Review and Progress Open Access

Environmental and Genetic Factors Shaping the Global Expansion of Tilapia Aquaculture

Liting Wang [1] ✉, Baohua Dong [2]
1 Hainan Institute of Biotechnology, Haikou, 57022, Hainan, China
2 Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
✉ Corresponding author: liting.wang@hitar.org

International Journal of Aquaculture, 2025, Vol.15, No.3 doi: 10.5376/ija.2025.15.0013
Received: 15 May., 2025
Accepted: 10 Jun., 2025
Published: 25 Jun., 2025

Preferred citation for this article:
Wang L.T., and Dong B.H., 2025, Environmental and genetic factors shaping the global expansion of tilapia aquaculture, International Journal of Aquaculture, 15(3): 135-148 (doi: 10.5376/ija.2025.15.0013)

Abstract As an important farmed fish in the world, tilapia has been widely cultivated in dozens of countries around the world due to its advantages of strong adaptability, rapid growth and low breeding costs. This study summarizes the effects of environmental and genetic factors on the expansion of tilapia farming territory. First, tilapia exhibits excellent ecological adaptability and has ecological plasticity such as wide temperature and salt. It can grow and reproduce normally under different temperature and salinity conditions, and adapt to high-density breeding and low-oxygen environments through regulating physiological mechanisms. Global climate change is changing the suitable areas for tilapia. Rising temperatures have extended the tilapia farming map to high latitudes, and is expected to further expand in tropical and subtropical areas, but extreme environments may bring new breeding risks. Genetic improvement plays a key role in the optimization of tilapia species. The application of high-growth strain breeding, disease-resistant molecular breeding and gender control technology has greatly improved the production performance and stress resistance of tilapia. Through case analysis of the development of tilapia industry in typical countries such as China, Egypt, and Brazil, the impact of environmental conditions and genetic improvement on industrial layout is revealed. Finally, we will discuss the ecological invasion risks faced by global expansion of tilapia, the environmental pressures of high-density breeding and genetic pollution risks, and look forward to the application prospects of technologies such as precise breeding, gene editing, and intelligent breeding in improving the sustainable breeding of tilapia. This study aims to provide scientific basis and decision-making reference for the global layout and sustainable development of tilapia farming.

Keywords Tilapia; Ecological adaptability; Climate change; Genetic improvement; Sustainable breeding

1 Introduction

Tilapia (various species of *Oreochromis*) is native to Africa. It has been widely introduced to breed around the world for its fast growth, mixed food, strong reproductive ability and wide adaptability, and enjoys the reputation of "chicken in water". After decades of development, tilapia has become the third largest breeding catfish in the world, second only to carp and grass carp, and is farmed in more than 100 countries and regions around the world (Vicente and Fonseca-Alves, 2013). In 2018, the global tilapia farming output was about 4.5 million tons, accounting for nearly 10% of the world's total aquaculture fish production that year. China is the world's largest producer and exporter of tilapia, with annual output stable at 1.6 million to 1.7 million tons in recent years, accounting for nearly one-third of the global total output (Mohamad et al., 2021). The development of tilapia fish farming not only provides cheap and high-quality animal protein in developing countries, but also an important pillar for the livelihood of fishermen in many regions.

Despite the significant economic value and production potential of tilapia, the global aquaculture industry also faces many challenges in its rapid expansion. The impact of environmental factors on the tilapia farming map is becoming increasingly prominent. Increased water temperatures caused by climate change and the increase in extreme weather events are changing the appropriate distribution areas of tilapia; some high-latitude areas with low temperatures still face the problem of water temperatures lower than the tolerance range of tilapia in winter, and need to overcome the problem of overwintering. Water resources and water environmental conditions are also important factors that limit the expansion of tilapia farming. High-density farming may lead to problems such as water quality deterioration and disease outbreaks, which poses a test on environmental carrying capacity (Acosta-Pérez et al., 2022). Secondly, genetic factors play a key role in the improvement of tilapia species and the improvement of breeding performance. By introducing genetic selection and breeding technology, people have cultivated new varieties such as GIFT tilapia that grows faster, as well as anti-strepococcus strains with stronger disease resistance, providing an excellent seedling foundation for industry expansion. However, variety introduction and hybridization also bring ecological risks such as alien species invasion and genetic pollution, and it is necessary to take into account biosecurity and diversity protection while developing production.

