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REVIEW

Locus and Non-Locus Specific Technical Caveats: An Overview of Their Occurrence in Tilapiine Cichlids Genetic Data and Approaches to Salvage Loci

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Abstract

Many tilapia-related research papers make assumptions in relation to Locus- and Non-Locus-Specific Technical Problems (LTPs) that hinder the reaching of clear genetic monitoring conclusions. Since LTPs have implications for decisions related to fisheries and aquaculture management, an overview of the key LTPs affecting tilapia population studies will help geneticists not only to consider them, but also to know the gaps that exist in order to guide future research within the domain. Using a meta-analysis, we present approaches to distinguish the LTPs from each other, which is most often needed for tilapia genetic data before any statistical inference is made. Each LTP and the approaches to make the genetic data reliable are presented and discussed. Cultured tilapia populations are generally characterized by homogamy, heterogamy, heterosis, inbreeding and overdominance. In contrast, null alleles, allelic dropout, stuttering, homoplasy, genetic bottleneck and Wahlund effect are most often at issue in populations originating only from the wild. Future perspectives are needed about the components underlying the LTPs related to genotyping errors and biological factors.

Introduction

Global inland and marine water fish captures have remained relatively stable during the last three decades (1990 to 2018), increasing at a rate of 8% per annum. But, the stagnation during 2019 and 2020 was mainly linked to a decline in fisheries production owing in part to the impacts of the COVID-19 pandemic (FAO, 2020; Amoussou et al., 2022; FAO, 2024). This trend is a reflection of the decline of fish populations due to overharvest, overfishing and environmental disturbances to which the aquatic environments are subjected. Indeed, the aquatic environments are subject to both the effects of changing environmental factors and man-made threats including invasions of non-native aquatic species, water pollution (e.g., harmful algal blooms, contaminants, engineered nanomaterials, microplastic pollution, light and noise), destruction or degradation of aquatic habitat (due to expanding hydropower, sand-mining), flow modification, infectious fish diseases, freshwater salinization, cumulative stressors, and changing climate (Recino-Reyes et al., 2020; Amoussou et al., 2020; Nehemia & Umbayda, 2024). Tilapias and other cichlids represent the second most important group of fishes (after the first group composed of carps, barbel and other cyprinids)

exploited in inland waters (FAO, 2020; Tibihika et al., 2022), and are affected by some, if not all, of the above-mentioned disturbances. Compensating for the downward trend in fish catches from the wild, aquaculture is contributing to production of fisheries products. In fact, global aquaculture production increased by 527% from 1990 to 2018 (FAO, 2020), and this trend deserves to be maintained.

Tilapia species (Family Cichlidae) are usually divided into three major phylogenetic groups, the pelmatochromine, haplochromine cichlids, and tilapiine cichlids (Lowe-McConnell, 1991) and are of particular interest for genetic investigations probably because of their hybridization rate, and evolutionary adaptive diversification or radiation (Fatsi et al., 2020; Feller et al., 2020; Svardal et al., 2021; Kariuki, et al., 2021; Singh et al., 2021; Fischer et al., 2021; Geraerts et al., 2022; Tibihika et al., 2024). The above-mentioned environmental and anthropogenic issues affect the consistency of genetic diversity estimates as well as assessment of biodiversity integrity. Yet, knowledge of the genetic diversity and spatiotemporal population structure has proven important to studies of evolutionary biology, ecology, and conservation biology, and to have implications for the choice of conservation strategies (Balloux & Lugon-Moulin, 2002). The conservation of tilapia resources will ensure the sustainability of aquaculture as well as fisheries (Hilsdorf & Hallerman, 2014, 2021). In this context, the need for future use of genetic conservation tools is obvious, as units for conservation must be identified and protected, and as hybridization between invasive and native species is among the major and pernicious threats to aquatic biodiversity (Firmat et al., 2013; Anane-Taabeah et al., 2019).

The integration of molecular tools into aquatic resource management is gaining momentum in part in response to recognition of the manmade threats and climate change. Owing to the remarkable progress of molecular techniques, many studies have been conducted on tilapias, particularly in the fields of population genetics, selective breeding, hybrid identification, species identification, and ecological and conservation biology (Amoussou et al., 2019; Morelos-Castro et al., 2024). Nevertheless, many of these studies have been affected by genotyping errors as well as problems related to fish reproduction and demography. These problems are known to bias estimates of population genetic differentiation and genetic diversity. Hence, the consideration of the effects of genotyping errors, typing errors and reproduction systems, often neglected, deserve greater attention (Bonin et al., 2004).

Genotyping of microsatellite markers is usually straightforward. However, due to the frequent presence of null alleles and limited number of DNA markers, complications arise (Liu, 2007; Ahmed et al., 2023) as they affects disproportionally frequencies of ancestral alleles, minor alleles and rare alleles (Hoey et al., 2022). Genotyping technical problems, like null alleles, stuttering, short allele dominance (SAD) or large allele dropouts (LAD) are frequent consequences of poor PCR amplifications, in particular for microsatellite markers (Manangwa et al., 2019), leading to artefactual deviations from Hardy-Weinberg expectations. These issues unevenly affect loci, and increase the perceived relative inbreeding of individuals and subpopulations by producing a positive F_{IS} with variation across loci, sometimes with significant outliers (De Meeûs, 2018). The causes, consequences and solutions of technical genotyping errors are already documented (Pompanon et al., 2005). Genotyping errors might lead to incorrect allele identification or incorrect genotype frequencies, resulting in incorrect *F*-statistics estimates, errant estimated migration rates, or false inference of population bottleneck or selection. In this latter context, such genotyping problems open the gate to apparent as opposed to real genetic hitchhiking selection events. Indeed, during the selective sweep of a favourable allele, any neutral alleles sufficiently tightly linked to the selected sequence will be dragged along. In other words, when a selectively favourable mutation occurs in a population and is subsequently fixed in that population, this process will alter the frequencies of alleles at other linked loci. Thus, a neutral allele may be carried along because of the selective advantage of the associated allele (Scribner et al., 2001). Moreover, several studies show that these markers are not neutral and/or do not display constant evolution (Gerber et al., 2001; Bazin et al., 2006; Galtier et al., 2009; Papadopoulou et al., 2010). Considering these different contingencies, all loci must satisfy several criteria including clearly defined peaks, reproducibility and consistency of amplifications, absence of stutter bands, presence of specific bands, presence of correct motif sizes, levels of heterozygosity, and high polymorphism information content (PIC) values (Landínez-García et al., 2020) before any statistical inference can be made.

Many mating system-related problems also exhibit remarkably significant homozygote excess relative to Hardy–Weinberg Equilibrium (HWE). The sexual system of a lineage has important evolutionary and ecological implications, affecting the levels of genetic variation as well as having longer-term consequences for the formation of new species and the risk of extinction (Ashman et al., 2014). In the context of aquaculture, such problems may be caused by poor broodstock management (Romana-Eguia et al., 2004), which increases associations between alleles. Indeed, such issues, often created by earlier genetic mismanagement, may generate not only high linkage disequilibrium (i.e., physical linkage) between pairs of loci but may, as well, lead to substantial outliers in tests of selection (Amoussou et al., 2018; De Meeûs et al., 2006). Such problems could undermine the effectiveness of any marker-assisted selection program (Ponzoni et al., 2009). In other words, many of such issues can lead to false estimates of genotype frequency

that can create an artificial excess of homozygotes, false departure from HWE, and overestimation of inbreeding or unreliable inferences about population substructures (Bonin et al., 2004).

Many studies dealing with fish genetic data have overlooked the above-mentioned Locus-specific Technical Problems (LTPs) before making subsequent inferences, thereby obliging reanalysis and reinterpretation of some published data sets. Yet, to fully assess the evolutionary genetics of tilapias, possible key problems associated with particular loci must be identified before reaching any genetic inferences. In addition, very few authors have used corrected datasets when assessing fish population genetics. This remains a challenge, and also as an opportunity for fisheries and aquaculture geneticists to detect and solve such technical caveats. Hence, summarizing the usually overlooked technical issues will guide fish geneticists on their solution. There is thus a need of making genetic problems' information available for a global audience. The paper attempts to provide insights into technical issues affecting genetic and genomics analyses in tilapias. In particular, this review involves examining what other studies have already contributed to this field of interest in order to reduce the influence of LTPs on biological conclusions. We have also provided, marker by marker, the approaches or tools needed to identify each LTP to help better understand where to go next.

Material and Methods

Bibliographic Sources

The approach used in this study was to gather relevant peer-reviewed journal articles. In-depth search techniques were used to retrieve the best and most relevant contents from scholarly journals. In order to conduct an effective literature search, the information retrieval process was based exclusively on peer-reviewed journal articles as primary sources, review papers as secondary sources, and books as tertiary sources. Information resources were evaluated regarding authority, accuracy, objectivity, coverage, and currency. Major information sources were scientific journals in agriculture, biological and environmental sciences. Our survey was based on Google Scholar, ISI Web of Science, Scopus search engine, and discipline-specific programmes (Research4Life and AGORA), AGRICOLA online catalog, and the TEEL database.

Scientific Information Extraction

The wealth of information resources makes selection of both articles and books necessary. Access tools grouped by content coverage were targeted without losing sight of the fact that information platforms are not all free. In order to find relevant articles, the searches included ten management levels including removal of duplicates, article accessibility, article relevance to the scope of the review, etc. (Figure 1). The survey of publications and information on the topic were based on both basic and systematic searches. The basic search referred to a single search term or phrase (e.g., "tilapia null allele"). The systematic search consisted of identifying search items, using Boolean terms (AND, OR), advanced search techniques, and building queries (Supplementary Material, Table S1). Using Boolean commands helped to narrow the search results by obtaining only relevant articles.

Two steps preceded the extraction of data. The first step was the articulation of terms and a detailed description of the search process. Thus, for the identification of the pertinent documentation, we combined the search terms "locus genotyping error" OR "loci genotyping error" OR "locus genotyping problem*" OR "loci genotyping problem*" OR "non-locus genotyping error" OR "non-loci genotyping error" OR "non-locus genotyping problem*" OR "non-loci genotyping problem*" with descriptions (or keywords) related to LTPs. The use of * in before a search term is an indication that the word has been used halfway. The LTPs were reconceptualized as including only null alleles, allele dropout, stuttering, homoplasy, Wahlund effect, overdominance, underdominance, homogamy (or assortative mating), heterogamy (or disassortative mating), heterosis, endogamy, inbreeding, and genetic bottleneck. The second step was to describe the inclusion and exclusion criteria. The papers included were those published in English. The publication types were article, review, book chapter, or book. Papers must be in the area of genetics or genomics. The paper must address at least one of the LTP pillars (i.e., null allele, allele dropout, stuttering, homoplasy, Wahlund effect, overdominance, underdominance, homogamy, heterogamy, heterosis, endogamy). We also made sure that the text included sufficient detail to allow data analysis.

Data and Statistical Treatment

Reliable, accurate, up-to-date scientific information retrieved from literature searches were stored in a bibliographic database. The bibliographic database helps build a ready-to-compute statistical database. Based on the defined criteria, a total of 131 papers dealing with technical issues were selected and considered for statistical inferences (Figure 2). For each selected paper, the data recorded in the statistical database were the name of the author(s), year of publication, source type, species group, biogeographical region of the samples/study, subject area, genetic markers, stock type, presence or absence of each LTP (null alleles, allelic dropout, short allele dominance, stuttering, Wahlund effect, underdominance, overdominance, heterogamy, homogamy, heterosis, and endogamy) (Figure 2). The data that emerged from the survey were all qualitative variables. Since we opted for a systematic review, the years of publication ranged

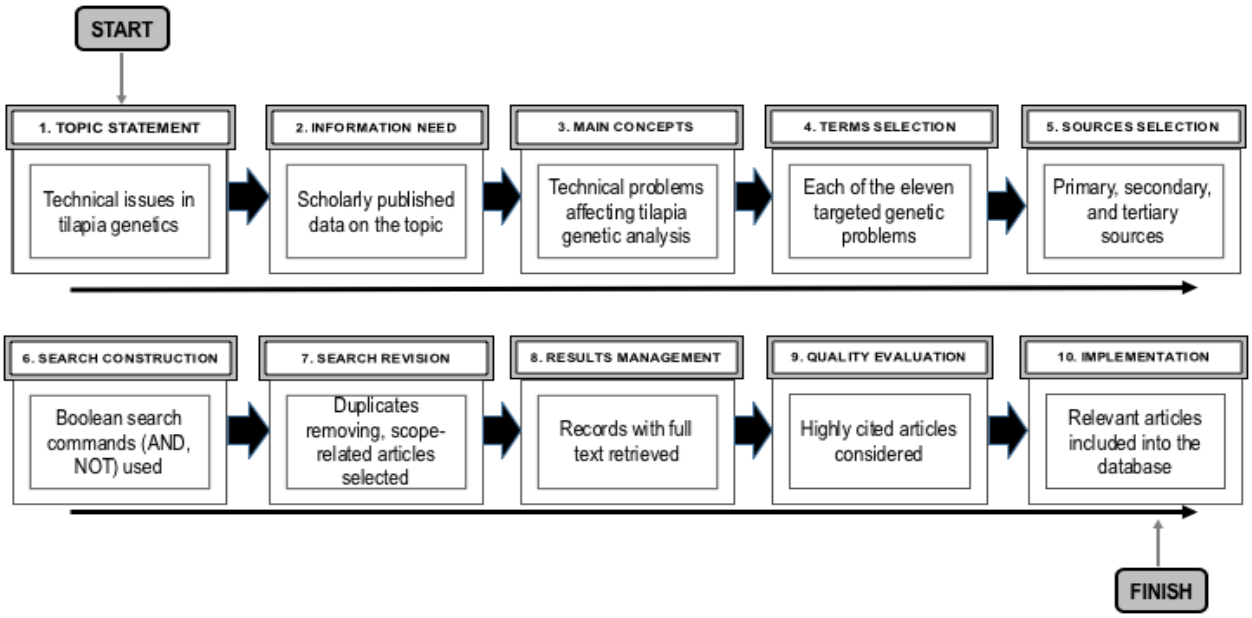

Figure 1. Diagram of search strategy considering 10 steps.

