The program aimed to enhance growth performance, disease resistance, and production efficiency in aquaculture. After multiple cycles of genetic selection, the WorldFish Center distributed specimens to other countries, including Malaysia, where the line continued to be improved before being introduced to Brazil (Ponzoni et al., 2011). Today, these imported strains have allowed Brazil to become self-sufficient in both tilapia fingerling production and grow-out operations. However, nearly all stocks are produced without any genetic information, which hinders the development of effective genetic improvement programs. In this context, it is crucial to first evaluate the genetic profile of pre-breeding individuals introduced into breeding nuclei, and then maximize growth trait performance under Brazilian environmental conditions, resistance against specific pathogens that infect Brazilian tilapia stocks such as *Streptococcus agalactiae* serotype Ib (Oliveira-Neto et al., 2024), and other traits of interest.

Tilapia breeding programs globally have achieved substantial advancements, driven by the necessity to satisfy the escalating demand for fish within the expanding aquaculture sector (Yáñez, Joshi, & Yoshida, 2020a,b). The success of a sustainable genetic improvement program is strictly dependent on how the pre-breeding population is constructed, as the initial genetic variability available in the broodstock will determine the progress of genetic gain in individuals over the future generations (Villanueva et al., 2022). With the advancement of genotyping technologies, an increasing amount of genomic information has been utilized to enhance the understanding and management of genetic diversity in aquaculture stocks (Nguyen, 2016; Yáñez, Joshi, & Yoshida, 2020a,b).

The application of single-nucleotide polymorphisms (SNPs) is considered an effective technique for the assessment of genetic diversity within aquaculture populations in sustainable breeding programs (Houston et al., 2020). SNP panels have been widely applied in genetic improvement programs for aquaculture species, gathering large volumes of population-level SNPs for genotyping (Houston et al., 2020; Yáñez, Joshi, & Yoshida, 2020a,b; You et al., 2020). However, the high genotyping costs can restrict the routine use of high-density SNP panels for the entire tilapia production in Brazil, and low-density genotyping appears to be a promising solution for enabling access to a broader range of fish producers. Several assessments of genetic diversity in productive stocks using lower densities of SNPs have been conducted in aquaculture species and seem to be a cost-effective way of genetic management for the development of effective genetic improvement programs (Martinez et al., 2023; Mastrochirico-Filho et al., 2024; Silva et al., 2022).

Considering the short reproductive cycle (less than one year) in Nile tilapia, along with the absence of inbreeding control in cultivated populations and limited introductions of this species in Brazil, the necessity to utilize monitoring tools for genetic variability becomes urgent. Additionally, genomic data regarding genetic variability is crucial for implementing pre-breeding strategies, offering guidance on maintaining variability within a breeding nucleus. Therefore, the objective of the present study was to assess the genetic diversity of nine distinct farmed populations of Nile tilapia in Brazil, using SNPs. Additionally, this work will serve as a model for establishing new breeding nuclei through the investigation of the genetic profile of pre-breeding populations.

Additionally, it will provide valuable insights for effective genetic management within Nile tilapia breeding programs from Brazil.

2. Material and methods

2.1. Ethics statement

This study was conducted in strict accordance with the recommendations of the National Council for Control of Animal Experimentation (CONCEA) (Brazilian Ministry for Science, Technology and Innovation) and was approved by the Ethics Committee on Animal Use (CEUA number 004650/24) of Faculdade de Ciências Agrárias e Veterinárias, UNESP, Campus Jaboticabal, SP, Brazil.

2.2. Experimental population and genotyping

Samples were previously collected by the Brazilian Fish company (Santa Fé do Sul, SP, Brazil) and provided for analysis in the present study. Fin clips were collected from each fish under benzocaine anesthesia (80 mg/L) and all efforts were made to minimize suffering. Fin samples were stored in 95% ethanol at −20 °C.

The experimental pre-breeding population consisted of 600 Nile tilapia individuals, comprising samples from nine commercial fish farms (Pop1 – Pop9), as detailed in Table 1. These fish farms are located in the Southeast and South regions of Brazil, which are the main production areas for this species. To ensure confidentiality, the commercial identities and exact locations of the farms were not disclosed. These animals will be used as founders to create a novel breeding programs aiming at economic traits in Brazil. Genotyping of all samples were performed by the Center of Aquaculture Technologies (CAT) (San Diego, CA, USA), using the AQUAarray LD for tilapia, containing 192 SNPs. This SNP panel does not cover all regions of the genome, but it is strategically used for fish farms and researchers to provide insights into the genetic architecture of populations, parentage testing, and inbreeding analysis, at a lower cost compared to a higher-density panel (<https://aquatechcenter.com/species/nile-tilapia/>).

The genotyping data underwent a quality control (QC) process before population analyses. The PLINK software v. 1.9 (Purcell et al., 2007) was used to exclude individuals with low genotyping rates (<90 %) and high missing genotyping rates (>10 %). In addition, low minor allele frequencies (MAF <0.01) and high deviations from the Hardy-Weinberg equilibrium (HWE) ($P < e^{-6}$) were detected in each population and discarded.

2.3. Genetic diversity analyses and inbreeding

The number of polymorphic loci (N_P), MAF values, expected (H_E) and observed (H_O) heterozygosity, and deviations from the

Table 1
Population, number of samples (N), total genotyped loci, and quality control parameters (SNP call-rate, minor allele frequency (MAF) and Hardy-Weinberg equilibrium (HWE)) for 9 Brazilian Nile tilapia populations.

Population ^a	Sample (N)	Genotyped Loci	SNP call-rate (90 %)	MAF (>0.01)	HWE (>1e ⁻⁰⁶) ^b
Pop1	50	192	175	156	149
Pop2	50	192	175	169	168
Pop3	50	192	175	168	168
Pop4	100	192	175	164	155
Pop5	50	192	175	168	168
Pop6	100	192	175	168	164
Pop7	100	192	175	163	157
Pop8	50	192	175	167	166
Pop9	50	192	175	168	168

^a Population genotyped and evaluated using the low density 192 SNP array.
^b P-value for Hardy-Weinberg equilibrium.

Hardy–Weinberg equilibrium (HWE) were predicted at each locus using PLINK software v. 1.9 (Purcell et al., 2007). The statistical significance of the difference between the mean H_O and H_E was evaluated for each population using the Mann–Whitney test ($P = 0.05$). For HWE, the P were adjusted within each population according to the false discovery rate (FDR) method of Benjamini and Hochberg, to a significance level of 0.05.

The inbreeding coefficient (F_{IS}) was estimated within each population to assess heterozygote deficiency in the populations using HIERF-STAT (Goudet, 2005). Bootstrapping over loci were performed per population to extract the significance of F_{IS} estimates using the option *boot.ppfis* of HIERFSTAT, adopting 1000 bootstraps and quantiles of 0.05 and 0.95. The effective population size (N_e) for each population was calculated using the linkage disequilibrium method in NeEstimator V2.01 ($P < 0.05$) (Do et al., 2014). To optimize this analysis, rare alleles were discarded in the quality control process (details in section 2.2). The N_e estimates were used for a gross estimation of the rate of inbreeding (ΔF) in the analyzed populations, following the formula: $\Delta F = 1/2N_e$ (Gjedrem & Baranski, 2009).