The research on global expansion of tilapia is of great significance. On the one hand, analyzing the impact of environmental adaptability and climate change on the tilapia farming map will help predict the change trends of future farming areas and guide countries to reasonably plan their breeding layout. On the other hand, summarizing the role of genetic improvement in the development of the tilapia industry can provide ideas for further improving breeding efficiency and stress resistance. This study systematically explains how environmental and genetic factors shape the global pattern of tilapia aquaculture based on environmental adaptability, climate change impacts, genetic improvement, germplasm resources, typical national cases, ecological risks and future technical outlooks, hoping to provide reference for industry managers and scientific researchers.

2 Environmental Adaptability: Ecological Plasticity of Tilapia

2.1 The performance of wide temperature and wide salt characteristics in different ecological regions

Tilapia is known for its wide temperature properties and can adapt to a variety of water temperature environments from subtropical to tropical. In Africa, Nile tilapia (*Oreochromis niloticus*) can survive in the water temperature range of 1 438 °C, with an optimal growth temperature of about 2 532 °C; extreme temperatures below 15 °C or above 40 °C can cause stress and death (Zhou et al., 2022). In the introduced regions, tilapia exhibits excellent temperature adaptability. Farming practices in southern China show that high temperatures in summer (the lake water temperature often reaches above 30 ℃) do not affect the feeding and growth of tilapia; and when the water temperature drops to around 15 ℃ in winter, tilapia can still survive and survive the winter even though the feeding intake drops. This is because tilapia can cope with temperature changes by regulating metabolic rates and activity behavior, reducing oxygen consumption and eating to preserve energy when water temperatures decrease (Figure 1) (Liu et al., 2022). In addition, there are differences in the cold tolerance of different species of tilapia. Blue tilapia (*Oreochromis aureus*) is relatively cold-resistant and can tolerate low temperatures around 10 °C, so it is often used to hybridize with Nile tilapia to improve cold resistance. There are studies that have obtained strong cold-resistant tilapia strains through hybrid selection and survival rates significantly higher than those of ordinary strains in acute cooling tests.

2.2 Water quality adaptability and aquaculture density regulation

Tilapia not only can adapt to different water temperatures, but also has a wide tolerance range to salinity, showing wide salt properties. Although tilapia is native to freshwater basins, it can survive in salty freshwater and offshore high salinity environments. Experiments have shown that Nile tilapia can grow normally in salt water with a salinity of 15‰~20‰, and some individuals can even tolerate short-term exposure of seawater salinity (about 30‰) (Mirera and Okemwa, 2023). Field surveys on the Brazilian coast recorded tilapia invasion of estuary and coastal wetland ecosystems, showing that the species has the potential to utilize brackish and seawater environments. The general salt adaptability of tilapia is partly attributed to its well-developed osmotic pressure regulation mechanism in the body: when in a high-salt environment, tilapia excretes excess salt in the body by increasing the number of chlorine cells in the gills and drinking water, maintaining fluid balance (Huang et al., 2025). In addition, tilapia has a strong tolerance to water quality and shows certain tolerance to higher concentrations of ammonia nitrogen and nitrite. A study based on carbonate alkalinity stress showed that the semi-lethal alkalinity (pH in carbonate) of Nile tilapia at 96 hours acute exposure ranged from 6.25 g/L to 9.01 g/L, which is weaker than extremely alkali-resistant fish but is more tolerant than most freshwater fish. Under the conditions of gradual domestication, increasing the alkalinity of water can significantly improve the alkali resistance of tilapia juvenile fish. Therefore, whether in brackish ponds, saline-alkali waters, or in intensive breeding systems with large water quality fluctuations, tilapia can adapt to survival better. This broad salt and water quality adaptability provides the possibility for tilapia to breed in unconventional environments such as coastal tidal flats and brackish bays, and also helps them to colonize and spread in foreign waters.