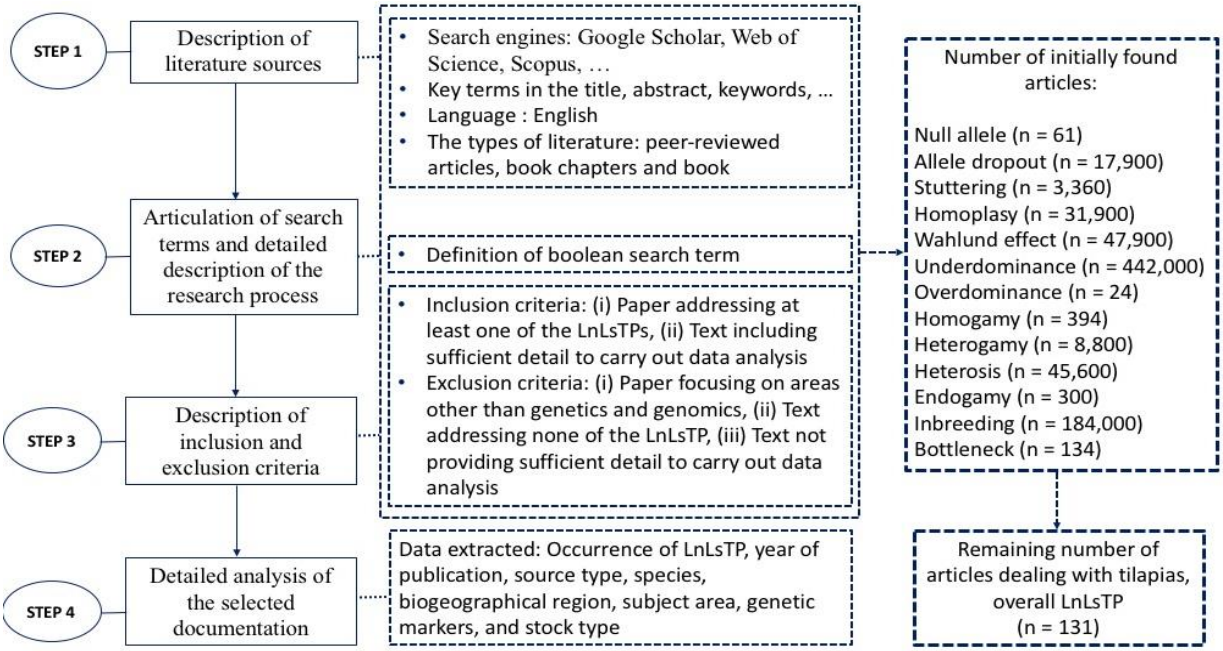

Figure 2. Diagram of the data extraction process prior to analysis. The procedure of data extraction was conducted in 4 steps.

from 1928 to 2021 considering the overall species. But for papers dealing specifically with tilapia, the period was from 1975 to 2020. The modalities of the source type were: review paper, article, or book. The groups of species initially identified were: tilapias, other cichlids, other species. The modalities of the biogeographical region were: Australian, Ethiopian, Madagascan, Nearctic, Neotropical, Palearctic, Sino-Oriental, and Global. The biogeographic regions were defined according to the major global transition zones of freshwater fish species (Leroy et al., 2019). As for the subject areas, they were genetics and genomics. The genetic markers had as modalities: Amplified Fragment Length Polymorphism (AFLP), Allozyme, Expressed Sequence Tags (EST), Mitochondrial DNA (MtDNA), Quantitative Trait Locus (QTL), Random Amplified Polymorphic DNA (RAPD), Restriction Fragment Length Polymorphism (RFLP), Sex-linked marker, Single Nucleotide Polymorphism (SNP), Simple Sequence Repeats (SSR), and Variable Number Tandem Repeats (VNTR). The stock types were wild-type and cultured-type. Each of the LTPs identified (for instance, genotyping errors and biological factors) was characterized according to whether it was locus-specific or non-locus specific. The tilapia species in which each LTP was observed were listed as well. We also provided a rough description of the nature of each LTP. The genetic markers used in the identification of each LTP

were then compiled. For each genetic marker, the tools, the methods, or the approaches used to highlight each technical issue were documented.

A qualitative model was used to assess the nature of the interrelationships between the different technical issues. This consisted of a set of Multiple Correspondence Analysis (MCA) and Correspondence Analysis (CA) in order to draw up an assessment of the relationships (or proximity) between the different qualitative variables extracted from the selected papers. These analyses were performed either per variable or variables taken in pairs. In this way, the different papers identified were compared modality-by-modality in order to highlight the rarity or general nature of the modalities. This allowed the identification of variables that summarize the information contained in several qualitative variables. The information carried by the source type, the biogeographical region, the subject area and the stock type was studied in terms of their modalities. So, two modalities are more distant (high distance) if they have few papers in common. Moreover, the relationships between stock type and LTPs (i), genetic markers and LTPs (ii), biogeographic region and subject area (iii), as well as publication year and source type (iv) were analyzed. The MCA and CA were performed using R Studio Version 1.3.1093 (RStudio Team, 2020) after loading the FactoMineR package (Lê et al., 2008).

Results and Discussion

The results are presented and discussed in two main sections. The first section provides an overview of LTPs in natural and aquaculture populations of tilapia species, on the basis of the biogeographical region of the selected papers, the subject areas, the occurrence of LTPs by molecular marker, the occurrence of LTPs by stock type, etc. The second section presents each LTP as well as the usual approaches to detect and characterize them.

Overall Progress of Studies Focusing on LTPs in Natural and Aquaculture Populations of Tilapia

The number of papers dealing with genetics is greater than that dealing with genomics. Also, studies focusing on genomics have enough modalities in common with those focusing exclusively on genetics that they are hereafter considered together. In terms of stock type, papers involving aquaculture populations of tilapias are more numerous than those involving wild populations of tilapias. The number of papers that focused on both aquaculture and wild tilapia populations is midway between the number of papers that focused on these two stocks separately. Based on literature source, articles, reviews, and books have many modalities in common. However, the number of articles dealing with LTPs in tilapia is higher than the corresponding numbers of books and literature reviews. Regarding the biogeographic region of the tilapia populations studied, four groups were observed. The first group combined populations of the respective biogeographic regions, the Madagascan, Nearctic, Palearctic, and Sino-Oriental. The second, third and fourth groups included tilapia from the Australian, Ethiopian and Neotropical regions, respectively. The inertia (i.e., measure of spread around the mean) percentages associated with the two major factorial components of the MCA were overall low, at around 5.3% (Figure 3A). This is common because MCAs generally have lower inertia percentages than CAs. Among the papers selected, those paying attention to genotyping errors represented 42%, 29%, 20% and 9% respectively for null alleles, stuttering, allelic dropout, and homoplasy. Regarding the LTPs related to biological factors such as demographic problems and reproductive system problems, the proportions were: 40% (inbreeding), 18% (bottleneck), 14% (heterosis), 7% (heterogamy), 6% (Wahlund effect), 6% (homogamy), 5% (endogamy), 4% (overdominance) and 1% (underdominance) (Figure 3B, C). The plots presented in Figure 4 include the papers organized into groups of LTPs within stock type and genetic marker type, into groups of biogeographic region within subject area, and into publication year-class within literature source type. The two major factorial components were extracted and contributed 100% and 62.72% of the total variability respectively between the stock types and the LTPs, between the genetic marker types and the LTPs on one hand (Figure 4A, B); and contributed 33.48% and 39.64% of the total variability respectively between the biogeographic region of the study and the subject area, between the source type and the publication year-class of the literature on the other hand (Figure 4C, D). Overall, tilapia populations in the aquaculture environment and in the wild environment, taken separately, are characterized by LTPs such as: null allele, dropout, stuttering, Wahlund effect, heterogamy, heterosis, inbreeding, bottleneck. Aquaculture-only tilapia populations are generally characterized by LTPs such as: homogamy, heterogamy, heterosis, inbreeding and overdominance. Null alleles, allelic dropout, stuttering, homoplasy, genetic bottleneck and Wahlund effect are most often found in tilapia populations originating only from the wild. Studies focusing on both aquaculture and wild populations generally highlight LTPs such as underdominance and endogamy (Figure 4A). Genetic markers such as ESTs, sex-linked marker, and SSRs are mainly relevant to highlight null alleles, allelic dropouts, stuttering, and heterogamy patterns. ESTs and mtDNA markers are the most widely used genetic markers to highlight heterogamy, and genetic bottleneck (Figure 4B). Genetic studies were mainly intensified on tilapia populations from four biogeographic regions: Australian, Ethiopian, Madagascan, Neotropical, and Sino-Oriental. However, genomic studies focused to a lesser extent on tilapia populations from two biogeographic regions, the

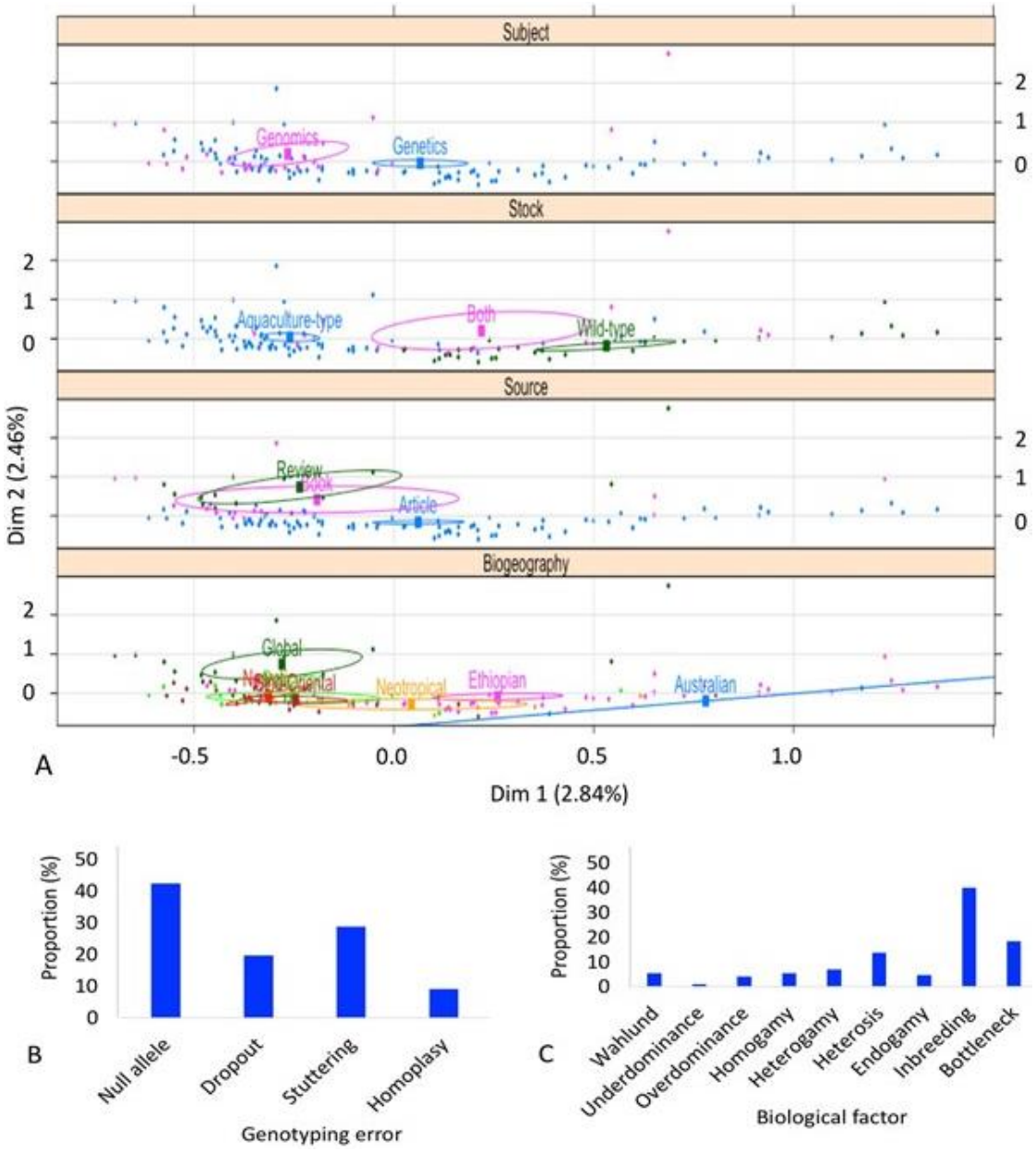

Figure 3. Plots from MCA (Multiple Correspondence Analysis) showing the confidence ellipses for the subject area, stock types, source types, and biogeographic regions of studies considering LTPs in tilapia (A) along with the occurrence diagram of LTPs in tilapia (B and C).

Nearctic and Palearctic (Figure 4C). Whether articles, books or review papers, studies highlighting LTPs in tilapia were mostly concentrated in the periods 1990 to 2020, probably because molecular tools received special attention in these periods (Figure 4D).

Detection and Characterization of the LTPs

Null Alleles (Non-amplified alleles)

A null allele is defined as any allele at a locus that is weakly or not visible (De Meeûs et al., 2007) due to mutational changes in the primer-binding site (Nguyen et al., 2006). This may occur in allozymes for alleles that are not functionally expressed anymore or enzymatically inactive (Amoussou et al., 2019). If the active site of the enzyme is mutated, for instance, and then does not foster degradation of the substrate following electrophoretic migration, no precipitate will occur and the corresponding allele will remain unseen (De Meeûs et al., 2007). Null alleles also occur in PCR-dependent marker systems like SSRs (Van Oosterhout et al., 2006; Chapuis & Estoup, 2007). The microsatellite-flanking sequence is mutated at one of the two primer-binding sites such that annealing does not occur, the corresponding allele is not amplified (Pompanon et al., 2005). Null alleles lead to an observed deficit of heterozygotes as compared to HW expectations (De Meeûs et al., 2007) and increase the genetic differentiation apparent between populations (Chapuis & Estoup, 2007). Null alleles do not affect all loci equally, and a typical signature of null alleles is a strong variance across loci of statistics measuring deviation from panmixia, such as Wright's F_{IS} (De Meeûs et al., 2007).

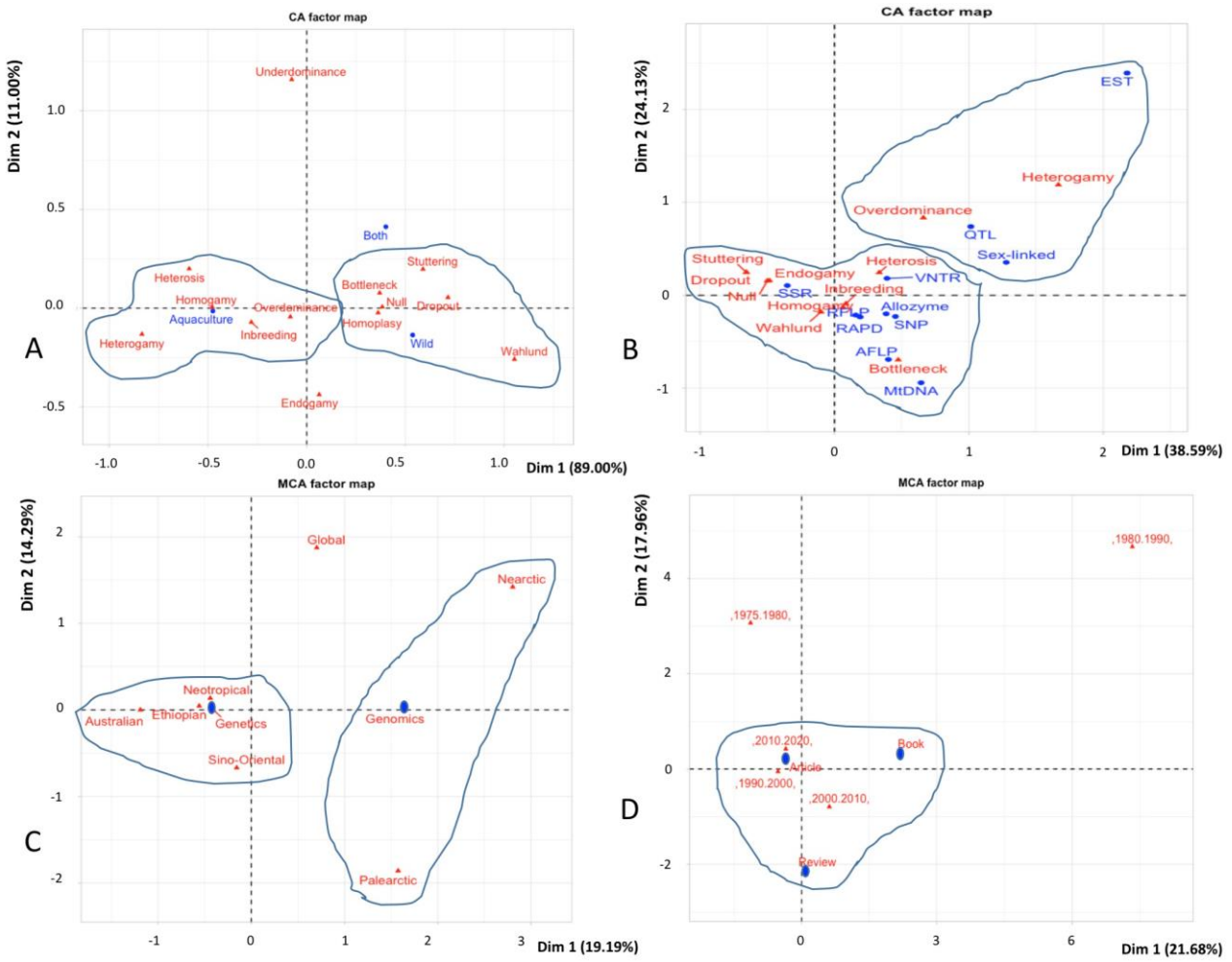

Figure 4. Biplot from CA (Correspondence Analysis) showing the relationship between the stock type and the LTPs and between the genetic markers and the LTPs (A and B) with biplot from MCA showing the relationship between the active modalities of the biogeographic region and the subject area (C) and between the active modalities of the publication year and the type of source dealing with LTPs in tilapia (D).