2.4. Population structure and admixture

The genetic structure of populations was evaluated using pairwise F_{ST} values, estimated by FSTAT software v. 2.9.4 (Goudet, 1995). Genetically distinct clusters among the populations were evaluated through discriminant analysis of principal components (DAPC) using ADEGENET software v. 2.1.9 (Jombart & Ahmed, 2011), and via Bayesian approach using STRUCTURE v2.3.4 (Pritchard et al., 2000). In the DAPC analysis, the *find.clusters* function determined the number of clusters using Bayesian Information Criterion (BIC). The *xvalDAPC* function was utilized to calculate the optimal number of principal components to retain for the analysis. For STRUCTURE analysis, we assessed the distribution of ΔK , a statistic based on the rate of change in log probability of data between successive K values. Clusters (K) ranging from 1 to 9 were adopted, with analysis comprising 90 replicated runs (i. e., 10 replicates for each K value) using 300,000 Markov chain Monte Carlo iterations after a burn-in period of 150,000 runs. The most likely K value to explain population structure was determined by the modal value of ΔK . Outputs of STRUCTURE analysis were visualized using the STRUCTURE SELECTOR program (Li & Liu, 2018) and CLUMPAK (Kopelman et al., 2015). A molecular variance analysis (AMOVA) based on the STRUCTURE and DAPC results was conducted using ARLEQUIN software v. 3.5.2.2 (Excoffier & Lischer, 2010) to assess the significance of the structuring formed among the clusters.

2.5. Relatedness estimates

For genetic analyses to control inbreeding, the relatedness coefficient between pairs of individuals from each population was estimated using PLINK software v. 1.9 (Purcell et al., 2007) through the *–make-rel* option. This option estimates the relatedness coefficient based on the unadjusted A_{jk} parameter described in Yang et al. (2011). Yang et al. (2011) define $A_{jk} > 0.025$ as a pair of individuals being related at least as second cousins.

3. Results

3.1. Experimental population and genotyping

Details of the QC process applied to the genotypes from the nine Nile tilapia populations are presented in Table 1. Of the 192 genotyped SNPs, 175 were successfully genotyped in at least 90 % of the individuals and were retained. Subsequently, SNPs with a MAF below 1 % and those showing significant deviations from HWE within the populations were excluded. As a result, a total of 169 high-quality SNPs obtained from the merging of genotypes were retained for the subsequent genetic diversity

analysis. Additionally, no individuals were removed during the QC analyses, as all individuals had a call rate higher than 90 %.

3.2. Genetic diversity analyses and inbreeding

The resulting genetic diversity parameters estimated for each population of Nile tilapia are summarized in Table 2. Considering the total of 169 high-quality genotyped SNPs from all studied populations, the number of polymorphic SNPs reached a minimum of 156 (92.3 %) in Pop1. In contrast, all 169 SNPs were polymorphic in Pop2 and Pop6. The mean MAF values were slightly different between populations, ranging from 0.24 (SD 0.15) in Pop1 to 0.30 (SD 0.13) in Pop5. The mean H_O was significantly higher than the mean H_E in Pop1 ($H_O = 0.38$, SD = 0.24; $H_E = 0.32$, SD = 0.16; $P < 0.05$). In the other populations, H_O and H_E were similar ($P > 0.05$), with values ranging from 0.34 to 0.39. Only in Pop6 the mean H_O (0.36, SD = 0.13) was lower than the mean H_E (0.38, SD = 0.12) suggesting heterozygote deficiency. The smallest number of loci in Hardy–Weinberg equilibrium (HWE) was found in Pop1 (137 loci, 81 % of the total) and Pop4 (150 loci, 88.8 % of the total), while in the other populations, loci in equilibrium ranged between 153 (90.5 %) and 168 (99.4 %). Negative F_{IS} values were found in Pop1 (-0.17 , $P < 0.05$), Pop4 (-0.01 , $P < 0.05$), and Pop5 (-0.02 , $P < 0.05$). For Pop6, the F_{IS} was positive (0.05) and significantly different from zero, while in Pop2, Pop3, Pop7, Pop8, and Pop9, the values have low variation and were not statistically different from zero.

The N_e values was exhibited in Table 3, and they showed significant variation among the studied populations. Pop1 ($N_e = 6.8$), Pop4 ($N_e = 15.4$), and Pop3 ($N_e = 19.7$) exhibited the smallest effective population sizes and, consequently, are at higher risk of losing genetic diversity within their respective populations. On the other hand, Pop7 ($N_e = 92.5$), Pop8 ($N_e = 77.6$), and Pop9 ($N_e = 57.3$) had much larger effective population sizes. With the reduced N_e values, the inbreeding rates (ΔF) were higher for Pop1 ($\Delta F = 0.07$) and Pop4 ($\Delta F = 0.03$), while for the other populations, the N_e values ranged between 0.02 and 0.01.

3.3. Population structure and admixture

The pairwise F_{ST} estimates are shown in Table 4. In summary, the pairwise F_{ST} values were not statistically different from zero ($P < 0.05$) between Pop7 and Pop8 ($F_{ST} = 0.003$), Pop2 and Pop8 ($F_{ST} = 0.005$), Pop5 and Pop9 ($F_{ST} = 0.005$), Pop2 and Pop6 ($F_{ST} = 0.006$), and Pop6 and Pop8 ($F_{ST} = 0.006$). Pop1 showed the highest F_{ST} estimates, being significantly differentiated from Pop7 ($F_{ST} = 0.12$); from Pop2, Pop5, pPop8, and Pop9 ($F_{ST} = 0.10$); from Pop3 ($F_{ST} = 0.09$); and from Pop6 ($F_{ST} = 0.005$). In contrast, the differentiation between Pop1 and Pop4 was less pronounced ($F_{ST} = 0.005$).

For structuring evaluation, the PC1 and PC2 axes of the PCA analysis represented 25.83 % and 16.91 % of the total variance among the data, respectively (Fig. 1). The data structure resulting from the PCA analysis revealed the formation of three distinct clusters: one cluster formed by Pop1 and Pop4, one cluster formed by Pop5 and Pop9, and a larger cluster formed by a mixture of Pop2, Pop3, Pop6, Pop7, and Pop8.

According to the Bayesian model-based clustering analyses, a K value of 2 was the most suitable to explain the population structure of the tilapia populations (Fig. 2a). Three putative clusters composed of (1) Pop1 and Pop4; (2) Pop2, Pop3, Pop6, Pop7 and Pop8; and (3) Pop5 and Pop9 were found (Fig. 2b). Moreover, cluster 3 seems to be an admixture between cluster 1 and cluster 2. The DAPC method identified a similar formation of clusters retaining 200 principal components (PCs) (Fig. 3a) and obtaining a minimum BIC of 6 (Fig. 3b) and 8 discriminants (Fig. 3c).

Despite the genetic structure among populations being confirmed by STRUCTURE and DAPC analyses, AMOVA analysis based on groups supported by the results of STRUCTURE and DAPC was exhibited in Table 5. The AMOVA results showed that the higher percentage of genetic variation was assigned to differentiation within individuals: 93.1

Table 2
Number of polymorphic loci (N_P), proportion of polymorphic loci ($\%N_P$), MAF values, expected (H_e) and observed (H_o) heterozygosity, SNPs not deviating from the Hardy–Weinberg equilibrium (HWE) and the inbreeding coefficient (F_{IS}) estimated for nine Brazilian Nile tilapia populations.