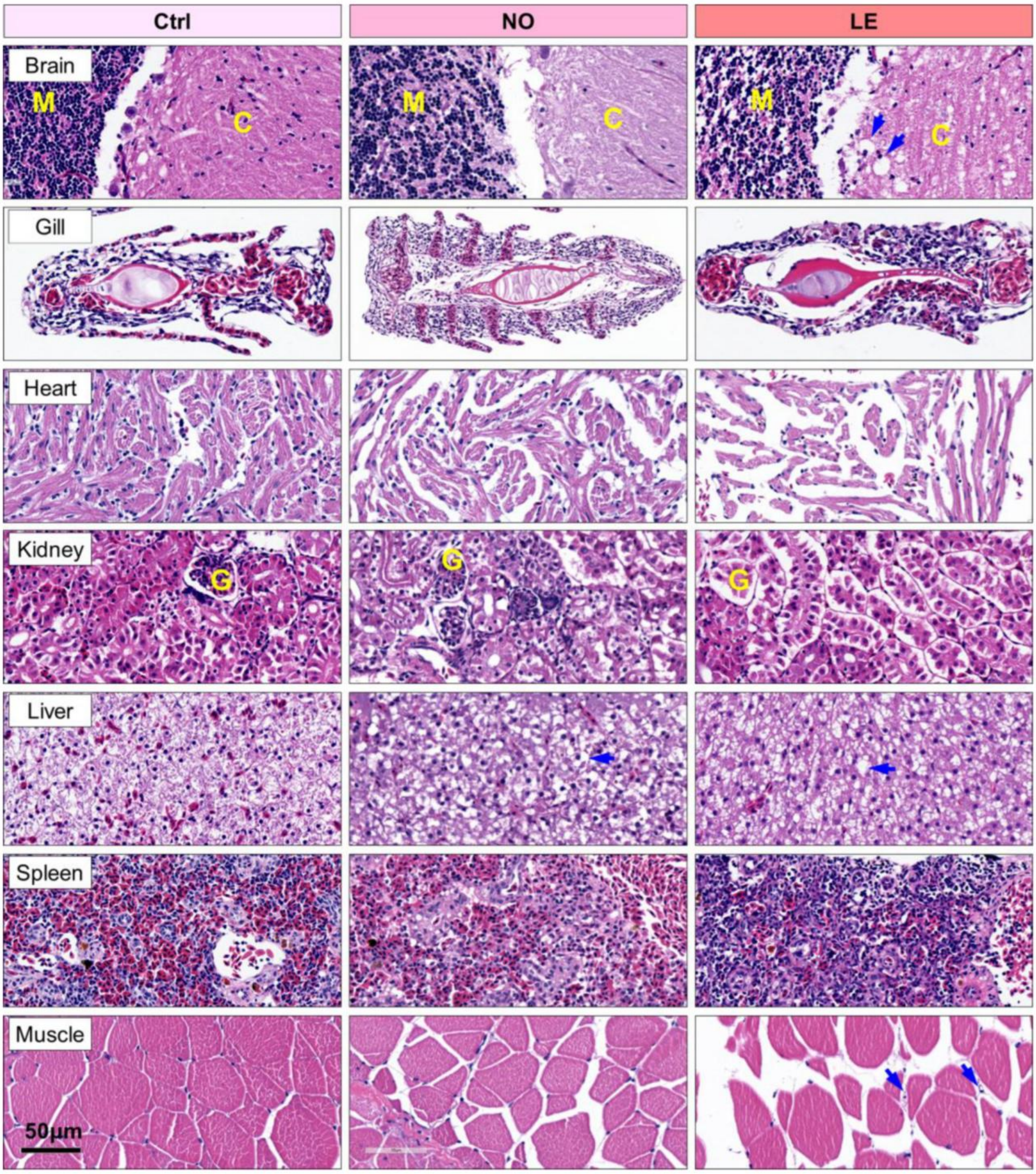

Figure 1 Exposure of Nile tilapia to lethal cold stress caused extensive tissue damage. After being held at 12 °C for 72 h, both the normal fish (NO, individuals that could swim normally at the sampling time) and those lost equilibrium (LE) were sampled. Ctrl indicates fish not exposed to cold stress (Adopted from Liu et al., 2022)

2.3 Hypoxic tolerance and environmental stress response mechanism

Under intensive breeding conditions, low dissolved oxygen is one of the common environmental stresses faced by fish. Compared with many sensitive fish, tilapia exhibits strong hypoxia resistance and corresponding physiological response mechanisms. When dissolved oxygen in the water drops, tilapia can absorb oxygen by increasing the swing frequency of the gill cover and floating to the water meter to breathe air to relieve hypoxia pressure (Obirikorang et al., 2023). In addition, the number of red blood cells and hemoglobin content in the blood can be upregulated under low oxygen conditions, improving the blood oxygen carrying capacity. Research has found that tilapia can reduce the metabolic rate and enter a metabolic inhibitory state under long-term hypoxia exposure, thereby reducing oxygen demand and increasing survival time. This is reflected in the field and in breeding practice: tilapia are often observed to gather on the water surface at night or in the early morning when dissolved oxygen is low, so as to pass the low oxygen period in the fish pond. In order to further enhance the anti-oxidant properties of tilapia, breeding experts have also carried out relevant breeding work. Chinese scientific researchers have successfully cultivated tilapia families with stronger hypoxia resistance, and screened individuals with higher survival rates for seed selection through the hypoxia-reoxygen alternating stress experiment. At the molecular level, tilapia activates hypoxia-inducing factor pathways such as HIF-1α under hypoxia stress, regulates the expression of a series of anti-stress genes, thereby enhancing the cell's tolerance to the hypoxia environment (Ma et al., 2023).