Occurrences of blank genotypes can be the signature of presence of null alleles in the homozygous state. Null allele frequencies can easily be estimated using procedures assuming panmixia, as in the Micro-Checker software (Van Oosterhout et al., 2004; Van Oosterhout et al., 2006). The null allele frequency can be merely estimated from heterozygote deficiency (Brookfield, 1996). Subdivision or genetic distance can be adjusted easily with FreeNA (Chapuis & Estoup, 2007) with which only null alleles with frequencies >8% are considered true (Dabrowski et al., 2014). Other authors consider that only markers exceeding a null allele frequency value of 0.2 should be excluded from subsequent inferences (Dakin & Avise, 2004).

Null alleles are locus-specific technical problems. They commonly occur for tilapia populations (Hassanien & Gilbey, 2005; McKinna et al., 2010; Agnèse et al., 2009; Yoboué et al., 2012; Amoussou et al., 2018), especially *Oreochromis* spp. and *Sarotherodon* spp. (Table 1). Null alleles explained F_{IS} (relative inbreeding of individuals as compared to subsample inbreeding) variation in tilapia *Sarotherodon melanotheron* (Amoussou et al., 2018). In tilapia, null alleles have been observed with genetic markers such as SSRs, allozymes, SNPs and RAPDs. Regarding SSRs, tools such as FreeNA and MicroChecker are commonly used to highlight them (Table 1). When using FreeNA, applying the Expectation-Maximization Algorithm (EMA) allows highlighting of null allele frequencies. When using MicroChecker, the most commonly used approach is based on estimating the Brookfield index (Brookfield, 1996). With allozyme markers, it is advisable to perform gel electrophoresis analysis (GEA) to determine the presence or absence of a null allele (Fujio, 1984).

Allelic Dropout

Also referred to as short allele dominance (SAD), large allele dropout (Van Oosterhout et al., 2006), or upper allele dropout (Fessehaye, 2006), this problem is specific to PCR-based genetic markers. It occurs when the shorter allele is more often amplified than the longer one in a heterozygous individual. Allelic dropout occurs when the PCR applied for a given locus fails to amplify one or both alleles for a diploid individual. In the case where only one allele drops out, only one allele (band or

Table 1. Genetic and genomic methods for detecting and characterizing LTPs in tilapia species

Problem		Type	Tilapia species	Nature of the problem	Genetic markers	Approaches for detection/solving Tool/Software
Genotyping errors	Null allele	Locus-specific	*Oreochromis* spp., *Sarotherodon* spp.	Low or poorly amplified alleles leading to mutations at priming sites	SSR	Applying the Expectation-Maximization Algorithm (EMA) using FreeNA
						Estimating Brookfield index (Brookfield, 1996) using MicroChecker
					Allozyme	Gel electrophoresis analysis
					SNP	NS
					RAPD	NS
	Dropout	Locus-specific	*Oreochromis* spp., *Sarotherodon* spp.	Preferential amplification of short alleles i.e. non-amplified allele during PCR	SSR	MicroChecker
					AFLP	Genographer
					SNP	Genome-Independent imputation
					QTL	Maximum likelihood estimates computing
	Stuttering	Locus-specific	*Oreochromis* spp., *Sarotherodon* spp.	Scoring of stutter peaks due to the non-specificity of primers, and thus, to the breakdown of the Tap polymerase during the PCR amplification	SSR	MicroChecker
	Homoplasy	Locus-specific	*Oreochromis* spp., *Sarotherodon* spp., *Tilapia* sp.	Multiple substitutions (insertion or deletion) in the amplified fragment size	AFLP	Cauchy distribution analysis
					MtDNA	Tree-based method
					Allozyme	PAUP* (Homoplasy indices computation)
					SSR	Sequence analysis of electromorphs (alleles of the same size)
					Sex-linked marker	NS
					SNP	NS
Biological factors	Wahlund	Non-Locus-specific	*Tilapia* sp., *Oreochromis* spp., *Sarotherodon* spp.	Problem affecting the whole genome equally and consisting of a mixture of two or more subsamples having different allelic frequencies	SSR	FSTAT (Comparing the jackknife standard errors of *F*-statistics over loci)
						Maximum likelihood (ML) analysis
					MtDNA	NS
					Allozyme	NS
					AFLP	Bayesian framework analysis
					SNP	Multimodelling analysis
	Overdominance	Locus-specific	*Oreochromis* spp., *Coptodon* sp.	Excess of heterozygous individuals at a given locus	SSR	Computing the product $N_e r$, where r is the recombination fraction between the marker and the selected locus, and N_e the effective population size
					Allozyme	Computing the correlation between the weight and the degree of heterozygosity
					QTL	Compare the effect of new mutations in homozygous and heterozygous individuals
	Underdominance	Locus-specific	*Sarotherodon* spp.	Selection that disadvantages heterozygotes while favouring chromosomal excess of homozygotes	SSR	Search for heterozygous deficient loci
						Analysing the relation between the frequency of private alleles and the effective numbers of immigrants per generation
Biological factors	Homogamy (Assortative mating)	Locus-specific	*Tilapia* sp., *Oreochromis* spp., *Sarotherodon* spp.	Homospecific mating system where sexual partners or gametes are more likely attracted by genetically similar individuals at loci responsible for the trait (e.g., color morphs)	SSR	Identifying sex-linked DNA markers (loci/genes)
					RFLP	NS
					Allozyme	NS
					Sex-linked marker	Sex chromosome differentiation
						BLASTN to align sex-specific markers to the homogametic sex data sets
						Karyotypic analysis
					MtDNA	Computing the probability of assortative mating under cytonuclear association models
	Heterogamy (Disassortative mating)	Locus-specific	*Oreochromis* spp., *Tilapia* sp.	Heterogamic systems favour mating between individuals carrying different alleles at loci responsible for the trait	Sex-linked marker	Ultrastructural analyses of synaptonemic complexes
						Applying dRAD-seq (double digest restriction site – associated DNA sequencing) to identify sex-specific genotypic markers
						Cross-combinations of genotype and phenotype
						Analysis of sex ratios from single-pair matings
					SSR	Analysing the inheritance of sex-linked alleles by sex-determining locus on linkage groups
					SNP	Using Perl script to analyse the sex biased inheritance of parental SNPs
Biological factors	Heterosis	Non-locus-specific	*Oreochromis* spp.	Selective phenomenon affecting the whole genome equally	SNP	Determining the optimal interstrain crosses using SNP markers
						Identifying the ribosomal protein-related genes
					Sex-linked marker	Matings using sex-specific DNA markers
					None	Compare crossbred progenies with the average of the parental line/strain
						Compare the crossbred progenies with the average of the better parental line/strain

Table 1. *Continued*

Problem		Type	Tilapia species	Nature of the problem	Genetic markers	Approaches for detection/solving Tool/Software
						Using Fisher's model to predict heterosis
						Computing the least squares means (LSM) estimations
	Endogamy	Locus-specific	*Sarotherodon* spp., *Oreochromis* spp.	Non-random union of gametes (e.g., from sib mating) affecting the genotypic distribution at all loci (all loci loose heterozygosity)	SSR	Computing the selfing rate
						Computing sib mating rate
						Computing the kinship coefficient
						SPAGeDi to compute the individual endogamy coefficient
					Allozyme	NS
Biological factors	Inbreeding	Non-locus specific	*Oreochromis* spp., *Sarotherodon* spp., *Coptodon* sp.	A multi-loci non-random union of gametes affecting the whole genome	SSR	FSTAT
						Testing deviations from HWE on the basis of the inbreeding coefficient, using ARLEQUIN
						GENEPOP
						POPGENE
						IDENTIX
						Computing the per-generation rate of inbreeding
						GenAlEx
						POWERMARKER
						GENETIX
						Performing MCMC (Markov chain Monte Carlo) Bayesian method (e.g., GENEPOP)
						diveRsity
						GENODIVE
					SNP	ADEGENET
						STACKS
						STACKS-2
						diveRsity
						VCFTOOLS
						GENEPOP
						Test for inbreeding depression, by fitting linear model, with individual heterozygosity as a single predictor of growth residuals, followed by a linear mixed model, using the lme function of R package nlme, to control for random differences in environmental effects at birth. When fitting the linear mixed model, consider the birth year as a single random effect, individual heterozygosity as a single fixed predictor
					QTL	Using BLUP (Best Linear Unbiased Prediction) approaches for genetic evaluation to monitor inbreeding
					VNTR	NS
					MtDNA	ARLEQUIN
						Performing a generalised skyline plot analysis to compute the inbreeding effective population size
						GENIE
					AFLP	Using Bayesian F-model to compute population-specific inbreeding coefficient
					Allozyme	GENEPOP
						diveRsity
					RFLP	NS
					RAPD	POPGENE
					None	PEDIGREE package
Biological factors	Bottleneck	Non-locus-specific	*Oreochromis* spp.	A deviation from neutrality (i.e. deviation from mutation/drift balance) always accompanied by either heterozygosity excess or heterozygosity deficit	SSR	Performing Wilcoxon sign-rank test and Wilcoxon sign test using BOTTLENECK
						Computing G-W (Garza–Williamson) Index using ARLEQUIN
						Performing M-ratio (M) statistic (Garza and Williamson, 2001) with EXCEL using the output from GENALEX
						Performing tests of alternative introduction scenarios using DIYABC
						Performing M-ratio (M) statistic (Garza and Williamson, 2001) using ARLEQUIN
						Using the *F*model in historical inference to detect occurrence of population bottleneck
						Using the predicting model of DemoDivMs
					MtDNA	Computing the the standardized square difference (SSD) and the raggedness index using ARLEQUIN
						Test of population demographic expansion of neutrality using Tajima's D and Fu's Fs approaches under ARLEQUIN
						Performing a generalised skyline plot analysis to differentiate between alternate population bottlenecks
						Performing Tajima's D and Fu's F tests using DnaSP
					SNP	Reconstruct past fluctuations in N_e by using demographic modeling and methods that estimate historical coalescence rates from whole-genome SNP data
						Using genome-wide runs of homozygosity to infer correlation between the sum total length of runs and the total number of runs

HWE: Hardy–Weinberg Equilibrium; NS: Not Studied

peak) is then revealed and the individual is thus mis-scored as homozygous at that locus. This is a random event (either of the two alleles is as likely to undergo the phenomenon). Several phenomena can lead to allelic dropout: poor matching between primers and the primer-binding DNA sequence flanking the marker, low-quality template DNA, low-quality reagents, poor precision or reliability of DNA quantification or amplification equipment, or use of an inappropriate protocol (Pompanon et al., 2005) and when the melting temperatures of the forward and reverse primers substantially vary. Allelic dropouts are thus, most of the time, expected to be locus-specific. This LTP is most often reported in fish-specific loci (e.g., Landínez-García et al., 2020).

Here, competition for the polymerase exists such that shorter alleles have an amplification advantage over longer ones. This phenomenon is problematic as it changes both F_{IS} and genotype frequency estimates (De Meeûs et al., 2004). A simple way to check for it is to regress F_{IS} measured on each allele against allele size (Wattier et al., 1998; De Meeûs et al., 2004). MicroChecker also identifies when this phenomenon is present (Van Oosterhout et al., 2006). Low quality or quantity of DNA can favour short allele dominance (Pompanon et al., 2005) probably owing to the quality of the reagents and protocols. Short allele dominance has been demonstrated at PCR-analysed SSR and minisatellite loci (Armour et al., 1996; Wattier et al., 1998; De Meeûs et al., 2004), but seems to rarely occur in tilapia species (McKinna et al., 2010).

Allelic dropout can also cause missing genotypes (if both alleles drop out) (Séré et al., 2014), thereby decreasing effective population sizes and genetic diversity. In cichlid fishes, the dropout of genomic regions often affects SSRs (Henning et al., 2014). It leads to an overestimation of inbreeding coefficients since heterozygous individuals are erroneously genotyped as homozygous (Bonin et al., 2004). To remedy this, DNA extraction and amplification protocols should be well suited to the species. This loci-specific problem has been observed in *Oreochromis* spp. and *Sarotherodon* spp. for many genetic markers including SSRs, AFLPs, SNPs, and QTLs (Table 1). This problem is distinguished by a preferential amplification of short alleles, i.e., non-amplified alleles during PCR using these markers. Software packages such as MicroChecker (Van Oosterhout et al., 2004) and Genographer (Benham et al., 1999) can be used to identify allelic dropouts for SSRs and AFLPs, respectively (Table 1). When using SNPs and QTLs, one can perform Genome-Independent imputation (Ward et al., 2013) and Maximum Likelihood Estimates computing (Miller et al., 2002), respectively.