Pop	N^a	N_P (%)	MAF ^b	H_e^b	H_o^b	HWE (%) ^c	F_{IS}^d
Pop1	169	156 (92.3)	0.24 (0.15)	0.32 (0.16)	0.38 (0.24)	137 (81.0)	−0.17*
Pop2	169	169 (100)	0.27 (0.13)	0.36 (0.13)	0.36 (0.16)	163 (96.4)	0.02
Pop3	169	168 (99.4)	0.28 (0.13)	0.36 (0.13)	0.36 (0.15)	160 (94.7)	0.02
Pop4	169	167 (98.8)	0.26 (0.15)	0.34 (0.16)	0.35 (0.19)	150 (88.8)	−0.01
Pop5	169	168 (99.4)	0.30 (0.13)	0.39 (0.12)	0.39 (0.15)	168 (99.4)	−0.02*
Pop6	169	169 (100)	0.28 (0.12)	0.38 (0.12)	0.36 (0.13)	153 (90.5)	0.05*
Pop7	169	167 (98.8)	0.26 (0.14)	0.34 (0.14)	0.34 (0.16)	155 (91.7)	0.02
Pop8	169	167 (98.8)	0.26 (0.13)	0.35 (0.13)	0.35 (0.15)	165 (97.6)	0.03
Pop9	169	168 (99.4)	0.29 (0.13)	0.39 (0.12)	0.39 (0.14)	168 (99.4)	0.001

^a High-quality SNPs after QC process.
^b The standard deviation (SD) of the MAF, H_e and H_o are presented in parentheses.
^c Number of SNPs (relative %) not deviating from the Hardy–Weinberg Equilibrium (p -value > 0.05, adjusted within each population according to the false discovery rate (FDR) method of Benjamini and Hochberg).
^d The F_{IS} values with an asterisk represent values that are statistically different from zero.

Table 3
Effective population size (N_e) parameter and its 95 % confidence interval (N_e 95 % CI) based on linkage disequilibrium and inbreeding coefficient ($\Delta F = 1/2N_e$) for nine Brazilian Nile tilapia populations.

Pop	N_e	N_e 95 % CI	ΔF
Pop1	6.8	6.3–7.4	0.07
Pop2	31.1	28.6–33.8	0.02
Pop3	19.7	18.5–21.1	0.02
Pop4	15.4	14.7–16.2	0.03
Pop5	33.4	30.8–36.4	0.01
Pop6	39.1	36.9–41.5	0.01
Pop7	92.5	83.8–102.8	0.01
Pop8	77.6	66.8–91.8	0.01
Pop9	57.3	51.0–64.9	0.01

% ($P < 0.05$). The estimated variation between groups (FCT) was only 5.78 % ($P < 0.05$). In addition, the variation among populations and within groups (FSC) presented 1.6 % of the genetic variation ($P < 0.05$), and among individuals within populations −0.46 % (Table 5).

3.4. Relatedness estimates

The mean relatedness coefficient for each population ranged from 0.04 (SD = 0.05) to 0.06 (SD = 0.09) (Fig. 4a; Table S1). Essentially, all populations had a higher proportion of nonrelative individuals, with at least 61 % being unrelated (Fig. 4b–Table S1). The percentage of relatives was higher in Pop1 (38.6 %), Pop6 (37 %) and Pop4 (34.2 %). This indicates a significant probability of mating between related breeders in these populations (Fig. 4b). Although the other populations had a lower proportion of relative individuals, the results presented here will be used for effective genetic management in the breeding program (Fig. 4b).

4. Discussion

The production of Nile tilapia in Brazil has experienced significant

growth in recent decades, positioning the country among the top five global producers of this species. As production advances, genetic management in tilapia farms using genomic information has become necessary; however, large-scale genotyping involves high costs. This study employed a cost-effective genotyping approach, making genetic monitoring more economically viable for producers. While higher-density SNP arrays may provide additional resolution, the selected low-density panel was effective in identifying genetic diversity patterns relevant to stock management.

Studies have shown that when carefully selected, low-density SNP panels can still provide reliable results for broad-scale population structure and genetic diversity analyses (Silva et al., 2022). The increasing adoption of low-density SNP genotyping panels in aquaculture reflects their demonstrated utility in preventing inbreeding, monitoring genetic variability and guiding strategic mating plans (Holman et al., 2017; Martinez et al., 2023; Saint-Pé et al., 2019; Silva et al., 2022). Accordingly, this study presented the first large-scale genetic evaluation of a pre-breeding population of Nile tilapia using a low-density SNP, as has been assessed for other species (Mastrochirico-Filho et al., 2019). Previous research has shown that genotyping costs for Nile tilapia populations using low-density SNP panels can be reduced by up to 70 % compared to genotyping with higher-density SNP panels (Yoshida et al., 2019), making them a more accessible tool for Nile tilapia producers in general.

Unlike our study, the diversity analyses of Brazilian Nile tilapia stocks have mostly been conducted using RAPD and microsatellite markers and were limited to a few individuals and focused on specific regions of Brazil (Lupchinski et al., 2011; Oliveira et al., 2011; Petersen et al., 2012; Rodriguez-Rodriguez et al., 2013; Silva et al., 2020). Although these techniques have been very useful in population studies, they have lower reproducibility and require more manual steps, making them more time-consuming and labor-intensive, thus limiting access for producers. In addition to using a larger number of individuals from Nile tilapia populations across different parts of Brazil in this study, the use of SNP genotyping panels offers significant advantages for population

Table 4
Pairwise F_{st} between nine Brazilian Nile tilapia populations (estimates in bold are not statistically different from zero, $p < 0.05$).

Population	Pop1	Pop2	Pop3	Pop4	Pop5	Pop6	Pop7	Pop8	Pop9
Pop1	–	0.10	0.09	0.05	0.10	0.08	0.12	0.10	0.10
Pop2		–	0.01	0.07	0.06	0.006	0.01	0.005	0.05
Pop3			–	0.06	0.05	0.01	0.02	0.01	0.04
Pop4				–	0.08	0.06	0.09	0.08	0.07
Pop5					–	0.05	0.08	0.07	0.005
Pop6						–	0.01	0.006	0.04
Pop7							–	0.003	0.07
Pop8								–	0.06
Pop9									–

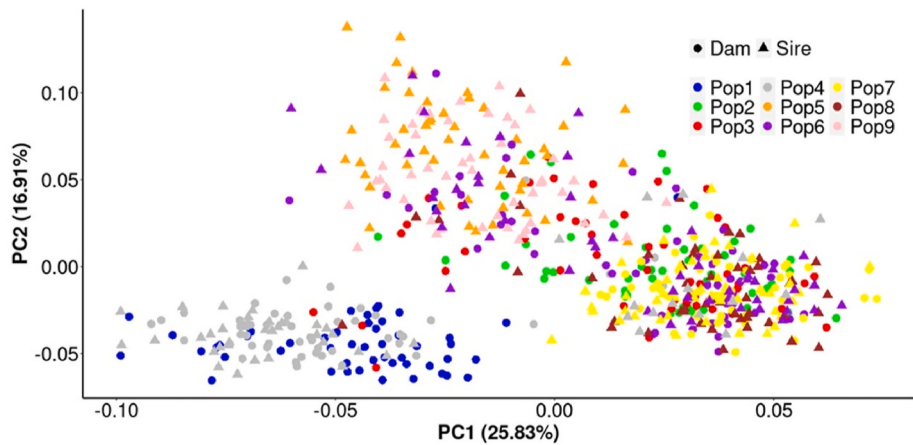


Fig. 1. Genetic structure of nine Brazilian Nile tilapia populations based on principal component analysis (PCA) using the genomic relationship matrix (GRM) with 192 SNPs. Sires and dams are identified by different shapes. Only SNPs with minor allele frequency ≥ 0.10 were considered to compute the GRM.