3 Analysis of Climate Change and Geographical Suitability

3.1 Changes in the breeding area in the context of global warming

Global warming is profoundly affecting the spatial pattern of aquaculture, especially for tropical fish such as tilapia. As the average temperature rises, high-latitude areas that are traditionally too cold to be suitable for tilapia to overwinter may become new breeding suitable areas in the future. In recent years, there have been reports of experimental overwintering tilapia in coastal provinces such as Zhejiang and Fujian in China. The success rate has gradually increased, which is a reflection of the reduction of local extreme low-temperature events in winter due to the warming. In addition to China, some previously marginalized areas in southern Japan and southern United States may have the conditions for seasonal breeding of tilapia in the future. Northward migration of distribution has become one of the trends of global expansion of tilapia: A study on the invasion potential of tilapia shows that climate warming will cause the centroid of high-risk invasion areas of tilapia to migrate to high latitudes, and temperate areas with strong climate restrictions may have an outbreak of alien tilapia populations under warm winter conditions. However, global warming is not unilaterally beneficial to tilapia farming. Excessive water temperatures may exceed the optimal range of tilapia, thereby inhibiting its growth and reproductive efficiency. Especially in tropical areas, the temperature of many aquaculture water bodies is close to the upper limit of tilapia tolerate in summer. Further heating may lead to enhanced stress response and decreased immune function, thereby increasing the risk of disease outbreaks. Studies have found that when the water temperature rises from 28 ℃ to 34 ℃, the gill tissue structure of tilapia is damaged, and its tolerance to hypoxia is significantly reduced (Zhou et al., 2022).

3.2 Prospects of aquaculture expansion in tropical and subtropical regions

Tropical and subtropical regions have always been the areas with the most concentrated tilapia farming, and these regions will still be the main force of industrial growth in the future. In Africa, many countries are actively expanding their breeding scale due to the rich local resources and strong market demand. For example, Egypt, as Africa's largest producer of tilapia, relies on the water resources and high temperature climate in the Nile River Basin to expand its breeding to a wider range of waters, including the use of drainage ditches and reservoirs to develop high-density cage farming. Other sub-Saharan African countries, such as Nigeria and Kenya, have suitable climatic conditions, and have also regarded tilapia as an important way to improve protein supply and promote agricultural development, and there is a lot of room for improvement in future output. In Southeast Asia, tilapia farming has become very popular. Countries such as the Philippines, Indonesia, Thailand and other countries will continue to optimize varieties and breeding models to improve unit yield and product quality. Especially in monsoon areas with abundant rainfall, by developing flood-resistant cage farming, tilapia can continue to produce in water-stalk areas and reservoirs in the rainy season. For example, the Haor wetlands in northeastern Bangladesh are flooding year by year. The local government is trying to raise tilapia in floating cages during the flood season to explore new models of livelihoods in floodplain areas. The experimental results show that the survival rate of cage tilapia under different densities is above 90%, and the unit water output can reach 25 kg per cubic meter, showing good climate adaptability potential (Burggren et al., 2019). Subtropical areas such as Brazil and Mexico in Latin America have developed rapidly in recent years. These areas have sufficient sunshine and a large number of reservoirs are available. The Brazilian state of São Paulo and other places use reservoirs to carry out cage farming of tilapia, with an annual output of hundreds of thousands of tons. In the future, it has the potential for replication and promotion in a wider inland waters.

3.3 Prediction and regulation strategies for future distribution by climate model

In order to quantitatively predict the changes in the potential adaptive range of tilapia under climate change scenarios, the researchers used species distribution models and climate model data for analysis. Simulation results generally show that by around 2050, the total area of suitable tilapia farming areas around the world will expand, and the center of high-suitability areas will be shifted. China's model forecast points out that the area of high-risk invasion areas will increase in the future, and the center will move from south China to north China (Esmaeili and Barzoki, 2023). Rising temperatures and changes in precipitation patterns in winter are considered to be the main climate factors driving this trend. On a global scale, some currently marginalized warm temperate areas or seasonal suitable areas may become suitable areas throughout the year after warming. However, some studies have also emphasized that the impact of extreme climate events on future distribution of tilapia should be considered. For example, an increase in climate variability may lead to abnormal cold waves in some years, which will hit the northern margin breeding areas. To this end, adaptive strategies need to be followed up simultaneously. First, breeding units can adopt wintering guarantee measures, such as building temperature-controlled greenhouses and hot spring water heating in high-latitude areas to cope with occasional low temperatures and safely push the tilapia breeding scope to the marginal area. Secondly, varieties should be actively selected and breeded to cultivate corresponding stress-resistant strains based on the climatic characteristics of different regions. Improve the breeding risk warning system and use meteorological forecasts to guide farmers to prevent extreme weather in a timely manner.