Stuttering (Stutter-related Scoring)

Stuttering is a result of scoring error, particularly with di-nucleotide repeat motif markers, and can result in some homozygote samples being scored as heterozygotes (Simbine et al., 2014). Although stuttering is not a problem in genetic mapping studies where the number and type of possible alleles are known, it is a cause of concern in population genetics where scoring errors can lead to an artificial excess of heterozygotes (O'Connell & Wright, 1997). Stutter peaks are caused by polymerase slippage during PCR amplification, which results in secondary products containing one or more repeat units less or more than the primary allelic band (Liu & Cordes, 2004). Technically, if the PCR primers do not cling well, it is possible that the *Taq* polymerase stutters and amplifies different sizes for the same allele so that individuals homozygous for two alleles similar in size will appear as heterozygous individuals. Polymerase stuttering may be indicated when the microsatellite alleles are observed as a series of bands, and not a single discrete band (scoring of stutter peaks or "phantom bands") (O'Connell & Wright, 1997; Chenuil, 2006) leading to elevated frequencies of genotypes with alleles of one repeat unit difference (Karlsson & Mork, 2005). Depending on quality of primer synthesis, stuttering is an issue for SSR data (Moradi & Keyvanshokooh, 2013) and can be detected by Micro-Checker (Van Oosterhout et al., 2004). It is also generally higher in fish SSRs with larger repeat arrays (O'Connell &d Wright, 1997). One possible approach to avoid this problem is to select and screen tetranucleotide instead of dinucleotide loci (Sekar et al., 2009). A second method for reducing the potential scoring difficulties is to use dinucleotide loci with a small product size (<120 bp) (O'Reilly & Wright, 1995; Sekar et al., 2009).

There was no evidence for band stuttering in the Genetically Improved Farmed Tilapia strain (McKinna et al., 2010), but the problem is nevertheless reported for other fish-specific SSR loci (Landínez-García et al., 2020). In the same way, this problem has also been reported on unimproved tilapia *Oreochromis* spp. and *Sarotherodon* spp. stocks, both wild and aquaculture types (Table 1). For investigations using SSRs, the MicroChecker software (Van Oosterhout et al., 2004) can be used to detect loci subject to issues of allelic stuttering.

Homoplasy (Allele Size Homoplasy)

Homoplasy refers to the phenomenon of two alleles that are scored as identical but do not share a common ancestry, which are then said to be identical in state as opposed to identical by descent (De Meeûs et al., 2007). In other words, homoplasy refers to the coexistence of identical variants of independent evolutionary origins and process (Chenuil, 2006; De Santis, 2024). Indeed, variants of base-pair size are assumed to derive from a recent common ancestor (Chistiakov et al., 2006), and homoplasy problems are due to high mutation rates (Lemaire et al., 2000) that allows the same allele (at a given locus) to arise multiple times (Chistiakov et al., 2006). The terminology also

refers to a character that arises twice in the course of evolution (Haubold & Wiehe, 2006), downplaying the effect of heterozygosity (Meirmans & Hedrick, 2011). This locus-dependent problem caused by multiple substitutions at a single nucleotide site can lead to difficulties in grouping closely related haplotypes (Nguyen et al., 2006). Microsatellite DNA markers are known to be characterized by high levels of size homoplasy (Balloux & Lugon-Moulin, 2002). With microsatellites, the problem may contribute to biased genetic analyses of natural populations, thereby limiting their utility for identification of conservation units (Chistiakov et al., 2006). Thus, fragment-size homoplasy can cause incorrect scoring of bands across gels (Dudgeon et al., 2012) and can lead to extreme outliers in tests for the signature of selection (Foll et al., 2010).

Multiple substitutions (insertion or deletion) in the amplified fragment are commonly reported in tilapias, *Oreochromis* spp., *Sarotherodon* spp. and *Tilapia* sp. (Table 1). Homoplasy caveats are locus-specific and are most often reported for molecular markers such as AFLPs, mtDNA, allozymes, SSRs, sex-linked markers, and SNPs. Their assessment is based on Cauchy distribution analysis (Carrillo et al., 2010), tree-based method (Seehausen, 2004), computation of homoplasy indices (Swofford, 1991), and sequence analysis of electromorphs, i.e., of alleles of the same size (Estoup et al., 1995).

Wahlund Effect

This analytic problem was first described by Wahlund (Wahlund, 1928) and results from the mixing of genetically distinct populations. The Wahlund effect is manifested as observation of a heterozygote deficit relative to Hardy-Weinberg expected genotypic frequencies (Hartl & Clark, 2007), which arises when two or more populations with different allele frequencies are mixed within a sample (Karlsson & Mork, 2005; Nyingi et al., 2009; Foll et al., 2010). Wahlund effect can occur when a sample is composed of individuals that belong to several and differentiated cohorts, subpopulations or even cryptic species (Hassanien & Gilbey, 2005; Larsson et al., 2007). Within a population, a heterozygote deficiency generated by an inter-family Wahlund effect may arise, and may mask any heterozygote excess (Nomura, 2008) while creating linkage disequilibrium (Waples, 2006). F_{ST} being a measure of the probability that an allele is identical between sub-samples, represents an estimate of the Wahlund effect (Balloux & Lugon-Moulin, 2002).

In fish, the Wahlund effect may be either spatial or temporal (Landínez-García et al., 2020). This non-locus-specific problem affects the whole genome equally. So far, Wahlund effect has attracted little attention in tilapia genetic studies, with the exception of a few studies (e.g., Agnèse et al., 2009; Nyingi et al., 2009; Amoussou et al., 2018). Tilapia species that usually exhibit the Wahlund effect are *Tilapia* spp., *Oreochromis* spp. and *Sarotherodon* spp. (Table 1). Many genetic analyses based on markers such as SSRs, mtDNAs, allozymes, AFLPs and SNPs have revealed this phenomenon in tilapia populations. The problem is most often evidenced by genetic structure analysis. The most commonly used tool to detect this problem with SSRs in tilapias is the FSTAT software (Goudet, 2003) which compares the jackknife standard errors of *F*-statistics over loci (Table 1). The most commonly used approaches are based on Maximum Likelihood (ML) analysis (Swofford, 2000), Bayesian Framework (BF) analysis (Foll et al., 2010), and Multi-Modelling (MM) analysis (Manangwa et al., 2019), for SSRs, AFLPs and SNPs, respectively (Table 1).

Over- or Under-Dominance

Overdominance refers to the state when the performance of the heterozygote exceeds the performance of either of the two respective homozygotes (Crow, 2008). In practice, the stabilization of selection on diploid organisms can lead to overdominance at individual loci, thus maintaining high genetic diversity (Barton, 2001). Many selective breeding programs, especially those based on crossbreeding or hybridization, are designed to capitalize on overdominance (Crow, 2008). Typically, the phenomenon occurs in aquaculture when the heterozygous is superior to the two homozygous genotypes (Fjalestad, 2005). This biology-related problem is locus-specific, leading to an excess of heterozygous individuals at a given locus. It is most commonly reported in tilapia *Oreochromis* spp. and *Coptodon* sp. (Table 1). It often affects SSR, allozyme, and QTL molecular markers. In SSRs, it is quite simply assessed by computing the product Ner , where r is the recombination fraction between the marker and the selected locus, and N_e is the effective population size (Ohta & Kimura, 1970). With allozymes, overdominance was proposed to explain the correlation between weight-at-age and the degree of heterozygosity (Zouros et al., 1980). With QTLs, it is about comparing the effect of new mutations in homozygous and heterozygous individuals (Crow, 2008).

Underdominance is a selective process in which heterozygous individuals (at a given locus) show a reduced survival, reproductive success, or other trait (Thomas et al., 2010). In such a system, there is a fitness advantage of homozygotes relative to heterozygotes. Unlike tilapias, this problem is commonly encountered in rainbow trout (Miller et al., 2004) and in seabass *Dicentrarchus labrax* and *D. punctatus* (Ky et al., 2012). However, the problem has previously been hypothesized in the tilapia *Sarotherodon* spp. (Amoussou et al., 2019). It is a locus-specific selection process that disadvantages heterozygotes while favouring chromosomal excess of homozygotes. In tilapias, the problem has been evident at SSRs (Table 1) either by searching for heterozygous-deficient loci (De

Meeûs, 2018) or by analysing the relation between the frequency of private alleles and the effective numbers of immigrants per generation (Barton & Slatkin, 1986).

Genetic Bottleneck

Sometimes caused by a founder event, a bottleneck is a demographic historical process during which a population undergoes a strong and rapid reduction in size (Ellegren & Galtier, 2016), especially the number of founder or mating individuals. Population bottlenecks can result in loss of allelic diversity and low genetic diversity as population size declines (Nguyen et al., 2006; Ndiwa et al., 2023; Imamoto et al., 2024) and loss of major sex-determinant genomic region (Triay et et al., 2022). In the Cichlidae Lamprologus lethops, a bottleneck may be mediated by directional selection for degenerative physiological and phenotypic traits including eye loss and pigment deficiency (Aardema et al., 2020). A fish population bottleneck may result from species introduction (e.g., invasive alien species) or reintroduction, reducing many population genetic parameters (the observed number of alleles, the effective number of alleles and the expected heterozygosity, etc.) (Dunham, 2011) and may be important in some modes of speciation (Cournet & Luikart, 1996). A direct introduction history is characterized by a single bottleneck event, while an indirect route of introduction history may encompass two or more bottleneck events (Wood et al., 2018). Environmental changes like rainy seasons and dry seasons fluctuations, water level fluctuations, overfishing, droughts, or glaciation periods can create bottleneck processes in fish populations by changing or maintaining their genetic variation (Espinosa-Lemus et al., 2009; Dudgeon et al., 2017; Laroche et al., 1999; Simbine et al., 2014; Tibihika et al., 2018; 2020; Tibihika et al., 2020). An ecotoxicological origin of bottlenecks has been proven in European Eel and the problem may affect the genetic variability in a population (Maes et al., 2005) by generating genetic drift (Nielsen et al., 1997). In fish, in case of high genetic diversity among populations, it is important to find out whether this is due to gene flow or a history of bottlenecks (Nikolic et al., 2009). The problem can be observed in populations of aquatic organisms other than fishes. The stocks of the swimming crab *Portunus trituberculatus* in Panjin, China are experiencing the bottleneck phenomenon (Liu et al., 2018). In cyprinids, the problem has been suggested to be due to another environmental factor, e.g., fluctuations in water levels (Laroche et al., 1999).

Bottleneck problems have been known for tilapias (Romana-Eguia et al., 2004; Sanudi et al., 2020) as a factor limiting population-level conservation (Ponzoni et al., 2009). In tilapias, the problem most often arises from a low number of founder individuals of a population (Yoboué et al., 2012), hence leading to low genetic polymorphism (Nyingi et al., 2009). Genetic bottlenecks have been evidenced in tilapias species *Oreochromis* spp. with a documented example, *Oreochromis mossambicus* from the Limpopo, Incomati, Umbeluzi and Sabié rivers in Mozambique (Simbine et al., 2014). Genetic bottleneck is a non-locus specific problem, being by nature a deviation from neutrality (i.e., deviation from mutation/drift balance) often accompanied by either heterozygosity excess or heterozygosity deficit. With SSRs, the assessment of genetic signal of past, recent or present demographic bottleneck in natural and cultured tilapia populations is commonly done by performing Wilcoxon sign-rank test and Wilcoxon sign test using BOTTLENECK (Piry et al., 1999). Alternative approaches are : (i) computing the G-W (Garza–Williamson, 2001) index using ARLEQUIN (Excoffier & Lischer, 2010) or with EXCEL using the output from GENALEX (Peakall & Smouse, 2012) (ii) performing tests of alternative introduction scenarios using DIYABC (Cornuet et al., 2014), or (iii) using the predicting model of DemoDivMs (Nikolic et al., 2009). One can also use the *F*model in historical inference to detect occurrence of population bottleneck with SSR markers (Falush et al., 2003). The benefit of using the mtDNA markers to detect population bottlenecks is the restricted number of haplotypes detected. In the case of allozyme markers, only the examination of genetic variation can be considered for this purpose. In addition, due to the large number of alleles present at VNTR markers, these markers are particularly well suited to the study of populations previously subject to bottlenecks (Ferguson et al., 1995). Such demographical changes are examined by estimating the standardized square difference (SSD) (also referred to as the “sum of squared deviations”) and the raggedness index (Harpending, 2013; Barasa et al., 2016) using ARLEQUIN (Table 1). Higher values of SSD and raggedness index suggest static or bottlenecked tilapia populations (Kavembe et al., 2014). Again, with mtDNA markers, one can perform a test of population demographic expansion of neutrality using Tajima’s *D* and Fu’s *Fs* approaches using ARLEQUIN. The Tajima’s *D* and Fu’s *F* tests can also be performed using DnaSP (Librado & Rozas, 2009). A final approach is performing a generalised skyline plot analysis to differentiate between alternate population bottlenecks (Strimmer & Pybus, 2001) with mtDNA markers.

Homogamy and Heterogamy

In a system of homogamy (i.e., with assortative mating), the parental species becomes differentiated into two new species, morphologically similar but sexually isolated from each other (Kosswig, 1963). Homogamy occurs when sexual partners or gametes are more likely attracted by genetically similar individuals at loci responsible for a trait (De Meeûs et al., 2007). In cichlid fishes, males as well as females show conditional mating preferences (Baldauf et al., 2013) that suggest non-random mating. The major consequence of assortative mating pattern at a molecular marker is

heterozygote deficiency, indicating a departure from HWE. Among tilapia species, sex-linked color polymorphisms provide a basis for sexual selection and assortative mating (Kocher et al., 2005). Assortative mating is also reported in Atlantic cod (Karlsson & Mork, 2005).

Heterogamy (disassortative mating) is a sexual reproduction process in which individuals are more attracted to one another for mating if they differ genetically at gene(s) that encode a trait (De Meeûs et al., 2007). In one case of such a system, an organism of a particular sex carries two different types of sex chromosomes (Ellegren & Galtier, 2016). Genetic sex-determining systems including male heterogamy (XY) and female heterogamy (ZW), can be regarded as a form of heterogamy (Luo et al., 2011; Fowler & Buonaccorsi, 2016; Du et al., 2023). Either system can have monogenic or polygenic sex determination. Both systems exist in teleost fishes, with a higher proportion for the XY system than the WZ system (Bao et al., 2019). Both systems exist within the tilapia group (Chen et al., 2018), where, for example, Nile tilapia *Oreochromis niloticus* and Mozambique tilapia *Oreochromis mossambicus* have an XY system, whereas blue tilapia *Oreochromis aureus* has a WZ system (Cnaani et al., 2008; Campos-Ramos et al., 2003). In the ZW–ZZ genetic sex determination system, the ovum is the sex determiner of the progeny, while in the XX-XY genetic sex determination system, the sperm determines the sex of the progeny (Joshi et al., 2018).

Homogamy has been demonstrated using various molecular markers, including SSRs, RFLPs, allozymes, sex-linked markers, and mtDNA in tilapias such as *Tilapia* sp., *Oreochromis* spp. and *Sarotherodon* spp. (Table 1). It is a locus-specific technical issue. The presence of homogamy in genetic data of tilapia often is detected by identifying sex-linked DNA markers (loci/genes) (Cnaani et al., 2008) or by karyotypic analysis (Devlin & Nagahama, 2002). One can also use the sex chromosome differentiation approach (Mawaribuchi et al., 2017). BLASTN (Camacho et al., 2009) also can be used to align sex-specific markers to the homogametic sex data sets. With mtDNA markers, the recommended approach is computing the probability of assortative mating under cytonuclear association models (Scribner et al., 2001).