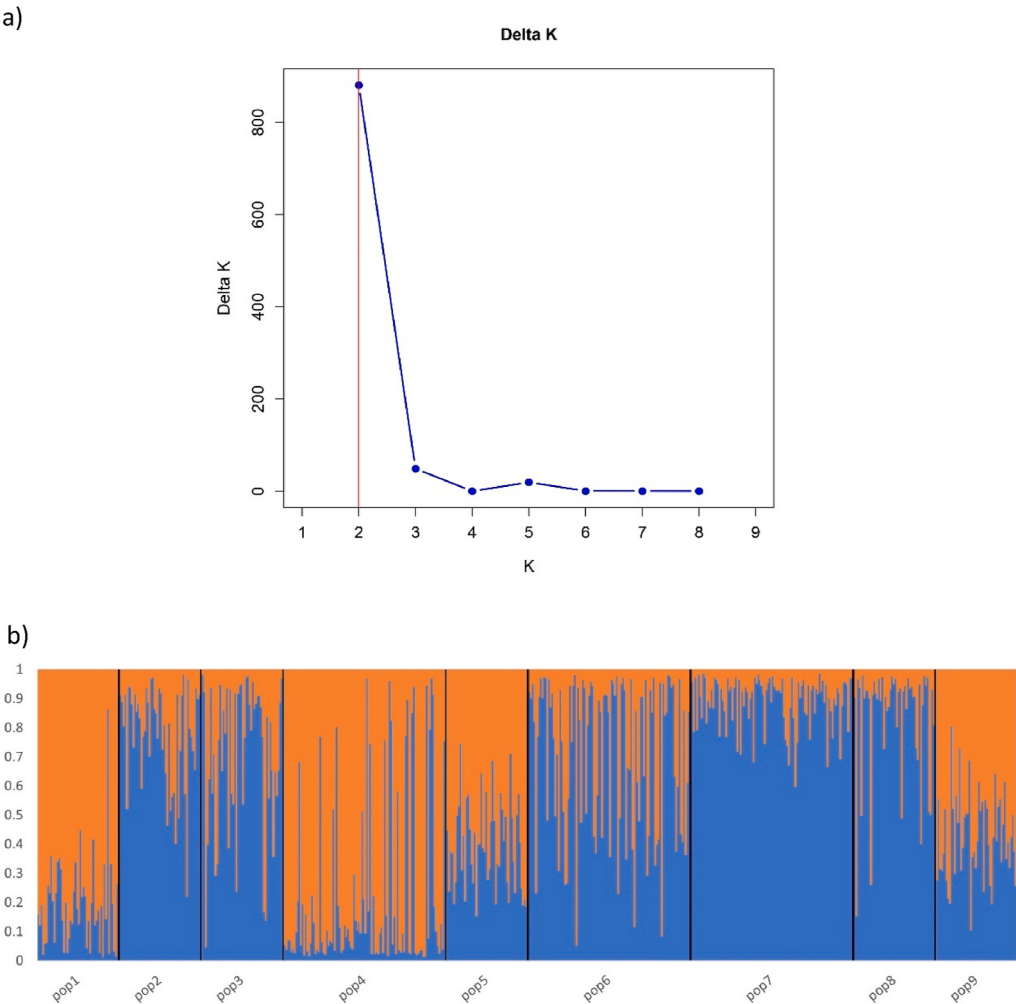


Fig. 2. (a) Admixture clustering of nine Nile tilapia populations ($K = 2$) using 192 SNPs. (b) The animals are grouped by population and each individual is represented by a vertical bar. Each color represents a different cluster.

studies in terms of marker density, reproducibility, automation, and cost-effectiveness. These characteristics have become attractive for production and make SNPs a preferred choice in many research contexts, such as maintaining the genetic diversity of fish stocks.

Databases of informative SNPs have been provided for conservation management, diversity, and structure analyses of cultivated populations of Nile tilapia strains from Africa (Kajungiro et al., 2019; Lind et al., 2019; Robledo et al., 2024; Van Bers et al., 2012), Asia (Hamilton et al.,