4 Genetic Improvement Promotes Variety Optimization

4.1 Breeding and genotype analysis of high growth lines

Genetic breeding plays a central role in the development of the tilapia breeding industry. One of the most representative results is the cultivation of the "GIFT tilapia" line. In the late 1980s, WorldFish, in conjunction with scientific research institutions in many countries, successfully cultivated GIFT tilapia with significantly improved growth rates by collecting wild populations of Nile tilapia from many places in Africa, and applying family breeding and index selection methods. After multiple generations of breeding, the growth rate of GIFT tilapia has increased by about 85% to 100% compared with the basic population, and the bait conversion efficiency and survival rate have also been significantly improved (Bentsen et al., 2017). In recent years, with the development of molecular genetic technology, genotype analysis of tilapia growth traits has made in-depth progress (Liang et al., 2024). Genome-wide association analysis (GWAS) and genome-wide selection (GS) are used to discover key QTL sites that affect growth, thereby accelerating the genetic improvement process. For example, Yáñez et al. (2020) reported progress in genome selection research on traits such as tilapia growth and disease resistance, demonstrating that using genome breeding value (GEBV) selection can achieve a genetic gain of 5% to 10% per generation (Yáñez et al., 2020). Multi-trait selection is also one of the directions for breeding of strains. In a Mexico trial, a comprehensive evaluation of growth, survival and feed utilization was performed on several new lines, and the results showed that some new lines such as "Silver YY" grew fast but had slightly lower survival, while GIFT showed a balanced performance in various traits. This suggests that different traits need to be weighed during breeding.

4.2 Selection of molecular markers related to improving disease resistance

The intensification of tilapia farming has made the disease problem increasingly prominent, and traditional drug and vaccine measures have limited effect in large-scale farming. Therefore, improving the disease resistance of tilapia through genetic improvement has become one of the important solutions. In recent years, breakthroughs have been made in the research on disease-resistant breeding of major diseases of tilapia (such as streptococcosis, tilapia lake virus, etc.). On the one hand, family breeding has been used to screen disease-resistant strains (Joshi et al., 2020). On the other hand, molecular marker assisted breeding provides tools for rapid improvement of disease resistance. Through genome-wide association analysis, researchers found the main-effect QTL sites related to

Streptococcus resistance in tilapia (Gao et al., 2019). Especially in terms of Tilapia Lake virus (TiLV) resistance, a 2021 study identified a region on chromosome 22 in tilapia that had a significant impact on disease-resistant survival: the mortality rate of individuals carrying resistance alleles was only 11%, while the mortality rate of homozygous susceptible alleles was as high as 43%. This finding means that relevant molecular markers can be used to select disease-resistant individuals for breeding at the seedling stage. Currently, WorldFish and other institutions are integrating TiLV resistance markers into the tilapia breeding program to cultivate tilapia strains that are highly resistant to the virus. In addition, using RNA sequencing and proteomics technology, people have deeply analyzed the immune response mechanism of tilapia after infection with pathogens, and found that the polymorphisms of immune genes such as MHC and TLR are closely related to disease resistance. These results provide clues for screening candidate genes for disease-resistant breeding.

4.3 Gender control technology and single-sex population cultivation

Tilapia has the characteristics of early reproduction and high reproduction frequency. It is prone to overpropagation in a breeding environment, resulting in individual growth stagnation and irregular specifications. Therefore, achieving gender control to produce single-sex groups (usually all-male groups) is an important need in tilapia farming. All male tilapia grows faster and avoids reproductive energy consumption. Generally, the yield can be increased by more than 30% compared with mixed breeding groups. At present, the main preparation techniques for single-sex seedlings of tilapia include hormone hermaphrodite induction and YY supermale breeding. The Chinese scientific research team has achieved remarkable results in this field. For example, the "Yuemin No. 1" tilapia cultivated by the Pearl River Aquatic Products Research Institute is a new strain cultivated by Olia tilapia hybridization and backcrossing through multiple generations, combined with YY superhero technology. The father of "Yuemin No. 1" is a supermale Nile tilapia with chromosome type YY, and the mother is an excellent Nile tilapia female. The male rate of their offspring can reach more than 98%, and the growth rate is about 23.8% higher than that of the GIFT tilapia bred during the same period (Chen et al., 2018). The promotion of "Yuemin No. 1" has made large-scale hormone-free all-male seedling production possible, which is a milestone in China's tilapia industry. In addition to YY technology, modern molecular biology also provides new tools for gender control. Knockout of key genes on the gender-determining pathway such as *DMRT1* or *Foxl2* by gene editing can lead to gender reversal. Japanese studies have found that CRISPR knocking out the *foxl2* gene of XX tilapia will transform its gonads from ovaries to semen, achieving genetic maleization.