As with homogamy, heterogamy is also a locus-specific problem usually reported in *Oreochromis* spp., *Tilapia* sp. (Table 1). With sex-linked markers, one can: (i) perform ultrastructural analyses of synaptonemic complexes (Devlin & Nagahama, 2002), (ii) apply ddRAD-seq (double digest restriction site – associated DNA sequencing) to identify sex-specific genotypic markers (Fowler &d Buonaccorsi, 2016), (iii) apply the cross-combinations of genotype and phenotype (Cnaani et al., 2008), or (iv) analyse sex ratios from single-pair matings (Mair et al., 1991). For SSR data, it has been recommended to analyze the inheritance of sex-linked alleles by the sex-determining locus in linkage groups (Cnaani et al., 2008). With SNPs, data can be accurate by using perl script to analyse the sex-biased inheritance of parental SNPs (Furman & Evans, 2016).

Heterosis

Heterosis (hybrid vigour) in tilapias was described in a previously published paper (Amoussou et al., 2019). It is a non-locus-specific selective phenomenon affecting the whole genome equally. Heterosis most often has been scored in tilapia *Oreochromis* spp. because of the interest of these species in selective breeding programmes. In non-marker assisted selection, heterosis can be measured: (i) by comparing crossbred progenies with the average of the parental line/strain, or (ii) by comparing the crossbred progenies with the average of the better parental line/strain (Fjalestad, 2005). Other approaches include using Fisher's model to predict heterosis (Barton, 2001) and computing the least squares means (LSM) estimations (Tayamen et al., 2002). One can also determine the optimal inter-strain crosses when using SNP markers (Delomas et al., 2019). It was also advised to identify the ribosomal protein-related genes (Hedgecock et al., 2007) when using SNPs. One can also refer to the matings using sex-specific DNA markers (Chen et al., 2018).

Endogamy

Endogamy, most often equated with selfing or self-fertilization or sib-mating in view of their similar consequences, is a reproductive system in which related individuals mate. In fish, it can be achieved through selfing (in hermaphrodites) (Kanamori et al., 2006; 2016) and sib mating. Sib-mating occurs when individuals tend to prefer to mate with members of the same family. On the other hand, hermaphrodites can mate with each other and benefit from the advantages of sex by mixing their genes; however, when it is difficult to find partners, progeny may be produced from one individual that fertilizes its own ovules with its own spermatozoids (Bachtrog et al., 2014). The process of selfing or self-fertilization or sib-mating is an extreme form of inbreeding (mating between relatives), because in this case the mating is one's own self (Hartl & Clark, 2007). An endogamic system is known to increase associations between alleles (Stapley et al., 2017), as well as linkage between loci or linkage disequilibrium (De Meeûs et al., 2007). It leads to deficiency of heterozygous genotypes compared to that expected under panmixia (De Meeûs et al., 2007). It most often appears in plants and invertebrates (Thomas et al., 2010; Griffiths et al., 2013). In fish, selfing has been reported in the cyprinodonts *Rivulus marmoratus* (Schartl, 2004) and *Kryptolebias marmoratus* (Kanamori et al., 2006; 2016). It may occur in rainbow trout *Oncorhynchus mykiss* males (Chevassus et al., 1988) and *Clarias lazerea* (Liu & Yao, 1995) when hermaphrodites are induced. When siblings mate, the offspring of these crosses are more susceptible to be

homozygous for any locus and have a great risk for a hereditary disease (Griffiths et al., 2013). In fish strains, endogamy most often leads to low reproductive performance manifested as low growth rate, survival and fecundity (Garduno-Lugo et al., 2004; Neves et al., 2009) through inbreeding depression. F_{IS} can measures the probability that both alleles in an individual come from the same copy of a common ancestor (Griffiths et al., 2013) and thus may be a measure of the rate of endogamic matings in the population. Endogamic matings have been reported for tilapia species such as *Sarotherodon melanotheron* (Yoboué et al., 2012; Yoboue et al., 2014) and *Oreochromis niloticus* (Neves et al., 2009). It is a non-random union of gametes (e.g., from sib mating) affecting the genotypic distribution at all loci (all loci lose heterozygosity). This locus-specific technical issue is commonly evident at SSR markers (Table 1). Several approaches can be employed to assess endogamy in tilapia genetic data: computing the selfing rate (De Meeûs et al., 2007), sib mating rate (Amoussou et al., 2018), or kinship coefficient (Fessehaye et al., 2009). In addition, the software SPAGeDi (Hardy & Vekemans, 2002) can be used to compute the individual endogamy coefficient.

Inbreeding (Sib-mating)

Inbreeding increases homozygosity (Lenormand et al., 2016) in the whole genome without changing the respective allele frequencies (Nguyen et al., 2006). In fact, it increases numbers of recessive genotypes, which is often associated with decreased fitness known as inbreeding depression, in selective breeding programs (Neira et al., 2006; Oh, 2012) and in the wild. It refers to the probability that two randomly selected alleles from the same individual are identical by descent from a common ancestor (Balloux, 2004). Inbreeding depression is among the major problems encountered by fish genetic resources management (Amoussou et al., 2019; Pavlova et al., 2024), as its immediate repercussions are low-fitness (Bachtrog et al., 2014), low survival (Dunham, 2011), reduced fecundity (Osure & Phelps, 2006) and weak disease resistance (Nielsen et al., 2010). It may also cause greater deviation from expected sex ratios in tilapia culture (Abucay et al., 1999). In cichlid fishes, inbreeding opposes outbreeding that involves unfamiliar non-kin (Thunken et al., 2007). High inbreeding rates could thus be a driver of heterozygote deficit in tilapia accessions (Nyingi et al., 2009). In population genetics, for a hierarchy with three levels (individual, sub-population and total), the unbiased estimator of Wright's inbreeding coefficient F_{IS} estimates refer to relative inbreeding of individuals as compared to per-site inbreeding (Amoussou et al., 2018; Lind, 2009; Delomas et al., 2019) by testing whether it is significantly larger than zero. Here again in this hierarchy model, F_{IT} refers to the inbreeding of individuals resulting both from non-random union of gametes within demes and from population structure (De Meeûs et al., 2006).

Many random factors such as population size, limited dispersal, or active mate choice for relatives may favor inbreeding in cichlid fishes (Thunken et al., 2007). Effective population size (N_e) depends strongly on mating systems and has a direct relationship with inbreeding (Lind et al., 2012; Fessehaye, 2006; Ansah et al., 2014). Excessive inbreeding results in lower heritabilities due to reduced genetic variation (Ansah et al., 2014). In fact, if the size of any isolated population decreases, the rate of genetic drift increases, along with the rate of inbreeding, accumulation of detrimental genes, and loss of adaptive variation (Dudgeon et al., 2012). Heterozygosity-fitness correlations also can help to assess the impact of inbreeding in natural populations (Szulkin et al., 2010). Accordingly, high levels of genetic diversity in genetically improved farmed tilapia is required to prevent possible negative impacts of inbreeding (McKinna et al., 2010). On the other hand, inbreeding can be useful if reference is made to an increase in homozygous individuals for certain good genes (Dunham, 2011).

Many tilapia species usually have fecundity rate (ranging from 2000 to 8000) that can contribute to inbreeding and inbreeding depression (Amoussou et al., 2018; 2019). The pattern of shoaling behaviour in tilapias is suggested to contribute to direct inbreeding, implying preferential reproduction between related individuals (Bezault et al., 2011). To maintain a low level of inbreeding in mass selection programmes in aquaculture, it has been recommended to spawn at least 50 pairs of broodstock in each generation and to restrict or even standardize the number of tested progeny in each pair (Bentsen & Olesen, 2002). In fact, reducing the number of broodstock pairs might increase the rate of inbreeding to as much as 6–8% per generation (Bentsen & Olesen, 2002) and lead to changes in additive genetic variances (Ponzoni et al., 2013) by increasing the dominant and epistatic variances. Aquaculture stakeholders are advised that a continuous improvement of relevant traits requires a well-designed selective breeding program where the pedigree of broodfish is monitored to increase the accuracy of selection and to restrict inbreeding (WorldFish Center, 2004). In fact, the problem can be restricted by avoiding mating of full-sibs, half-sibs or cousins (Hamzah et al., 2014). Inbreeding has proven to be a genetic cause of sperm quality variation in fish (Gennotte et al., 2012), and genetic markers can contribute to monitoring and control (Davis & Hetzel, 2000). In well-designed breeding programs, this threat must be avoided as much as possible (Cross, 2000) by targeting a limited number of selection goals (Iversen et al., 2016). Diallel-cross mating within the base population followed by optimum contribution selection in subsequent generations can reduce the inbreeding to 0.5% per generation (Zenger et al., 2019).

Inbreeding is the most extensively documented non-locus specific problem in the three species (*Oreochromis* spp., *Sarotherodon* spp. and *Coptodon* sp.) of the tilapia group. With SSR data, there are a variety of software programs that can be used to assess inbreeding. These include FSTAT (Goudet, 2003), GENEPOP (Rousset, 2015), POPGENE (Yeh et al., 1999), IDENTIX (Belkhir et al., 2002), GenAlEx (Peakall & Smouse, 2012), POWERMARKER (Liu & Muse, 2005), GENETIX (Belkhir et al., 2004), diveRsity (Keenan et al., 2013), and GENODIVE (Meirmans, 2020) (Table 1). One may prefer testing deviations from HWE on the basis of the inbreeding coefficient using ARLEQUIN (Excoffier & Lischer, 2010). One also can apply the MCMC (Markov Chain Monte Carlo) Bayesian method (e.g., GENEPOP) (Ayres & Balding, 1998), or compute the per-generation rate of inbreeding (Falconer & Mackay, 1996). With SNP markers, there is a portfolio of tools including: ADEGENET (Jombart & Ahmed, 2011), STACKS (Catchen et al., 2013), STACKS-2 (Rochette et al., 2019), diveRsity (Keenan et al., 2013), VCFTOOLS (Danecek et al., 2011), and GENEPOP (Rousset, 2015) (Table 1). With QTLs, BLUP (Best Linear Unbiased Prediction) approaches can be employed for genetic evaluation to monitor inbreeding (Henderson, 1973). With mtDNA markers, performing a generalised skyline plot analysis to compute the inbreeding effective population size (Strimmer & Pybus, 2001), can be a good option. ARLEQUIN (Excoffier & Lischer, 2010) and GENIE (Pybus & Rambaut, 2002) programs also can be used when dealing with mtDNA markers. However, estimating an accurate inbreeding coefficient with standard binary AFLP data remains a challenge (Foll & Gaggiotti, 2008). It was nevertheless proposed to use Bayesian *F*-model to compute population-specific inbreeding coefficient (Foll et al., 2010) when using AFLP makers. For allozyme markers, GENEPOP (Rousset, 2015) and diveRsity (Keenan et al., 2013) can be used, while for RAPDs, POPGENE (Yeh et al., 1999) is preferred (Table 1).

Conclusions and Future Directions

This work provides technical guidance for geneticists working on fishes, particularly tilapia species, to make the appropriate choice of genetic marker and analytic approaches for their genetic investigations. The work also sheds light on the challenges related to the LTPs observable in the allelic and genotypic records of tilapias. It appears from the review that eleven molecular markers – i.e., allozymes, AFLPs, indels (insertions/deletions), SSRs, mtDNA, RAPDs, VNTRs, RFLPs, SNPs, ESTs and SSCPs (single-strand conformation polymorphisms), are commonly used for genetic analysis of tilapias. Several of these markers can display PCR amplification (genotyping) errors resulting potentially from mutations at priming sites (null alleles), or preferential amplification of short alleles (large allele dropout), or scoring of stutter peaks (stuttering), or typing error during data collection. Among these genetic markers, only eight (allozymes, ESTs, mtDNA, RAPDs, RFLPs, SNPs, SSRs, and VNTRs) have been investigated for LTPs in tilapias. In addition to these genotyping errors, several biological factors – such as the Wahlund effect, underdominance, overdominance, homogamy, heterogamy, heterosis, endogamy, inbreeding, and bottleneck – are known to affect the genetic analysis of tilapia. Many of these demographic and reproduction-related processes lead to introgressive hybridization by introducing genes from one species into the gene pool of another genetically related species. Most of these processes affect the whole genome equally: inbreeding (sib-mating), heterosis, Wahlund effect or genetic bottleneck. Like genotyping errors, many demographic or reproduction-related processes such as underdominance, overdominance, homogamy (assortative mating), heterogamy (disassortative mating), and endogamy are locus-specific. Indeed, the demographic changes affect all loci, whereas selection is expected to be locus-specific which can be distinguished if multiple loci are analyzed. It also appears from the review that SSR markers are more sensitive, i.e., easier to use than the other markers, in the detection of LTPs. Depending on their reliability, the data analyst can choose one tool or the other depending on the genetic marker in use. A critical perspective also can be brought to bear on the effectiveness and usefulness of the different approaches used to avoid unrecognized analysis of any selection-affected outlier loci in the genetic data. It will also be necessary to shed some light on the genomic basis and the genomic components (i.e., coding and non-coding genomic regions) underlying the LTPs that are related to both genotyping errors and biological factors.

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Author Contribution

The authors contributed equally to the work.

Conflict of 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.

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References

Aardema, M.L., Stiassny, M.L.J., & Alter, S.E. (2020).Genomic Analysis of the Only Blind Cichlid Reveals Extensive Inactivation in Eye and Pigment Formation Genes. Genome Biology and Evolution, 12(8), 1392–1406.

Abucay, J.S., Mair, G.C., Skibinski, D.O.F., & Beardmore, J.A. (1999). Environmental Sex Determination: The Effect of Temperature and Salinity on Sex Ratio in *Oreochromis niloticus* L. Aquaculture, 173 (1–4), 219–234.

Agnèse, J.F., Adépo-Gourène, B., Nyingi, D. (2009). Functional Microsatellite and Possible Selective Sweep in Natural Populations of the Black-Chinned Tilapia Sarotherodon melanotheron (Teleostei, Cichlidae). Marine Genomics, 1 (3–4), 103–107.

Ahmed, S.M., Hordofa, B., Meressa, B.H., Tamiru, M. (2023). Population structure and genetic diversity of Nile tilapia (*Oreochromis niloticus*) using microsatellite markers from selected water bodies in southwest Ethiopia. Veterinary Medicine and Science, 9(5), 2095-2106.

Amoussou, T.O., Dessouassi, C.E., Yong, D.N., Fagnon, S.M., Houngbe, L., Millogo, V., Imorou Toko, I., & Frimpong, E.A. (2022). The multifactorial aquaculture-related COVID-19 shock in Benin, West Africa: A socio-economic perspective of mitigating the disruptive impacts on the small-scale and subsistence producers. Aquaculture, Fish and Fisheries, 2(6), 507–521.

Amoussou, T.O., Filipe, A.F., Kunda, C.F., Yong Njé, D., Millogo, V., & Alhassan, E.H. (2021). Anticipating the Effects of Increasing Rivers' Water Salinity for Sustainable Conservation of Tilapia Resources in Rural Coastal Zone of Benin, West Africa. Tanzania Journal of Science, 47(5), 1890–1900.

Amoussou, T.O., Youssao Abdou Karim, I., Dayo, G.-K., Imorou Toko, I., Séré, M., Chikou, A., & Toguyéni, A. (2018). Genetic Characterization of Benin's Wild Populations of Sarotherodon melanotheron melanotheron Rüppell, 1852. Molecular Biology Reports, 45 (6), 1981–1994.