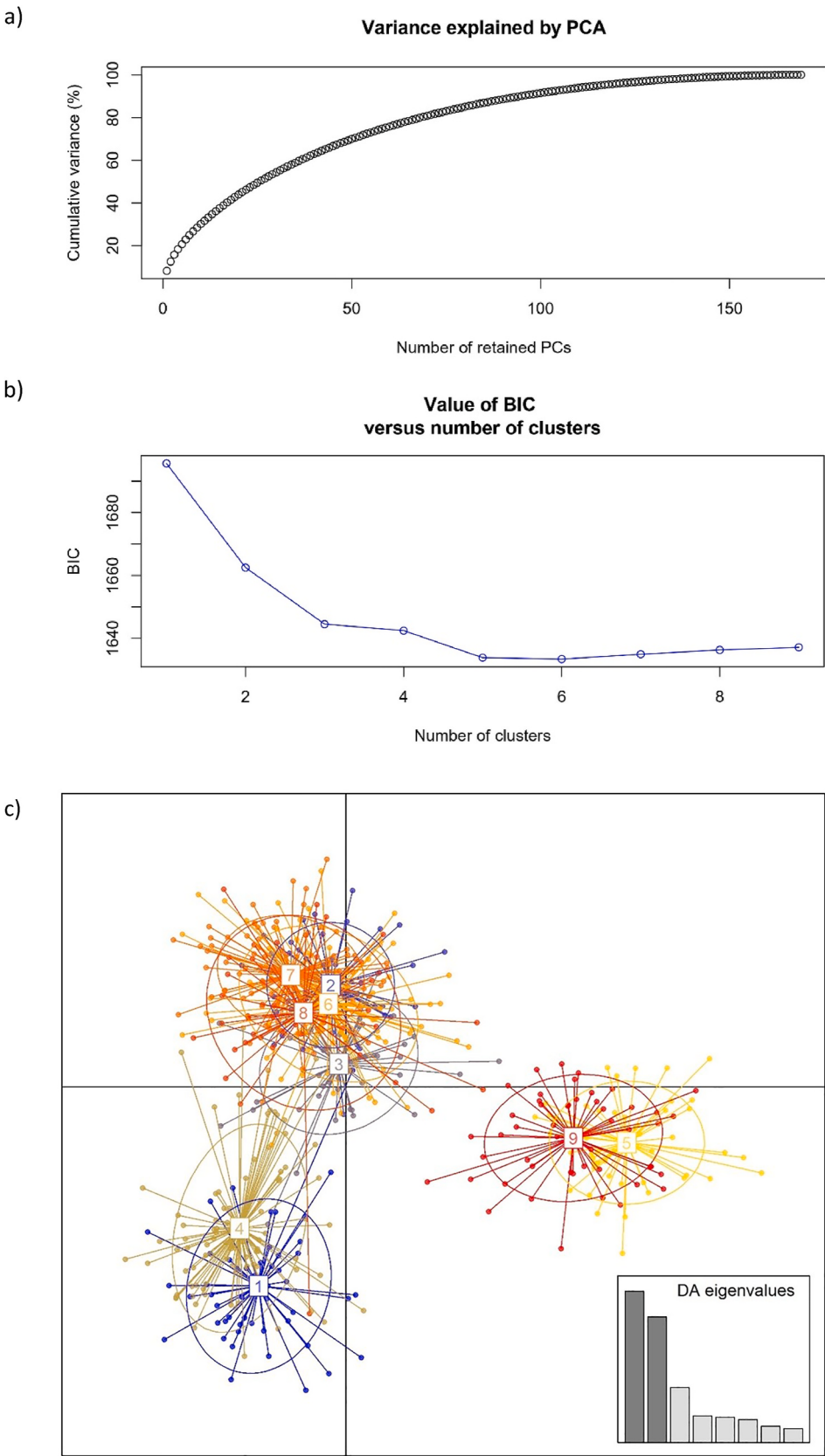


Fig. 3. Discriminant analysis of principal components (DAPC) for 600 genotypes of nine Nile tilapia populations. The axes represent the first two linear discriminants, each circle represents a cluster and each dot represents an individual. Numbers represent the different subpopulations identified by DAPC.

Table 5
AMOVA analysis for the partitioning of variation in 9 Brazilian Nile tilapia populations.

Source of variation	d.f.	Sum of Squares	Variance components	Percentage of variation
Among groups	2	1475.913	1.87037 Va	5.78
Among populations within groups	6	570.659	0.50438 Vb	1.56
Among individuals within populations	591	17647.78	(-0.14914) Vc	-0.46
Within individuals	600	18095.5	30.15917 Vd	93.13
Total	1199	37789.853	32.38477	
Fixation Indices				
FIS	-0.00497			
FSC	0.01653			
FCT	0.05775			
FIT	0.06872			

2020; Xia et al., 2014, 2015), and the Americas (Yáñez, Joshi, & Yoshida, 2020a,b). However, genetic diversity and stock structure evaluations, inbreeding estimates, and analyses related to strategic matings, as presented in this study, have not been utilized using SNPs in tilapia populations produced in Brazil.

With the intensification of the Nile tilapia production, the need for monitoring the genetic profile of stocks, as presented here, also increases. Without genetic information on populations within a commercial farm, occurrences of inbreeding can lead to the fixation of deleterious genes and a decline in productivity, undermining the potential of the strain. Considering previous studies, the first three generations of the GIFT line (G0, G1, G2, and G3) produced in Brazil, specifically in the state of Paraná (southern region of Brazil), were subjected to genetic analyses using RAPD markers (Oliveira et al., 2011) and microsatellites (Rodríguez-Rodríguez et al., 2013), where high genetic variability was detected and maintained throughout the three generations. A high number of polymorphic loci and genetic variability were also identified using microsatellite markers (Petersen et al., 2012; Silva et al., 2020) in genetic groups disseminated to the state of Santa Catarina. However, even years after the introduction of Nile tilapia in Brazil for commercial production, recent studies on genetic diversity using SNPs remain scarce for both the GIFT strain and other lines farmed in the country.

For comparative purposes, only one study by Yáñez, Joshi, & Yoshida, 2020a,b used a high-density SNP panel (50K SNP panel) to characterize the genetic diversity of Nile tilapia populations from Central America and a population from a fish farm located in the southeastern region of Brazil. Unlike the results found in our study, the Brazilian population exhibited H_E values of 0.28 and a H_O estimate of 0.20, indicating lower genetic diversity. However, these results may be related to lower segregation of SNPs in the panel for the analyzed Brazilian population or effects caused by ascertainment bias, which led to the decline in performance of the SNP panel when analyzing this population (Lachance & Tishkoff, 2013; Yáñez, Joshi, & Yoshida, 2020a,b). According to our results, out of the 192 SNPs genotyped, 169 high-quality SNPs (88 %) were successfully segregated among the 9 populations analyzed and showed satisfactory mean MAF values ranging from 0.24 to 0.30. The estimates of heterozygosity (H_O and H_E) were high in our study, higher than those found by Yáñez, Joshi, & Yoshida, 2020a,b, and similar to those found in genetic diversity analyses of lakes and fish farms in Africa (Robledo et al., 2024). In general, the mean estimates of H_O and H_E were similar within the populations, and the populations appeared to be in Hardy-Weinberg equilibrium. However, Pop1 exhibited greater variation, with a mean H_O (0.38, SD = 0.24) higher than the mean H_E (0.32, SD = 0.16) and an F_{IS} coefficient of -0.17 ($P < 0.05$). Despite the few differences found regarding genetic

diversity among the populations, Pop5 and Pop9 exhibited the highest genetic diversity.

However, the N_e estimates showed that both Pop1 and Pop4 had reduced effective population sizes compared to the other populations. This indicates that these populations were formed by a limited number of breeders or were subject to ineffective breeder management that did not maximize genetic diversity. Therefore, without proper genetic management, there is an increased risk that future generations on the fish farm will lose genetic diversity and exhibit signs of inbreeding.

The results regarding the within-population genetic diversity of the Nile tilapia populations likely influenced the genetic structure among populations. Both the population differentiation coefficient (F_{ST}) results and the genetic clustering analyses indicated that Pop1 and Pop4 were genetically differentiated from the other populations. These two populations clustered together, likely due to their lower genetic diversity and increased risk of inbreeding, which can be attributed to their smaller effective population sizes and a higher proportion of genetically related individuals. Conversely, the cluster formed by Pop5 and Pop9 represents populations with the highest genetic diversity and a larger proportion of loci in Hardy-Weinberg equilibrium. The cluster composed of Pop2, Pop3, Pop6, Pop7, and Pop8 represents populations with intermediate genetic diversity values. Despite the distinct clusters and population structuring, the greatest genetic variation is observed within individuals rather than between populations or population clusters. This suggests that a random sampling of individuals from each population may be the best strategy for forming the breeding nucleus of the fish farm. Alternatively, individuals could be separated into different groups based on phenotypic traits (such as growth rate), followed by random sampling within each group.

Despite the high genetic diversity and higher proportion of unrelated individuals observed in the pre-breeding populations, some exhibited parameters suggesting potential future risks of genetic diversity loss and inbreeding, as previously discussed. Even populations in equilibrium with high genetic diversity may experience a decline in diversity if not properly managed. For instance, Pop1 and Pop4 displayed lower genetic diversity, reduced effective population sizes, and, along with Pop6, had a higher proportion of related individuals compared to other populations. A key strategy for maintaining genetic diversity involves incorporating genetic material from other populations through breeder renewal. Introducing genetic diversity from populations with higher variability, such as Pop5 and Pop9, can help mitigate the effects of inbreeding. In addition to genetic material incorporation, monitoring genetic relationships among individuals using pedigree records or genomic tools, as presented in this study, is essential to minimize mating between related individuals and ensure a balanced contribution of breeders to the next generation. Increasing the effective population size can reduce inbreeding risks, which can be achieved by maintaining a larger breeding population, periodically rotating breeders, and preventing the overuse of a few individuals. Without proper knowledge of the genetic profile of farmed populations, as characterized in the present study, the well-established performance of the Nile tilapia could be compromised by genetic diversity loss due to the absence of genomic information.