5 Germplasm Resources and Genetic Diversity of Tilapia

5.1 Analysis of the genetic lineage of major breeding lines in the world

The extensive introduction and breeding of tilapia around the world has formed several representative breeding varieties. The origin and kinship of these lines can be revealed through genetic lineage and molecular marker analysis. GIFT tilapia (GIFT) is a multi-source group breeding group. Its gene bank is fused with wild Nile tilapia blood from Egypt, Kenya, Senegal, Ghana and other places. Microsatellite and single nucleotide polymorphism (SNP) analysis showed that the genetic diversity level of the Jifu strain was high, with an average heterogeneity of about 0.62, indicating that although breeding was performed, there were still abundant alleles (Yan et al., 2014). In contrast, Taiwan’s red tilapia is a red variant produced by interspecies hybridization of Nile tilapia and Mozambique tilapia. Its genetic component contains about 50% of the background of Mozambique tilapia, so it can be distinguished from purebred Nile tilapia strains on some molecular marker seats. The Chitralada strain in Thailand originated from a few tilapia individuals introduced from Japan in the 1960s. They were bred for many years by a royal Thai farm. Because the foundation group is small and the long-term atresia breeding is low, the genetic variation is low. Some studies have found that the average number of alleles is significantly less than that of the Jifu strain. In addition, localized strains in various countries often have a certain degree of genetic confusion. Taking China as an example, the early introduction of "Taiwanese tilapia" and "Thai tilapia" often hybridize during folk breeding, which makes many breeding groups today be hybrids of multiple strains. DNA band analysis confirmed that the characteristic alleles of the Jifu and Thai lines existed in the tilapia breeding population in South China.

5.2 Hybrid breeding strategies and gene flow risks

Hybrid breeding is a common strategy in tilapia modification, especially for binding to excellent traits of different species or lines. However, gene flow from hybridization can also pose ecological and genetic risks. Different species within the genus tilapia have a high degree of proximity and can produce fertile hybrid offspring. For example, in order to improve cold resistance, Olia tilapia (cold-resistant) and Nile tilapia (fast-growing) are often used to hybridize. The obtained Oni hybrid generation has both parental advantages, and both survival rate and growth performance at lower temperatures are better than those of purebreds. However, if these hybrid offspring escape into the wild and mate with local wild tilapia populations, it may introduce exogenous genes to affect the purity of the local species' gene bank, thereby changing the adaptability of the original population. In actual cases, the hybridization of Mozambique tilapia (*O. mossambicus*) and Nile tilapia was widely used to breed red tilapia, but its escape caused hybrid populations to appear in waters of many countries, causing genetic erosion to indigenous Mozambique tilapia (*Oreochromis mossambicus*). In addition, hybridization may also cause ecological invasion problems: if hybrid progeny is more environmentally adaptable than the parent, it may spread faster, aggravate the risk of foreign invasion. Therefore, the pros and cons need to be weighed in the application of hybrid breeding strategies.

5.3 Integration and localization adaptation between local and imported products

During the promotion of tilapia fish farming, countries often hybridize or breed and integrate the introduced improved varieties with local original varieties to obtain varieties that are adapted to the local environment and have excellent performance. This localization adaptation process is very important for the long-term development of the aquaculture industry. The imported strain usually has the advantages of fast growth, but direct transplantation to a new environment may cause disagreement in the water and soil, such as lack of resistance to local pathogens or inadequate to local feed and water quality conditions. By hybridizing with local lines, the excellent traits of the introduced lines can be combined with the characteristics of the local lines' long-term adaptation. After the introduction of the gimot tilapia into the Philippines, it crossed with locally cultivated strains and cultivated the "Genomar Supreme Tilapia" (GST) strain. It is reported that its production performance in Philippine waters is better than that in pure gimot gimot and has a higher survival rate (Ansah et al., 2014). In Guangdong, China, researchers hybridized the Jifu strain with the local "pioneer" strain, and the survival rate of the obtained offspring in the low-temperature season was significantly improved, while maintaining the rapid growth characteristics (Malik et al., 2014). This localized breeding takes into account local low temperatures and epidemic bacteria in winter and spring, and enhances the adaptability of the strain. In Egypt and other places, it is also common to cross local Nile tilapia with imported GIFT tilapia, which increases yield to a certain extent, but at the same time leads to gene confusion in wild populations, causing concerns about the loss of genetic diversity. To this end, it is suggested that when integrating the strain, the reinforcing and other methods should be used as much as possible to make the local germplasm account for the main share to maintain a high degree of adaptation to the local environment. In addition, a complete breeding system for breeding of good varieties should be established to prevent blind hybridization between introduced lines and local lines from being blindly mixed without planning, thereby avoiding the problems of germplasm degradation or instability. Practice has proved that the strains that have been selected systematically locally perform more stably in commercial breeding.