Amoussou, T.O., Youssao Abdou Karim, I., Dayo, G.-K., Kareem, N., Imorou Toko, I., Chikou, A., & Toguyeni, A. (2019). An Insight into Advances in Fisheries Biology, Genetics and Genomics of African Tilapia Species of Interest in Aquaculture. Aquaculture Reports, 14, 1–15.

Anane-Taabeah, G., Frimpong, E.A., & Hallerman, E. (2019). Aquaculture-Mediated Invasion of the Genetically Improved Farmed Tilapia (Gift) into the Lower Volta Basin of Ghana. Diversity, 11 (188), 1–23.

Ansah, Y.B., Frimpong, E.A., & Hallerman, E.M. (2014). Genetically-Improved Tilapia Strains in Africa: Potential Benefits and Negative Impacts. Sustainability, 6 (6), 3697–3721.

Armour, J.A.L., Crosier, M., & Jeffreys, A.J. (1996). Distribution of Tandem Repeat Polymorphism within Minisatellite MS621 (D5S110). Annals of Human Genetics, 60 (1), 11–20.

Ashman, T.-L., Bachtrog, D., Blackmon, H., Goldberg, E.E., Hahn, M.W., Kirkpatrick, M., Kitano, J., Mank, J.E., Mayrose, I., Ming, R., Otto, S.P., Peichel, C.L., Pennell, M.W., Perrin, N., Ross, L., Valenzuela, N.M., & Vamosi, J.C. (2014). Tree of sex: A database of sexual systems. Ecology, Evolution and Organismal Biology, 1, 1–8.

Ayres, K.L., & Balding, D.J. (1998). Measuring Departures from Hardy–Weinberg: A Markov Chain Monte Carlo Method for Estimating the Inbreeding Coefficient. Heredity, 80 (6), 769–777.

Bachtrog, D., Mank, J.E., Peichel, C.L., Kirkpatrick, M., Otto, S.P., Ashman, T.-L., Hahn, M. W., Kitano, J., Mayrose, I., Ming, R., Perrin, N., Ross, L., Valenzuela, N., & Vamosi, J.C. (2014). Sex determination: why so many ways of doing it? PLoS Biology, 12(7), 1–13.

Baldauf, S.A., Engqvist, L., Ottenheym, T., Bakker, T.C.M., & Thünken, T. (2013). Sex-specific conditional mating preferences in a cichlid fish: Implications for sexual conflict. Behavioral Ecology and Sociobiology, 67(7), 1179–1186.

Balloux, F. (2004). Heterozygote Excess in Small Populations and the Heterozygote-Excess Effective Population Size. Evolution, 58(9), 1891–1900.

Balloux, F., & Lugon-Moulin, N. (2002). The estimation of population differentiation with microsatellite markers. Molecular Ecology, 11(2), 155–165.

Bao, L., Tian, C., Liu, S., Zhang, Y., Elaswad, A., Yuan, Z., Khalil, K., Sun, F., Yang, Y., Zhou, T., Li, N., Tan, S., Zeng, Q., Liu, Y., Li, Y., Li, Y., Gao, D., Dunham, R., Davis, K., … & Liu, Z. (2019). The Y chromosome sequence of the channel catfish suggests novel sex determination mechanisms in teleost fish. BMC Biology, 17(6), 1–17.

Barasa, J. E., Abila, R., Grobler, J. P., Agaba, M., Chemoiwa, E. J., & Kaunda-Arara, B. (2016). High genetic diversity and population differentiation in Clarias gariepinus of Yala Swamp: evidence from mitochondrial DNA sequences. Journal of Fish Biology, 89(6), 2557–2570.

Barton, N.H. (2001). The role of hybridization in evolution. Molecular Ecology, 10(3), 551–568.

Barton, N.H., & Slatkin, M. (1986). A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. Heredity, 56, 409–415.

Bazin, E., Glemin, S., & Galtier, N. (2006). Population size does not influence mitochondrial genetic diversity in animals. Science, 312(570), 570–572.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N., & Bonhomme, F. (2004). GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations (4.05; p. 19). Montpellier, France: Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II.

Belkhir, K., Castric, V., & Bonhomme, F. (2002). IDENTIX, a software to test for relatedness in a population using permutation methods. Molecular Ecology Notes, 2, 611–614.

Benham, J., Jeung, J.-U., Jasieniuk, M., Kanazin, V., & Blake, T. (1999). Genographer: A Graphical Tool for Automated Fluorescent AFLP and Microsatellite Analysis. Journal of Agricultural Genomics, 4(3), 1–3.

Bentsen, H.B., & Olesen, I. (2002). Designing aquaculture mass selection programs to avoid high inbreeding rates. Aquaculture, 204(3–4), 349–359.

Bezault, E., Balaresque, P., Toguyeni, A., Fermon, Y., Araki, H., Baroiller, J.-F., & Rognon, X. (2011). Spatial and temporal variation in population genetic structure of wild Nile tilapia (*Oreochromis niloticus*) across Africa. BMC Genetics, 12(102), 1–16.

Bonin, A., Bellemain, E., Eidesen, P.B., Pompanon, F., Brochmann, C., & Taberlet, P. (2004). How to track and

assess genotyping errors in population genetics studies. Molecular Ecology, 13(11), 3261–3273.

Brookfield, J.F. (1996). A simple new method for estimating null allele frequency from heterozygote deficiency. Molecular Ecology, 5(3), 453–455.

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., & Madden, T., L. (2009). BLAST+: Architecture and applications. BMC Bioinformatics, 10(421), 1–9.

Campos-Ramos, R., Harvey, S.C., McAndrew, B.J., & Penman, D.J. (2003). An investigation of sex determination in the Mozambique tilapia, Oreochromis mossambicus, using synaptonemal complex analysis, FISH, sex reversal and gynogenesis. Aquaculture, 221(1–4), 125–140.

Carrillo, R.E., Aysal, T.C., & Barner, K.E. (2010). A Generalized Cauchy Distribution Framework for Problems Requiring Robust Behavior. Eurasip Journal on Advances in Signal Processing, 312989, 19.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A., & Cresko, W.A. (2013). Stacks: an analysis tool set for population genomics. Molecular Ecology, 22(11), 3124–3140.

Chapuis, M.P., & Estoup, A. (2007). Microsatellite null alleles and estimation of population differentiation. Molecular Biology and Evolution, 24(3), 621–631.

Chen, J., Fan, Z., Tan, D., Jiang, D., & Wang, D. (2018). A Review of genetic advances related to sex control and manipulation in Tilapia. Journal of World Aquaculture Society, 49(2), 277–291.

Chenuil, A. (2006). Choosing the right molecular genetic markers for studying biodiversity: from molecular evolution to practical aspects. Genetica, 127, 101–120.

Chevassus, B., Devaun, A., Chourrout, D., & Jalabert, B. (1988). Production of YY Rainbow Trout Males by Self-Fertilization of Induced Hermaphrodites. Journal of Heredity, 79(2), 89–92.

Chistiakov, D.A., Hellemans, B., & Volckaert, F.A.M. (2006). Microsatellites and their genomic distribution, evolution, function and applications: A review with special reference to fish genetics. Aquaculture, 255(1–4), 1–29.

Cnaani, A., Lee, B.Y., Zilberman, N., Ozouf-Costaz, C., Hulata, G., Ron, M., D'Hont, A., Baroiller, J.-F., D'Cotta, H., Penman, D.J., Tomasino, E., Coutanceau, J.-P., Pepey, E., Shirak, A., & Kocher, T.D. (2008). Genetics of Sex Determination in Tilapiine Species. Sexual Development, 2(1), 43–54.

Cornuet, J.M., Pudlo, P., Veyssier, J., Dehne-Garcia, A., Gautier, M., Leblois, R., Marin, J.-M., & Estoup, A. (2014). DIYABC v2.0: a software to make approximate Bayesian computation inferences about population history using single nucleotide polymorphism, DNA sequence and microsatellite data. Bioinformatics, 30(8), 1187–1189.

Cournet, J., & Luikart, G. (1996). Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics, 144(4), 2001–2014.

Cross, T.F. (2000). Genetic implications of translocation and stocking of fish species, with particular reference to Western Australia. Aquaculture Research, 31(1), 83–94.

Crow, J.F. (2008). Mid-Century Controversies in Population Genetics. Annual Review of Genetics, 42, 1–16.

Dabrowski, M.J., Pilot, M., Kruczyk, M., Zmihorski, M., Umer, H.M., & Gliwicz, J. (2014). Reliability assessment of null allele detection: inconsistencies between and within different methods. Molecular Ecology Resources, 14(2), 361–373.

Dakin, E.E., & Avise, J.C. (2004). Microsatellite null alleles in parentage analysis. Heredity, 93(5), 504–509.

Danecek, P., Auton, A., Abecasis, G., Albers, C.A., Banks, E., DePristo, M.A., Handsaker, R.E., Lunter, G., Marth, G.T., Sherry, S.T., McVean, G., & Durbin, R. (2011). The variant call format and VCFtools. Bioinformatics, 27(15), 2156–2158.

Davis, G.P., & Hetzel, D.J.S. (2000). Integrating molecular genetic technology with traditional approaches for genetic improvement in aquaculture species. Aquaculture, Research 31(1), 3–10.

Delomas, T.A., Gomelsky, B., Vu, N., Campbell, M.R., & Novelo, N.D. (2019). Single-Nucleotide Polymorphism Discovery and Genetic Variation in YY- Male and Mixed-Sex Strains of Nile Tilapia Available in the United States. North American Journal of Aquaculture, 81(3), 1–6.

De Meeûs, T. (2018). Revisiting FIS, FST, Wahlund effects and null alleles. Journal of Heredity, 109(4), 446–456.

De Meeûs, T., Humair, P.F., Grunau, C., Delaye, C., & Renaud, F. (2004). Non-Mendelian transmission of alleles at microsatellite loci: An example in Ixodes ricinus, the vector of Lyme disease. International Journal for Parasitology, 34(8), 943–950.

De Meeûs, T., Lehmann, L., & Balloux, F. (2006). Molecular epidemiology of clonal diploids: A quick overview and a short DIY (do it yourself) notice. Infection, Genetics and Evolution, 6(2), 163–170.

De Meeûs, T., McCoy, K.D., Prugnolle, F., Chevillon, C., Durand, P., Hurtrez-Boussès, S., & Renaud, F. (2007). Population genetics and molecular epidemiology or how to "débusquer la bête." Infection, Genetics and Evolution, 7(2), 308–332.

De Santis, M.D. (2024). Homoplasy as an Evolutionary Process: An Optimistic View on the Recurrence of Similarity in Evolution. Biological Theory, 19, 267–278.

Devlin, R.H., & Nagahama, Y. (2002). Sex determination and sex differentiation in fish: An overview of genetic, physiological, and environmental influences. Aquaculture, 208(3–4), 191–364.

Dudgeon, C.L., Blower, D.C., Broderick, D., Giles, J.L., Holmes, B.J., Kashiwagi, T., Krück, N.C., Morgan, J.A.T., Tillett, B.J., & Ovenden, J.R. (2012). A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. Journal of Fish Biology, 80(5), 1789–1843.

Dudgeon, C.L., Coulton, L., Bone, R., Ovenden, J.R., & Thomas, S. (2017). Switch from sexual to parthenogenetic reproduction in a zebra shark. Scientific Reports, 7, 1–6.

Du, J., Liu, Q., & Zheng, Y. (2023). Screening and characterization of sex-specific sequences through 2b-RAD sequencing in American shad (Alosa sapidissima). PLoS ONE 18(3), 1-12.

Dunham, R.A. (2011). Aquaculture and fisheries biotechnology - Genetic approaches. Alabama, USA: Centre for Agriculture and Bioscience International (CABI).

Ellegren, H., & Galtier, N. (2016). Determinants of genetic diversity. Nature Reviews Genetics, 17, 422–433.

Espinosa-Lemus, V., Arredonto-Figueroa, J.L., & Barriga-Sosa, I.A. (2009). Morphometric and genetic characterization of tilapia (Cichlidae: Tilapiini) stocks for effective fisheries management in two mexican reservoirs. Hidrobiologica, 19(2), 95–107.

Estoup, A., Tailliez, C., Cornuet, J.M., & Solignac, M. (1995).

Size homoplasy and mutational processes of interrupted microsatellites in two bee species, Apis mellifera and Bombus terrestris (Apidae). Molecular Biology and Evolution, 12(6), 1074–1084.

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(3), 564–567.

Falconer, D.S., & Mackay, T.F.C. (1996). Introduction to quantitative genetics. 4th ed. Prentice Hall, Harlow: Oliver & Boyd, Edinburgh & London.

Falush, D., Stephens, M., & Pritchard, J. (2003). Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics*, 164(4), 1567–1587.

FAO (2020). The State of World Fisheries and Aquaculture 2020. Sustainability in Action. Food and Agriculture Organization of the United Nations: Rome, Italy.

FAO (2024). The State of World Fisheries and Aquaculture 2024. Blue Transformation in action. Food and Agriculture Organization of the United Nations: Rome, Italy.

Fatsi, P.S.K., Hashem, S., Kodama, A., Appiah, E.K., Saito, H., & Kawai, K. (2020). Population genetics and taxonomic signatures of wild Tilapia in Japan based on mitochondrial DNA control region analysis. *Hydrobiologia* 847, 1491–1504.

Feller, A.F., Selz, O.M., McGee, M.D., Meier, J.I., Mwaiko, S., & Seehausen, O. (2020). Rapid generation of ecologically relevant behavioral novelty in experimental cichlid hybrids. *Ecology and Evolution*, 10(14):7445–7462.

Ferguson, A., Taggart, J.B., Prodohl, P.A., Mcmeel, O., Thompson, C., Stone, C., Mcginnity, P., & Hynes, R.A. (1995). The application of molecular markers to the study and conservation of fish populations, with special reference to Salmo. *Journal of Fish Biology*, 47(sA), 103–126.

Fessehaye, Y. (2006). Natural mating in Nile tilapia (*Oreochromis niloticus* L.): implications for reproductive success, inbreeding and cannibalism. PhD Thesis, Wageningen University.

Fessehaye, Y., Bovenhuis, H., Rezk, M.A., Crooijmans, R., van Arendonk, J.A.M., & Komen, H. (2009). Effects of relatedness and inbreeding on reproductive success of Nile tilapia (*Oreochromis niloticus*). *Aquaculture*, 294(3–4), 180–186.

Firmat, C., Alibert, P., Losseau, M., Baroiller, J. F., & Schliewen, U.K. (2013). Successive Invasion-Mediated Interspecific Hybridizations and Population Structure in the Endangered Cichlid *Oreochromis mossambicus*. *PLoS ONE*, 8(5), 1–12.

Fischer, C., Koblmüller, S., Börger, C., Michelitsch, G., Trajanoski, S., Schlötterer, C., Guelly, C., Thallinger, G.G., & Sturmbauer, C. (2021). Genome sequences of *Tropheus moorii* and *Petrochromis trewavasae*, two co-morphologically divergent cichlid fishes endemic to Lake Tanganyika. *Scientific Reports*, 11, 1-22.

Fjalestad, K.T. (2005). Breeding Strategies. In Selection and Breeding Programs in Aquaculture. Springer Netherlands, 145–158.