5. Conclusion

The presented results will ensure that effective strategies are implemented during the pre-breeding stage of a novel tilapia genetic improvement nucleus in Brazil, supporting the maintenance of genetic diversity in the breeding stock. Low-density SNP panels can be a cost-effective way to assess the genetic diversity and structure of Brazilian tilapia stocks, in addition to providing genomic information for strategic mating. The results of this study revealed high genetic diversity in the pre-breeding population of the evaluated fish farm. The presence of reduced effective population sizes and a considerable proportion of related individuals in some pre-breeding populations could lead to

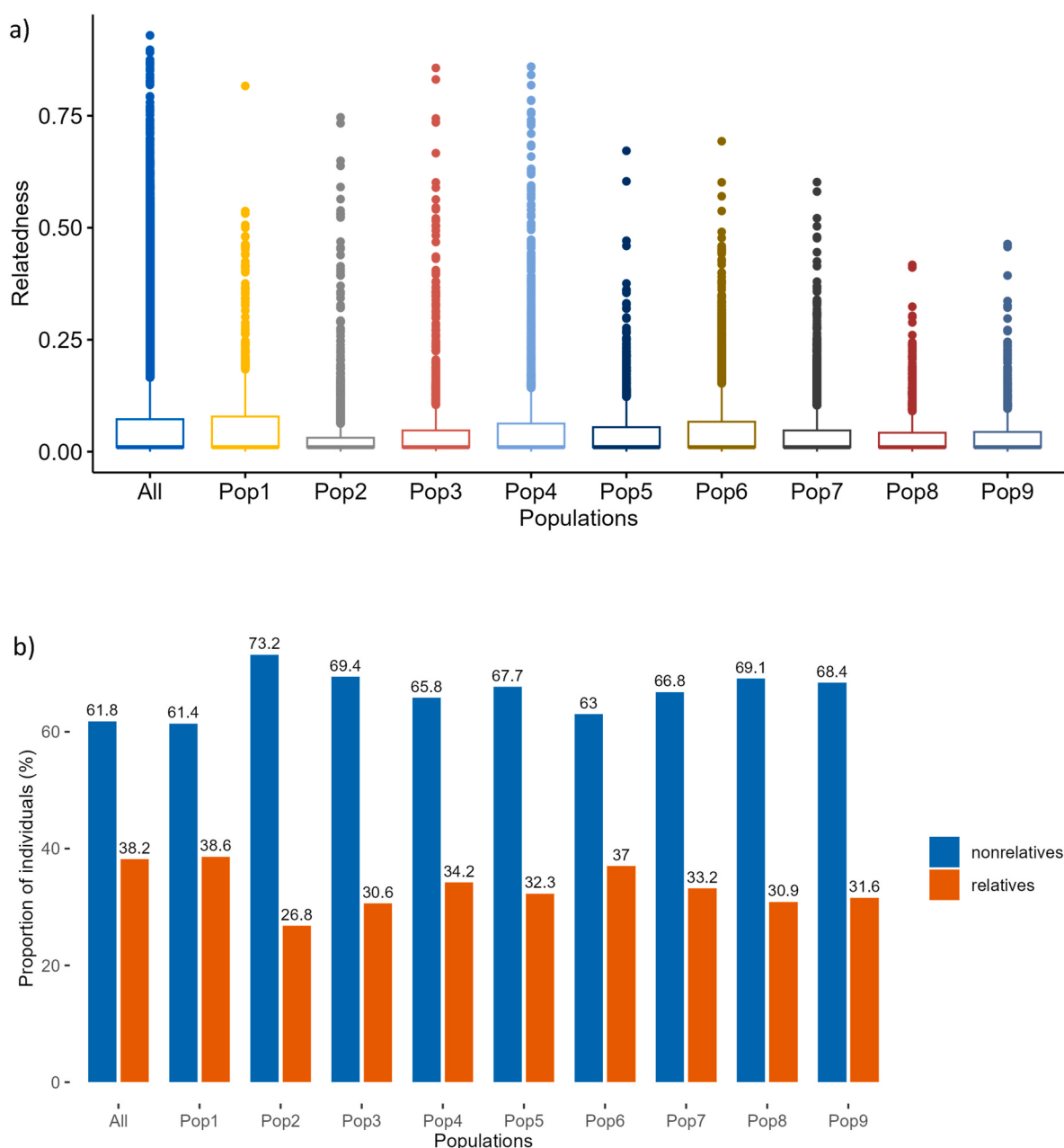


Fig. 4. (a) Mean relatedness coefficients and (b) distribution of nonrelative and relative individuals in 9 populations of Brazilian Nile tilapia.

inbreeding and a consequent loss of genetic diversity if not properly managed. Conversely, populations with higher genetic diversity exhibited larger effective population sizes and a greater proportion of unrelated individuals, reducing the risk of inbreeding. Populations at higher risk of inbreeding should be carefully managed when forming the pre-breeding population through management measures such as breeder renewal, controlled mating to ensure a balanced contribution of breeders to the next generation, and an overall increase in effective population size. Genetic diversity analyses, although rarely conducted, are essential to ensuring that the well-documented performance of Nile tilapia is not compromised by genetic diversity loss due to a lack of genomic information.

CRediT authorship contribution statement

Vito Antonio Mastrochirico-Filho: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Baltasar Fernandes**

Garcia: Writing – review & editing, Investigation, Formal analysis. **Lieschen Valeria Guerra Lira:** Writing – review & editing, Investigation. **Antonio Ramon do Amaral Neto:** Resources, Project administration. **Rodrigo Marín-Nahuelpi:** Formal analysis. **Jouseph Gallardo-Hidalgo:** Methodology. **Liane Ney Bassini:** Methodology. **Fabio Porto-Foresti:** Supervision. **Diogo Teruo Hashimoto:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

The data of the experiment are available upon request to the corresponding author.

Ethics statement

This study was conducted in strict accordance with the

recommendations of the National Council for Control of Animal Experimentation (CONCEA) (Brazilian Ministry for Science, Technology and Innovation) and was approved by the Ethics Committee on Animal Use (CEUA number 004650/24) of Faculdade de Ciências Agrárias e Veterinárias, UNESP, Campus Jaboticabal, SP, Brazil.

Declaration of generative AI in scientific writing

No generative AI technologies were used in the preparation of this manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aaf.2025.05.004>.