6 Case Analysis of the Expansion of Tilapia Industry in Typical Countries

6.1 China: Development of suitable and localized varieties in multi-ecological zones

China is a major tilapia breeding country, and its industrial expansion reflects the characteristics of multi-ecological zone development and localization of strains. The South China region (Guangdong, Guangxi, Hainan) located in the subtropical region has a warm climate and vast waters. Since the 1990s, tilapia farming has developed rapidly. In these areas, tilapia is widely used in different ecological farming models: for example, the Pearl River Delta region stocks tilapia in rice fields and lotus root ponds, and rice-fish symbiosis is implemented to improve comprehensive benefits; cage farming is developed in the main stream and reservoir of the Pearl River to obtain high yields (Sifa et al., 2008). At the same time, China is actively developing some non-traditional breeding areas in central and southwest China. For example, Yunnan and other southwestern plateau areas use hot spring water to carry out factory-based tilapia breeding to overcome high-altitude low-temperature environments; the middle and lower reaches of the Yangtze River achieve overwintering attempts through greenhouse heating, and introduce tilapia into the local market. This expansion of the southern and northern diversion of fish is inseparable from the localization improvement of the product. To this end, China has bred a number of new tilapia varieties to meet local needs. In addition to the large-scale application of the "Jifu" strain, "Longjiang No. 1", "Yuemin No. 1" and "Guiluo No. 1" have been successively bred: for example, "Guiluo No. 1" focuses on low-temperature resistance, improves cold resistance through hybridization and group selection, and can survive outdoors in northern Guangxi in winter; "Yuemin No. 1" aims to improve male rate and growth rate, and has become the dominant variety of large-scale all-male seedling production in South China. In the process of expanding the tilapia industry, China also attaches great importance to environmental management and by-product utilization. For example, in the Pearl River Delta region, the technology of circulating water aquaculture and pond tail water treatment is promoted, and high-level pond aquaculture and rice field wetlands are combined to reduce the discharge load of aquaculture wastewater. Some breeding companies adopt online water quality monitoring and intelligent feeding systems to improve breeding accuracy while reducing environmental pressure (Yuan et al., 2017). In addition, through the development of tilapia processing and comprehensive utilization, such as fish meat products export, fish skin leather and collagen extraction, the added value of the industrial chain has been increased and the industrial sustainability has been promoted.

6.2 Egypt: high-density aquaculture and water resource reuse strategies

Egypt is the most prominent country in Africa with tilapia farming, and its industrial characteristics can be summarized as high-density intensiveness and water resource recycling. The Nile Delta region of Egypt has a flat terrain and abundant water sources, making it very suitable for tilapia pond breeding. After decades of development, Egypt has become the world's second largest tilapia producer after China, with an annual output of more than 500 000 tons. In Egypt, tilapia are usually mixed with catfish in ponds, with stocking density up to thousands of tails per acre in order to pursue maximum output (Shaalan et al., 2018). This high-density farming benefits from Egypt's good water temperature conditions (the annual water temperature is mostly above 20 ℃) and sufficient feed investment. In addition, Egypt has adopted a unique water resource recycling model: many tilapia farms take water from the Nile irrigation canals, and the pond water is not directly disposal after fish farming, but flows into farmland to irrigate crops, achieving multi-use use of one water. Studies have evaluated the environmental sustainability of Egypt's family-style tilapia farms and found that through irrigation reuse, the impact of nutrient emissions from tilapia production on the surrounding environment has been significantly reduced. The Egyptian government also encourages this "fish-agricultural combination" model to ensure efficient use of water resources and pollution reduction while promoting tilapia farming. For example, pilot projects carried out in the Fayum area show that the use of aquaculture wastewater for growing aquatic vegetables can effectively absorb nitrogen and phosphorus from the breeding tail water, purify water quality and increase farmers' income. In terms of breeding technology, Egypt has also actively adopted modern means to improve the benefits of high-density breeding. For example, large-scale cage farming was deployed in the Nile tributaries, and the cage production in 2019 reached 119 000 tons, accounting for more than 10% of the national tilapia production. Cage farming makes full use of the fluidity of open water to reduce the dissolved oxygen pressure at high density of ponds (Radwan, 2020). At the same time, Egypt has effectively solved the problem of germplasm degradation caused by retail investors' self-propagation by establishing a centralized hatchery.