Foll, M., Fischer, M.C., Heckel, G., & Excoffier, L. (2010). Estimating population structure from AFLP amplification intensity. *Molecular Ecology*, 19(21), 4638–4647.

Foll, M., & Gaggiotti, O. (2008). A Genome-Scan Method to Identify Selected Loci Appropriate for Both Dominant and Codominant Markers: A Bayesian Perspective. *Genetics* ,180(2), 977–993.

Fowler, B.L.S., & Buonaccorsi, V.P. (2016). Genomic characterization of sex-identification markers in *Sebastes carnatus* and *Sebastes chrysomelas* Rockfishes. *Molecular Ecology*, 25(10), 2165–2175.

Fujio, Y. (1984). Study on genetic characteristics of fish and shelfishes in isozymic analysis. *Nosuisho Tokubetsu Shiken*, 1–65.

Furman, B.L.S., & Evans, B.J. (2016). Sequential Turnovers of Sex Chromosomes in African Clawed Frogs (*Xenopus*) Suggest Some Genomic Regions are Good at Sex Determination. *Genes, Genomes and Genomics*, 6, 3625–3633.

Galtier, N., Jobson, R.W., Nabholz, B., Glémin, S., & Blier, P.U. (2009). Mitochondrial whims: metabolic rate, longevity and the rate of molecular evolution. *Biology Letters*, 5(3), 413–416.

Geraerts, M., Vangestel, C., Artois , T., de Oliveira Fernandes, J.M., Jorissen, M.W.P., Manda, A.C., Mizani, C.D., Smeets, K., Snoeks, J., Sonet, G., Tingbao, Y., Steenberge, M.V., Vreven, E., Wamuini, S.L., Vanhove,M.P.M., & Huyse, T. (2022). Population genomics of introduced Nile tilapia (*Oreochromis niloticus* (Linnaeus, 1758)) in the Democratic Republic of the Congo: Repeated introductions since colonial times with multiple sources. *Molecular Ecology*, 31(12), 3304-3322.

Garduno-Lugo, M., Munoz-Cordova, G., & Olvera-Novoa, M.A. (2004). Mass selection for red colour in *Oreochromis niloticus* (Linnaeus 1758). *Aquaculture Research*, 35(4), 340–344.

Garza, J.C., & Williamson, E.G. (2001). Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology*, 10(2), 305–318.

Gennotte, V., François, E., Rougeot, C., Ponthier, J., Deleuze, S., & Mélard, C. (2012). Sperm quality analysis in XX, XY and YY males of the Nile tilapia (*Oreochromis niloticus*). *Theriogenology*, *78*(1), 210–217.

Gerber, A.S., Loggins, R., Kumar, S., & Dowling, T.E. (2001). Does nonneutral evolution shape observed patterns of DNA variation in animal mitochondrial genomes? *Annual Review of Genetics*, 35, 539–566.

Goudet, J. (2003). FSTAT (version 2.9.4), a program (for Windows 95 and above) to estimate and test population genetics parameters (2.9.4; p. 53). Department of Ecology & Evolution, Lausanne University, Switzerland.

Griffiths, A.J.F., Wessler, S.R., Carroll, S.B., & Doebley, J. (2013). Introduction à l'analyse génétique (6th ed.). 6th ed. Paris et Bruxelles: De Boeck.

Hallerman, E., & Hilsdorf, A.W.S. (2014). Conservation genetics of tilapias: Seeking to define appropriate units for management. *The Israeli Journal of Aquaculture - Bamidgeh*, 66, 2–19.

Hamzah, A., Ponzoni, R.W., Nguyen, N.H., Khaw, H.L., Yee, H.Y., & Mohd Nor, S.A. (2014). Performance of the genetically improved farmed tilapia (GIFT) strain over ten generations of selection in Malaysia. *Pertanika Journal of Tropical Agricultural Science*, 37(4), 411–429.

Hardy, O.J., & Vekemans, X. (2002). spagedi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes*, 2, 618–620.

Harpending, H.C. (2013). Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Human Biology*, 66(4), 591–600.

Hartl, D.L., & Clark, A.G. (2007). Principles of population genetics (4th ed.). 4th ed. Sunderland, MA, USA: Sinauer Associates.

Hassanien, H.A., & Gilbey, J. (2005). Genetic diversity and differentiation of Nile tilapia (*Oreochromis niloticus*) revealed by DNA microsatellites. *Aquaculture Research*, 36(14), 1450–1457.

Haubold, B., & Wiehe, T. (2006). Introduction to computational biology - An evolutionary approach. Basel - Boston - Berlin: Birkhäuser Verlag.

Hedgecock, D., Lin, J.Z., DeCola, S., Haudenschild, C.D., Meyer, E., Manahan, D.T., & Bowen, B. (2007). Transcriptomic analysis of growth heterosis in larval Pacific oysters (*Crassostrea gigas*). *Proceedings of the National Academy of Sciences of the United States of America*, 104(7), 2313–2318.

Henderson, C.R. (1973). Sire evaluation and genetic trends. Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr Jay L Lush, Champaign, IL, 10–41. Champaign, IL: American Society of Animal Science.

Henning, F., Lee, H. J., Franchini, P., & Meyer, A. (2014). Genetic mapping of horizontal stripes in Lake Victoria cichlid fishes: benefits and pitfalls of using dense linkage mapping in non-model organisms. *Molecular Ecology*, 23(21), 5224–5240.

Hilsdorf, A.W., & Hallerman, E.M. (2021). Tilapia Genetic Resources: Conservation and Use for Aquaculture. In J. F. López-Olmeda, F. J. Sánchez-Vázquez, & R. Fortes-Silva (Eds.), Biology and Aquaculture of Tilapia. CRC Press.

Hoey, J.A., Able, K.W., & Pinsky, M.L. (2022). Genetic decline and recovery of a demographically rebuilt fishery species. *Molecular Ecology*, 31(22), 5684-5698.

Iversen, M., Myhr, A.I., & Wargelius, A. (2016). Approaches for delaying sexual maturation in salmon and their possible ecological and ethical implications. *Journal of Applied Aquaculture*, 4438, 1–74.

Jombart, T., & Ahmed, I. (2011). adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics*, 27(21), 3070–3071.

Joshi, R., Árnyasi, M., Lien, S., Gjøen, H.M., Alvarez, A.T., & Kent, M. (2018). Development and validation of 58K SNP-array and high-density linkage map in Nile tilapia (*O. niloticus*). *Frontiers in Genetics*, 9(472), 1–15.

Kanamori, A., Sugita, Y., Yuasa, Y., Suzuki, T., Kawamura, K., Uno, Y., Kamimura, K., Matsuda, Y., Wilson, C. A., Amores, A., Postlethwait, J. H., Suga, K., & Sakakura, Y. (2016). A Genetic Map for the Only Self-Fertilizing Vertebrate. *Genes|Genomes|Genetics*, 6(4), 1095–1106.

Kanamori, A., Yamamura, A., Koshiba, S., Lee, J.-S., Orlando, E.F., & Hori, H. (2006). Methyltestosterone Efficiently Induces Male Development in the Self-Fertilizing Hermaphrodite Fish, *Kryptolebias marmoratus*. *Genesis*, 44(10), 495–503.

Kariuki, J., Tibihika, P.D., Curto, M., Alemayehu, E., Winkler, G. & Meimberg, H. (2021). Application of microsatellite genotyping by amplicon sequencing for delimitation of African tilapiine species relevant for aquaculture. Aquaculture, 537, 1-9.

Karlsson, S., & Mork, J. (2005). Deviation from Hardy-Weinberg equilibrium, and temporal instability in allele frequencies at microsatellite loci in a local population of Atlantic cod. *ICES Journal of Marine Science*, 62(8), 1588–1596.

Kavembe, G.D., Machado-Schiaffino, G., & Meyer, A. (2014). Pronounced genetic differentiation of small, isolated and fragmented tilapia populations inhabiting the Magadi Soda Lake in Kenya. *Hydrobiologia*, 739(1), 55–71.

Keenan, K., Mcginnity, P., Cross, T.F., Crozier, W.W., & Prodöhl, P.A. (2013). diveRsity: An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, 4(8), 782–788.

Kocher, T.D., Fernald, R., Hoffman, H., Meyer, A., Okada, N., Penman, D., Seehausen, O., & Baroiller, J.F. (2005). Genome Sequence of a Cichlid Fish: the Nile Tilapia (*Oreochromis niloticus*). Cichlid Genome Consortium.

Kosswig, C. (1963). Ways of Speciation in Fishes. *Copeia* 1963(2), 238–244.

Ky, C.-L., Vergnet, A., Molinari, N., Fauvel, C., & Bonhomme, F. (2012). Fitness of early life stages in F1 interspecific hybrids between *Dicentrarchus labrax* and *D. punctatus*. *Aquatic Living Resources*, 25(1), 67–75.

Landínez-García, R.M., Narváez, J.C., & Márquez, E.J. (2020). Population genetics of the freshwater fish *Prochilodus magdalenae* (Characiformes: Prochilodontidae), using species-specific microsatellite loci. *PeerJ*, 8(e10327), 1–26.

Laroche, J., Durand, J.D., Bouvet, Y., Guinand, B., & Brohon, B. (1999). Genetic structure and differentiation among populations of two cyprinids, *Leuciscus cephalus* and *Rutilus rutilus*, in a large European river. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(9), 1659–1667.

Larsson, L.C., Laikre, L., Palm, S., André, C., Carvalho, G.R., & Ryman, N. (2007). Concordance of allozyme and microsatellite differentiation in a marine fish, but evidence of selection at a microsatellite locus. *Molecular Ecology*, 16, 1135–1147.

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, 25(1), 1–18.

Lemaire, C., Allegrucci, G., Naciri, M., Bahri-Sfar, L., Kara, H., & Bonhomme, F. (2000). Do discrepancies between microsatellite and allozyme variation reveal differential selection between sea and lagoon in the sea bass (*Dicentrarchus labrax*)? *Molecular Ecology*, 9(4), 457–467.

Lenormand, T., Engelstädter, J., Johnston, S.E., Wijnker, E., & Haag, C.R. (2016). Evolutionary mysteries in meiosis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 1–14.

Leroy, B., Dias, M.S., Giraud, E., Hugueny, B., Jézéquel, C., Leprieur, F., Oberdorff, T., & Tedesco, P.A. (2019). Global biogeographical regions of freshwater fish species. *Journal of Biogeography*, 46(11), 2407–2419.

Librado, P., & Rozas, J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25(11), 1451–1452.

Lind, C.E. (2009). Population genetics, phylogeography and the effects of aquaculture on genetic diversity of the silver-lipped pearl oyster, Pinctada maxima (Jameson). James Cook University.

Lind, C.E., Brummett, R.E., & Ponzoni, R.W. (2012). Exploitation and conservation of fish genetic resources in Africa: issues and priorities for aquaculture development and research. *Reviews in Aquaculture*, 4(3), 125–141.

Liu, K., & Muse, S.V. (2005). PowerMarker: an integrated analysis environment for genetic marker analysis. *Bioinformatics*, 21(9), 2128–2129.

Liu, Q., Cui, F., Hu, P., Yi, G., Ge, Y., Liu, W., Yan, H., Wang, L., Liu, H., Song, J., Jiang, Y., Zhang, L., & Tu, Z. (2018). Using of microsatellite DNA profiling to identify hatchery-reared seed and assess potential genetic risks associated with large-scale release of swimming crab *Portunus trituberculatus* in Panjin, China. *Fisheries Research*, 207, 187–196.

Liu, S., & Yao, Z. (1995). Self-fertilization of hermaphrodites of the teleost *Clarias lazerea* after oral administration of 17-α-methyltestosterone and their offspring. *The Journal of Experimental Zoology*, 273(6), 527–532.

Liu, Z.J. (2007). Aquaculture Genome Technologies. 1st ed. Vol. 1. Iowa, USA: Blackwell.

Liu, Z.J., & Cordes, J.F. (2004). DNA marker technologies and their applications in aquaculture genetics. *Aquaculture*, 238(1–4), 1–37.

Lowe-McConnell, R.H. (1991). Ecology of cichlids in South American and African waters, excluding the African Great Lakes. In M. H. A. Keenleyside (Ed.), Cichlid Fishes – Behavior, Ecology and Evolution, 60–85. London, UK: Chapman & Hall.

Luo, K., Xiao, J., Liu, S., Wang, J., He, W., Hu, J., Qin, Q., Zhang, C., Tao, M., & Liu, Y. (2011). Massive production of all-female diploids and triploids in the crucian carp. *International Journal of Biological Sciences*, 7(4), 487–495.

Maes, G.E., Raeymaekers, J.A.M., Pampoulie, C., Seynaeve, A., Goemans, G., Belpaire, C., & Volckaert, F.A.M. (2005). The catadromous European eel *Anguilla anguilla* (L.) as a model for freshwater evolutionary ecotoxicology: Relationship between heavy metal bioaccumulation, condition and genetic variability. *Aquatic Toxicology*, 73(1), 99–114.

Mahboob, S., Al-Ghanim, K.A., Al-Misned, F., Al-Balawi, H.F.A., Ashraf, A., & Al-Mulhim, N.M.A. (2019). Genetic diversity in tilapia populations in a freshwater reservoir assayed by randomly amplified polymorphic DNA markers. *Saudi Journal of Biological Sciences*, 26(2), 363–367.

Mair, G.C., Scott, A.G., Penman, D.J., Beardmore, J.A., & Skibinski, D.O.F. (1991). Sex determination in the genus Oreochromis: Sex reversal, gynogenesis and triploidy in *O. niloticus* (L.). *Theoretical and Applied Genetics*, 82(2), 144–152.

Manangwa, O., De Meeûs, T., Grébaut, P., Ségard, A., Byamungu, M., & Ravel, S. (2019). Detecting Wahlund effects together with amplification problems: cryptic species, null alleles and short allele dominance in *Glossina pallidipes* populations from Tanzania. *Molecular Ecology Resources*, 19, 757–772.

Mawaribuchi, S., Takahashi, S., Wada, M., Uno, Y., Matsuda, Y., Kondo, M., Fukui, A., Takamatsu, N., Taira, M., & Ito, M. (2017). Sex chromosome differentiation and the W- and Z-specific loci in *Xenopus laevis*. *Developmental Biology*, 426(2), 393–400.

McKinna, E.M., Nandlal, S., Mather, P.B., & Hurwood, D.A. (2010). An investigation of the possible causes for the loss of productivity in genetically improved farmed tilapia strain in Fiji: Inbreeding versus wild stock introgression. *Aquaculture Research*, 41(11), e730–e742.

Meirmans, P.G., & Hedrick, P.W. (2011). Assessing population structure: FST and related measures. *Molecular Ecology Resources*, 11(1), 5–18.

Meirmans, P.G. (2020). GENODIVE version 3.0: Easy-to-use software for the analysis of genetic data of diploids and polyploids. *Molecular Ecology Resources*, 20(4), 1126–1131.

Miller, C.R., Joyce, P., & Waits, L.P. (2002). Assessing Allelic Dropout and Genotype Reliability Using Maximum Likelihood. *Genetics*, 160, 357–366.

Miller, L.M., Close, T., & Kapuscinski, A.R. (2004). Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. *Molecular Ecology*, 13(11), 3379–3388.