References

- Do, C., Waples, R. S., Peel, D., Macbeth, G. M., Tillett, B. J., & Ovenden, J. R. (2014). NeEstimator v2: Re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. *Molecular Ecology Resources*, 14(1), 209–214. <https://doi.org/10.1111/1755-0998.12157>
- Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under linux and windows. *Molecular Ecology Resources*, 10, 564–567. <https://doi.org/10.1111/j.1755-0998.2010.02847.x>
- FAO. (2023a). Demand for tilapia resumes growth despite higher prices. Retrieved from <https://www.fao.org/in-action/globefish/market-reports/resource-detail/en/c/1632900/>. (Accessed 29 March 2024).
- FAO. (2023b). *FishStatJ: Universal software for fishery statistical time series: Aquaculture production 1950–2021 (release date: March 2023)*. Rome: FAO.
- FAO. (2024). The state of world fisheries and aquaculture 2024 – blue transformation in action. Rome (Italy) <https://doi.org/10.4060/cd0683en>.
- Fitzsimmons, K., Martínez-García, R., & Gonzalez-Alanis, P. (2011). Why tilapia is becoming the most important food fish on the planet. *Proceedings of the ninth international symposium on tilapia in aquaculture*. Shanghai, China: Shanghai Ocean University, 22–24 April 2011.
- Freitas, D. D. G. C., Resende, A. L., da, S. S., Furtado, A. A. L., Tashima, L., & Bechara, H. M. (2012). The sensory acceptability of a tilapia (*Oreochromis niloticus*) mechanically separated meat-based spread. *Brazilian Journal of Food Technology*, 15 (2), 166–173. <https://doi.org/10.1590/S1981-67232012005000010>
- Gjedrem, T., & Baranski, M. (2009). *Selective breeding in aquaculture: An introduction*. Amsterdam: Springer Science & Business Media.
- Goudet, J. (1995). FSTAT (version 1.2): A computer program to calculate F-statistics. *Journal of Heredity*, 86(6), 485–486. <https://doi.org/10.1093/oxfordjournals.jhered.a111627>
- Goudet, J. (2005). Hierfstat, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes*, 5, 184–186. <https://doi.org/10.1111/j.1471-8286.2004.00828.x>
- Hamilton, M. G., Lind, C. E., Barman, B. K., Velasco, R. R., Danting, M. J. C., & Benzie, J. A. H. (2020). Distinguishing between Nile tilapia strains using a low-density single-nucleotide polymorphism panel. *Frontiers in Genetics*, 11, Article 594722. <https://doi.org/10.3389/fgene.2020.594722>
- Holman, L. E., Onoufriou, A., Hillestad, B., & Johnston, I. A. (2017). A workflow used to design low density SNP panels for parentage assignment and traceability in aquaculture species and its validation in Atlantic salmon. *Aquaculture*, 476, 59–64. <https://doi.org/10.1016/j.aquaculture.2017.04.001>
- Houston, R. D., Bean, T. P., Macqueen, D. J., Gundappa, M. K., Jin, Y. H., Jenkins, T. L., Selly, S. L. C., Martin, S. A. M., Stevens, J. R., Santos, E. M., Davie, A., & Robledo, D. (2020). Harnessing genomics to fast-track genetic improvement in aquaculture. *Nature Reviews Genetics*, 21, 389–409. <https://doi.org/10.1038/s41576-020-0227-y>
- IBGE - Instituto Brasileiro de Geografia e Estatística. (2023). *Produção da pecuária municipal 2022*. Rio de Janeiro: IBGE.
- Jombart, T., & Ahmed, I. (2011). Adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics*, 27(21), 3070–3071. <https://doi.org/10.1093/bioinformatics/btr521>
- Kajungiro, R. A., Palaikostas, C., Pinto, F. A. L., Mmochi, A. J., Mtolera, M., Houston, R. D., & de Koning, D. J. (2019). Population structure and genetic diversity of Nile tilapia (*Oreochromis niloticus*) strains cultured in Tanzania. *Frontiers in Genetics*, 10, 1269. <https://doi.org/10.3389/fgene.2019.01269>
- Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: A program for identifying clustering modes and packaging population structure inferences across K. *Molecular Ecology Resources*, 15(5), 1179–1191. <https://doi.org/10.1111/1755-0998.12387>
- Lachance, J., & Tishkoff, S. A. (2013). SNP ascertainment bias in population genetic analyses: Why it is important, and how to correct it. *BioEssays*, 35(9), 780–786. <https://doi.org/10.1002/bies.201300014>
- Li, Y. L., & Liu, J. X. (2018). StructureSelector: A web-based software to select and visualize the optimal number of clusters using multiple methods. *Molecular Ecology Resources*, 18(1), 176–177. <https://doi.org/10.1111/1755-0998.12719>
- Lind, C. E., Agyakwah, S. K., Attipoe, F. Y., Nugent, C., Crooijmans, R. P. M. A., & Toguyeni, A. (2019). Genetic diversity of Nile tilapia (*Oreochromis niloticus*) throughout west Africa. *Scientific Reports*, 9, 16767. <https://doi.org/10.1038/s41598-019-53295-y>
- Lupchinski, J. E., Vargas, L., Lopera-Barrero, N. M., Ribeiro, R. P., Povh, J. A., Gasparino, E., & Braccini, G. L. (2011). Genetic characterization of three Nile tilapia (*Oreochromis niloticus*) strains. *Archivos de Zootecnia*, 60, 985–995. <https://doi.org/10.4321/S0004-05922011000400015>
- Martinez, V., Galarce, N., & Setiawan, A. (2023). Developing methods for maintaining genetic diversity in novel aquaculture species: The case of *Seriola lalandi*. *Animals*, 13, 913. <https://doi.org/10.3390/ani13050913>
- Mastrochirico-Filho, V. A., Del Pazo, F., Hata, M. E., Villanova, G. V., Foresti, F., Vera, M., Martínez, P., Porto-Foresti, F., & Hashimoto, D. T. (2019). Assessing genetic diversity for a pre-breeding program in *Piaractus mesopotamicus* by SNPs and SSRs. *Genes*, 10(9), 668. <https://doi.org/10.3390/genes10090668>
- Mastrochirico-Filho, V. A., Garcia, B. F., Manso, S. C. S., Freitas, M. V., Porto-Foresti, F., Cáceres, P., Yáñez, J. M., & Hashimoto, D. T. (2024). Assessing accuracy of imputation using different SNP densities as strategy for breeding programs of the fish pacu *Piaractus mesopotamicus*. *Aquaculture Reports*, 36, Article 102140. <https://doi.org/10.1016/j.aqrep.2024.102140>
- Nguyen, H. N. (2016). Genetic improvement for important farmed aquaculture species with a reference to carp, tilapia and prawns in Asia: Achievements, lessons and challenges. *Fish and Fisheries*, 17(2), 483–506. <https://doi.org/10.1111/faf.12122>
- Oliveira, S. N., Ribeiro, R. P., Lopera, N. M., Candiotto, F. B., Resende, E. K. de, & Legat, A. P. (2011). Análise genética de três gerações de tilapia do Nilo (linhagem GIFT) utilizando o marcador RAPD. *Acta Scientiarum. Animal Sciences*, 33(2), 207–212. <https://doi.org/10.4025/actascianims.v33i2.9202>
- Oliveira-Neto, R. R., Mastrochirico-Filho, V. A., Assane, I. M., Ariede, R. B., Freitas, M. V., Agudelo, J. F. G., Borges, C. H. S., Gonçalves, T. G., Lira, L. V. G., Reis Neto, R. V., Pilarski, F., & Hashimoto, D. T. (2024). Resistance of juvenile Nile tilapia *Oreochromis niloticus* from Brazilian populations to *Streptococcus agalactiae* (serotype Ib and ST-NT). *Frontiers in Aquaculture*, 3, Article 1354029. <https://doi.org/10.3389/faquc.2024.1354029>
- Petersen, R. L., Mello, G., Garcia, J. E., Liedke, A. M. R., Sincero, T. C. M., & Grisard, E. C. (2012). Analysis of genetic diversity of farm-raised tilapia stocks from Santa Catarina State (Brazil) using microsatellite markers. *Boletim do Instituto de Pesca*, 38, 313–321.
- Ponzoni, R. W., Nguyen, N. H., Khaw, H. L., Hamzah, A., Bakar, K. R. A., & Yee, H. Y. (2011). Genetic improvement of Nile tilapia (*Oreochromis niloticus*, L. 1758) with special reference to the work conducted by the world fish center with the GIFT strain. *Reviews in Aquaculture*, 3(1), 27–41. <https://doi.org/10.1111/j.1753-5131.2010.01041.x>
- Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics (Austin, Tex.)*, 155(2), 945–959. <https://doi.org/10.1093/genetics/155.2.945>
- Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A., Bender, D., Maller, J., Sklar, P., de Bakker, P. I., Daly, M. J., & Sham, P. C. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *The American Journal of Human Genetics*, 81(3), 559–575. <https://doi.org/10.1086/519795>
- Ribeiro, V. S., Pedroza Filho, M. X., Rocha, H. S., & Ribeiro, J. B. (2024). Brazilian Tilapia production: A regional analysis using upgrading indicators. *Informe GEPEC*, 28(1), 366–383. <https://doi.org/10.48075/igepec.v28i1.32644>
- Robledo, D., Ogowang, J., Byakora, E., Schulze, J. N., Benda, K. K., Frasin, C., Salisbury, S., Solimo, M., Mayega, J. F., Peter, B., Masembe, C., Houston, R., & Mukibi, R. (2024). Genetic diversity and population structure of farmed and wild Nile tilapia (*Oreochromis niloticus*) in Uganda: The potential for aquaculture selection and breeding programs. *Genomics (San Diego, Calif.)*, 116(1), Article 110781. <https://doi.org/10.1016/j.ygeno.2024.110781>
- Rodriguez-Rodriguez, M. D. P., Lopera-Barrero, N. M., Vargas, L., Albuquerque, D. M., Goes, E. S. R., Prado, O. P. P., & Ribeiro, R. P. (2013). Caracterização genética de gerações de tilapia Gift por meio de marcadores microsatélites. *Pesquisa Agropecuária Brasileira*, 48(10), 1385–1393. <https://doi.org/10.1590/S0100-204X2013001000010>
- Saint-Pé, K., Leitwein, M., Tissot, L., Poulet, N., Guinand, B., Berrebi, P., Marselli, G., Lascaux, J., Gagnaire, P., & Blanchet, S. (2019). Development of a large SNPs resource and a low-density SNP array for brown trout (*Salmo trutta*) population genetics. *BMC Genomics*, 20, 582. <https://doi.org/10.1186/s12864-019-5958-9>

- Silva, N. M. L., Ianella, P., Yamagishi, M. E. B., Rocha, J. L., Teixeira, A. K., Farias, F. G., Guerrelhas, A. C., & Caetano, A. R. (2022). Development and validation of a low-density SNP panel for paternity and kinship analysis and evaluation of genetic variability and structure of commercial Pacific white shrimp (*Litopenaeus vannamei*) populations from Brazil. *Aquaculture*, 560, Article 738540. <https://doi.org/10.1016/j.aquaculture.2022.738540>
- Silva, B. C. da, Pereira, A., Massago, H., & Mariguela, K. H. (2020). Caracterização genética de tilápia-do-nilo selecionadas em Santa Catarina. *Semina: Ciências Agrárias*, 41(5), 1739–1754. <https://doi.org/10.5433/1679-0359.2020v41n5p1739>
- Van Bers, N. E. M., Crooijmans, R. P. M. A., Groenen, M. A. M., Dibbitts, B. W., & Komen, J. (2012). SNP marker detection and genotyping in tilapia. *Molecular Ecology Resources*, 12(5), 932–941. <https://doi.org/10.1111/j.1755-0998.2012.03144.x>
- Villanueva, B., Fernández, A., Peiró-Pastor, R., Penaloza, C., Houston, R. D., Sonesson, A. K., Tsigenopoulos, C. S., Bargelloni, L., Gamsiz, K., Karahan, B., Gökçek, E.Ö., Fernández, J., & Saura, M. (2022). Population structure and genetic variability in wild and farmed Mediterranean populations of gilthead seabream and European seabass inferred from a 60K combined species SNP array. *Aquaculture Reports*, 24, 101145. <https://doi.org/10.1016/j.aqrep.2022.101145>
- Xia, J. H., Bai, Z., Meng, Z., Zhang, Y., Wang, L., Liu, F., Jing, W., Wan, Z. Y., Li, J., Lin, H., & Yue, G. H. (2015). Signatures of selection in tilapia revealed by whole genome resequencing. *Scientific Reports*, 5(1), 14168. <https://doi.org/10.1038/srep14168>
- Xia, J. H., Wan, Z. Y., Ng, Z. L., Wang, L., Fu, G. H., Lin, G., Liu, F., & Yue, G. H. (2014). Genome-wide discovery and in silico mapping of gene-associated SNPs in Nile tilapia. *Aquaculture*, 432, 67–73. <https://doi.org/10.1016/j.aquaculture.2014.04.028>
- Yáñez, J. M., Joshi, R., & Yoshida, G. M. (2020a). Genomics to accelerate genetic improvement in tilapia. *Animal Genetics*, 51, 658–674. <https://doi.org/10.1111/age.12989>
- Yáñez, J. M., Yoshida, G., Barria, A., Palma-Véjares, R., Travisany, D., Díaz, D., Cáceres, G., Cádiz, M. I., López, M. E., Lhorente, J. P., Jedlicki, A., Soto, J., Salas, D., & Maass, A. (2020b). High-throughput single nucleotide polymorphism (SNP) discovery and validation through whole-genome resequencing in Nile Tilapia (*Oreochromis niloticus*). *Marine Biotechnology*, 22, 109–117. <https://doi.org/10.1007/s10126-019-09935-5>
- Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2011). GCTA: A tool for genome-wide complex trait analysis. *The American Journal of Human Genetics*, 88(1), 76–82. <https://doi.org/10.1016/j.ajhg.2010.11.011>
- Yoshida, G. M., Lhorente, J. P., Correa, K., Soto, J., Salas, D., & Yáñez, J. M. (2019). Genome-Wide association study and cost-efficient genomic predictions for growth and fillet yield in Nile Tilapia (*Oreochromis niloticus*). *G3 Genes | Genomes | Genetics*, 9(8), 2597–2607. <https://doi.org/10.1534/g3.119.400116>
- You, X., Shan, X., & Shi, Q. (2020). Research advances in the genomics and applications for molecular breeding of aquaculture animals. *Aquaculture*, 526, Article 735357. <https://doi.org/10.1016/j.aquaculture.2020.735357>