Moradi, A., & Keyvanshokooh, S. (2013). Microsatellite DNA marker in aquatic organisms. *Scientific Journal of Biological Sciences*, 2(9), 184–189.

Morelos-Castro, R.M., Aparicio-Simón, B., García-Morales, R., Cruz-Hernández, P., Campos-Ramos, R., Espinosa-Chaurand, D., Garza-Torres, R., & Maeda-Martínez, A.N. (2024). Exploring the presence of tilapia species in a central western Mexican reservoir using mitochondrial DNA control region sequencing. *Latin american journal of aquatic research*, 52(4), 575-585.

Nehemia, A., & Umbayda, T. (2024). The current population genetic status of *Oreochromis niloticus* (Linnaeus, 1758) along the Malagarasi River, Tanzania. *Ecological Genetics and Genomics*, 33, 1-3.

Neira, R., Díaz, N.F., Gall, G.A.E., Gallardo, J.A., Lhorente, J.P., & Manterola, R. (2006). Genetic improvement in Coho salmon (*Oncorhynchus kisutch*). I: Selection response and inbreeding depression on harvest weight. *Aquaculture*, 257(1–4), 9–17.

Neves, P.R., Natali, M.R.M., Ribeiro, R.P., Vargas, L., Maehana, K.R., & Marengoni, N.G. (2009). Morphological characteristics of ovarian development of two Nile tilapia (*Oreochromis niloticus*) strains in mixed-culture systems. *Arquivo Brasileiro de Medicina Veterinária e Zootecnia*, 61(5), 1173–1182.

Nguyen, T., Hurwood, D., Mather, P., Na-Nakorn, U., Komonrat, W., & Bartley, D. (2006). Manual on application of molecular tools in aquaculture and inland fisheries management - Part 2: Laboratory protocols and data analysis. Bangkok, Thailand: NACA.

Nielsen, E.E., Hansen, M.M., & Loeschcke, V. (1997). Analysis of microsatellite DNA from old scale samples of Atlantic salmon Salmo salar: a comparison of genetic composition over 60 years. *Molecular Ecology*, 6(5), 487–492.

Nielsen, H.M., Ødegård, J., Olesen, I., Gjerde, B., Ardo, L., Jeney, G., & Jeney, Z. (2010). Genetic analysis of common carp (*Cyprinus carpio*) strains. I: Genetic parameters and heterosis for growth traits and survival. *Aquaculture*, 304(1–4), 14–21.

Nikolic, N., Butler, J.R.A., Baglinière, J.-L., Laughton, R., McMyn, I.A.G., & Chevalet, C. (2009). An examination of genetic diversity and effective population size in Atlantic salmon populations. *Genetics Research*, 91(6), 395–412.

Nomura, T. (2008). Estimation of effective number of breeders from molecular coancestry of single cohort sample. *Evolutionary Applications*, 1(3), 462–474.

Nyingi, D., De Vos, L., Aman, R., & Agnèse, J.F. (2009). Genetic characterization of an unknown and endangered native population of the Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) (Cichlidae; Teleostei) in the Loboi Swamp (Kenya). *Aquaculture*, 297(1–4), 57–63.

O'Connell, M., & Wright, J.M. (1997). Microsatellite DNA in fishes. *Reviews in Fish Biology and Fisheries*, 7, 331–363.

O'Reilly, P., & Wright, J.M. (1995). The evolving technology of DNA fingerprinting and its application to fisheries and

aquaculture. *Journal of Fish Biology*, 47, 29–55.

Oh, S.H. (2012). Evaluation of optimum genetic contribution theory to control inbreeding while maximizing genetic response. *Asian-Australasian Journal of Animal Sciences*, 25(3), 299–303.

Ohta, T., & Kimura, M. (1970). Development of associative overdominance through linkage disequilibrium in finite populations. *Genetical Research*, 16(2), 165–177.

Osure, G.O., & Phelps, R.P. (2006). Evaluation of reproductive performance and early growth of four strains of Nile tilapia (*Oreochromis niloticus*, L) with different histories of domestication. *Aquaculture*, 253(1–4), 485–494.

Papadopoulou, A., Anastasiou, I., & Vogler, A.P. (2010). Revisiting the insect mitochondrial molecular clock: The mid-aegean trench calibration. *Molecular Biology and Evolution*, 27(7), 1659–1672.

Pavlova, A., Schneller, N.M., Lintermans, M., Beitzel, M., Robledo-Ruiz, D.A., & Sunnucks, P. (2024). Planning and implementing genetic rescue of an endangered freshwater fish population in a regulated river, where low flow reduces breeding opportunities and may trigger inbreeding depression. *Evolutionary Applications*, 17(4), 1-20.

Peakall, R., & Smouse, P.E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics*, 28(19), 2537–2539.

Piry, S., Luikart, G., & Cornuet, J.-M. (1999). BOTTLENECK: A program for detecting recent effective population size reductions from allele data frequencies. Montpellier Cedex, France: INRA.

Pompanon, F., Bonin, A., Bellemain, E., & Taberlet, P. (2005). Genotyping errors: causes, consequences and solutions. *Nature Reviews. Genetics*, 6(11), 847–859.

Ponzoni, R.W., James, J.W., Nguyen, N.H., Mekkawy, W., & Khaw, H.L. (2013). Strain comparisons in aquaculture species: a manual. Penang, Malaysia: CGIAR.

Ponzoni, R.W., Nguyen, N.H., & Khaw, H.L. (2009). Genetic Improvement Programs for Aquaculture Species in Developing Countries: Prospects and Challenges. Proceedings of the 18th Conference of the Association for the Advancement of Animal Breeding and Genetics, 342–349.

Pybus, O.G., & Rambaut, A. (2002). GENIE: estimating demographic history from molecular phylogenies. *Bioinformatics*, 18(10), 1404–1405.

Recino-Reyes, E.B., Lesher-Gordillo, J.M., Machkour-M'Rabet, S., Gallardo-Alvarez, M.I., Zenteno-Ruiz, C.E., Olivera-Gómez, L.D., Valdés-Marín, A., Gómez-Carrasco, G., Ríos-Rodas, L., Barragán-Vázquez, M.D.R., & Martínez, R.H. (2020). Conservation and Management of *Trachemys venusta venusta* in Southern Mexico: A Genetic Approach. *Tropical Conservation Science*, 13, 1–20.

Rochette, N.C., Rivera-Colón, A.G., & Catchen, J.M. (2019). Stacks 2: Analytical methods for paired-end sequencing improve RADseq-based population genomics. *Molecular Ecology*, 28(21), 4737–4754.

Romana-Eguia, M.R.R., Ikeda, M., Basiao, Z.U., & Taniguchi, N. (2004). Genetic diversity in farmed Asian Nile and red hybrid tilapia stocks evaluated from microsatellite and mitochondrial DNA analysis. *Aquaculture*, 236(1–4), 131–150.

Rousset, F., 2015. Genepop 4.4 for Windows/Linux/Mac OS X. Laboratoire Génétique et Environnement.

RStudio Team 2020. RStudio: Integrated Development for R. version 1.2.5019. Boston, MA:RStudio, Inc.

Schartl, M. (2004). Sex chromosome evolution in non-mammalian vertebrates. *Current Opinion in Genetics and Development*, 14(6), 634–641.

Scribner, K.T., Page, K.S., & Bartron, M.L. (2001). Hybridization in freshwater fishes: a review of case studies and cytonuclear methods of biological inference. *Reviews in Fish Biology and Fisheries*, 10(3), 293–323.

Seehausen, O. (2004). Hybridization and adaptive radiation. *Trends in Ecology and Evolution*, 19(4), 198–207.

Sekar, M., Suresh, E., Kumar, N.S., Nayak, S.K., & Balakrishna, C. (2009). Microsatellite DNA Markers, a Fisheries Perspective Part 1: The Nature of Microsatellites. Bangkok, Thailand: Aquaculture Asia Magazine.

Séré, M., Kaboré, J., Jamonneau, V., Belem, A.M.G., Ayala, F.J., & De Meeûs, T. (2014). Null allele, allelic dropouts or rare sex detection in clonal organisms: simulations and application to real data sets of pathogenic microbes. *Parasites & Vectors*, 7(331), 1–13.

Simbine, L., Viana da Silva, J., & Hilsdorf, A.W.S. (2014). The genetic diversity of wild *Oreochromis mossambicus* populations from the Mozambique southern watersheds as evaluated by microsatellites. *Journal of Applied Ichthyology*, 30(2), 272–280.

Singh, P., Ahi, E.P., & Sturmbauer, C. (2021). Gene coexpression networks reveal molecular interactions underlying cichlid jaw modularity. *BMC Ecology and Evolution*, 21(62), 1-17.

Stapley, J., Feulner, P.G.D., Johnston, S.E., Santure, A.W., & Smadja, C.M. (2017). Variation in recombination frequency and distribution across eukaryotes: patterns and processes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 1–18.

Strimmer, K., & Pybus, O.G. (2001). Exploring the Demographic History of DNA Sequences Using the Generalized Skyline Plot. *Molecular Biology and Evolution*, 18(12), 2298–2305.

Svardal, H., Salzburger, W., & Malinsky, M. (2021). Genetic Variation and Hybridization in Evolutionary Radiations of Cichlid Fishes. *Annual Review of Animal Biosciences*, 9, 55–79.

Swofford, D.L. (1991). Phylogenetic Analysis Using Parsimony (PAUP), version 3.0 for Macintosh computers. Champaign, USA: Illinois Natural History Survey.

Swofford, D.L. (2000). PAUP* (Phylogenetic Analysis Using Parsi- mony, version 4.0b8a). Sunderland, MA, USA: Sinauer Associates.

Szulkin, M., Bierne, N., & David, P. (2010). Heterozygosity-fitness correlations: A time for reappraisal. *Evolution*, 64(5), 1202–1217.

Tayamen, M.M., Reyes, R.A., Danting, M.J., Mendoza, A.M., Marquez, E.B., Salguet, A.C., Gonzales, R.C., Abella, T.A., & Vera-Cruz, E.M. (2002). Tilapia Broodstock Development for Saline Waters in the Philippines. The ICLARM Quarterly 25(1), 32–38.

Thomas, F., Lefèvre, T., & Raymond, M. (2010). Biologie évolutive. Edited by De Boeck. First Edit.

Thunken, T., Bakker, T.C., Baldauf, S.A., & Kullmann, H. (2007). Active inbreeding in a Cichlid fish and its adaptive significance. *Current Biology*, 17, 225–229.

Tibihika, P.D., Curto, M., Alemayehu, E., Waidbacher, H., Masembe, C., Akoll, P., & Meimberg, H. (2020). Molecular genetic diversity and differentiation of Nile tilapia (*Oreochromis niloticus*, L. 1758) in East African natural and stocked populations. *BMC Evolutionary*

Biology, 20(16), 1–20.

Tibihika, P.D., Curto, M., Dornstauder-Schrammel, E., Winter, S., Alemayehu, E., Waidbacher, H., & Meimberg, H. (2018). Application of microsatellite genotyping by sequencing (SSR-GBS) to measure genetic diversity of the East African *Oreochromis niloticus*. *Conservation Genetics*, 20, 357–372.

Tibihika, P.D., Aruho, C., Namulawa, V., Ddungu, R., Atukunda, G., Aanyu, M., Nkambo, M., Vijayan, T., Kwikiriza, G., Curto, M., & Meimberg, H. (2024). Unlocking Nile tilapia (*Oreochromis niloticus* Linn., 1758) selective breeding programmes in Uganda through geographical genetic structure mapping. *Aquaculture, Fish and Fisheries*, 4(4), 1-17.

Tibihika, P.D., Meimberg, H., & Curto, M. (2022). The Nile tilapia (*Oreochromis niloticus*) is the second-most-farmed worldwide. *African Zoology*, 57(4), 1-9.

Triay, C., Courcelle, M., Caminade, P., Bezault, E., Baroiller, J.-F., Kocher, T.D., & D'Cotta, H. (2022). Polymorphism of Sex Determination Amongst Wild Populations Suggestsits Rapid Turnover Within the Nile Tilapia Species. *Frontiers in Genetics*, 13, 1-15.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M., & Shipley, P. (2004). MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, 4(3), 535–538.

Van Oosterhout, C., Weetman, D., & Hutchinson, W.F. (2006). Estimation and adjustment of microsatellite null alleles in nonequilibrium populations. *Molecular Ecology Notes*, 6(1), 255–256.

Wahlund, S. (1928). Zusammensetzung von Populationen und Korrelationsers-chinungen von Standpunkt der Vererbungslehre aus betrachtet. *Hereditas*, 11, 65–108.

Waples, R.S. (2006). A bias correction for estimates of effective population size based on linkage disequilibrium at unlinked gene loci. *Conservation Genetics*, 7(2), 167–184.

Ward, J.A., Bhangoo, J., Fernández-Fernández, F., Moore, P., Swanson, J.D., Viola, R., Velasco, R., Bassil, N., Weber, C.A., & Sargent, D.J. (2013). Saturated linkage map construction in *Rubus idaeus* using genotyping by sequencing and genome-independent imputation. *BMC Genomics*, 14(2), 1–14.

Wattier, R., Engel, C.R., Saumitou-Laprade, P., & Valero, M. (1998). Short allele dominance as a source of heterozygote deficiency at microsatellite loci: Experimental evidence at the dinucleotide locus Gv1CT in *Gracilaria gracilis* (Rhodophyta). *Molecular Ecology*, 7(11), 1569–1573.

Wood, J.P., Beer, S.D., Campbell, T.S., & Page, R.B. (2018). Insights into the introduction history and population genetic dynamics of the Argentine black-and-white tegu (*Salvator merianae*) in Florida. *Genetica*, 146(6), 443–459.

WorldFish Center (2004). GIFT technology manual: An aid to Tilapia selective breeding. Edited by WorldFish Center. WorldFish. Penang, Malaysia

Yeh, F.C., Yang, R.C., & Boyle, T. (1999). POPGENE (version 1.3.1). Microsoft Window-Bases Freeware for Population Genetic Analysis. Alberta, Canada: University of Alberta and the Centre for International Forestry Research.

Yoboue, A.N., Adepo-Gourene, A.B., Agnese, J.F., & Laë, R. (2014). Diversité et structure génétique de *Sarotherodon melanotheron* (Pisces : Cichlidae) révélées par les microsatellites. *European Scientific Journal*, 10(33), 299–311.

Yoboué, A.N., Adepo-Gourène, B.A., Séka, D., Durand, J.D., Panfili, J., & Laë, R. (2012). Genetic diversity and adaptability of *Sarotherodon melanotheron* (Cichlidae) in coastal ecosystem. *Ethology Ecology & Evolution*, 24(3), 230–243.

Zenger, K.R., Khatkar, M.S., Jones, D.B., Khalilisamani, N., Jerry, D.R., & Raadsma, H.W., (2019). Genomic Selection in Aquaculture: Application, Limitations and Opportunities with Special Reference to Marine Shrimp and Pearl Oysters. *Frontiers in Genetics*, 9, 1–19.

Zouros, E., Singh, S.M., & Miles, H.E. (1980). Growth rate in oysters: An overdominant phenotype and its possible explanations. *Evolution*, 34(5), 856–867.