6.3 Brazil: conservation of genetic diversity and ecological integration breeding

As the fastest growing country in Latin America, Brazil has expanded its industrial concepts that focus on the conservation of genetic diversity and ecological integration. Brazil began introducing tilapia in the 1990s. With its abundant water resources (large large reservoirs) and warm climate, tilapia farming output has doubled several times in the past decade, exceeding 500 000 tons in 2022, making it the second largest farmed fish after Kalu (Barroso et al., 2019). In terms of strain, Brazil attaches great importance to the genetic management of introduction. Early introductions include the Chitralada series in Thailand and the GST series in the Philippines. In order to avoid inbreeding and line degeneration, Brazil has established a national-level breeding center to preserve the original species of multiple lines and conduct hybridization experiments. In terms of reservoir cage farming, the government strictly controls the cage delivery density and advocates "multi-nutritional integrated aquaculture (IMTA), that is, planting aquatic plants or stocking filter-feeding fish around the cage to absorb breeding waste and reduce environmental impact. Some cases show that in the reservoirs in northeastern Brazil, farms combine tilapia with local herbivorous carp and shellfish, and the water quality indicators have been significantly improved and the comprehensive benefits of breeding have been improved (Camarago and Amorim, 2020). In addition, Brazil pays great attention to preventing the impact of foreign invasion of tilapia on local organisms. Although tilapia has established self-producing groups in Brazilian waters, the government has explicitly prohibited the introduction of tilapia in ecologically sensitive areas (such as the Amazon River Basin) to protect the unique local fish diversity.

7 Ecological Risks and Sustainable Breeding Challenges

7.1 Ecological invasion caused by the spread of alien species

With its tenacious survival ability, tilapia has also become an alien fish with invasive potential while introducing it into breeding. Escaped tilapia populations have been found in the natural waters of many tropical and subtropical countries, which have had some impact on the local ecosystem. The risk of ecological invasion of tilapia is mainly reflected in the following aspects: After tilapia enters natural water bodies, due to lack of natural enemies and strong reproductive power, the population can grow rapidly, which may pose a threat to local fish through competition and predation. In the Shanmei Reservoir in South China, the invaded Qi's tilapia and hybrid tilapia have formed reproductive populations, occupying the main proportion of catches, causing significant squeeze on indigenous fish resources (Shuai and Li, 2022). Studies in Ethiopia, the Philippines and other places have also reported that the invasion of tilapia has led to a decline in some local cichlid populations. Secondly, tilapia can become a carrier of pathogens, bringing diseases in the breeding environment into the wild. The study found that Nile tilapia may introduce parasitic monoclonal flukes (such as *Cichlidogyrus sclerosus*) during foreign invasion, and local native fish have experienced healthy declines after infection with these parasites. The ecological engineering role of tilapia will also change the water environment. They feed on plankton and debris, and high-density tilapia populations may increase water turbidity and inhibit aquatic vegetation growth through feeding and agitation, thereby affecting ecosystem structure (Cassemiro et al., 2017).

7.2 The pressure of intensive aquaculture on water quality and soil systems

Although large-scale intensive farming of tilapia increases output per unit area, it inevitably generates environmental pressure, which is mainly reflected in the pollution and degradation of water quality and bottom quality. In high-density farming ponds, large amounts of bait and fish excretion will lead to eutrophication in the water: the content of ammonia nitrogen, nitrite and phosphorus increases, and the over-propagation of planktonic algae, causing large fluctuations in dissolved oxygen in the water day and night and even hypoxia. When the water quality of the pond deteriorates, not only will the fish be damaged in health, but pollutants will also be discharged into the surrounding water. Research shows that every ton of tilapia produced produces about 3 050 kg of nitrogen and 57 kg of phosphorus. If improperly disposal is discharged into rivers and lakes, it will cause algae blooms and water quality in local waters. In addition, in the long-term mode of not replacing the pool water or recycling, toxic metabolites such as hydrogen sulfide may accumulate at the bottom of the pool, threatening fish survival. High-density farming can also lead to deterioration of the pond bottom mud environment. The residual bait and fish manure are deposited at the bottom, decomposed by microorganisms to consume oxygen, forming a highly reducing black and odorous sludge, which not only releases harmful gases such as ammonia nitrogen and methane, but also destroys the beneficial microbial community at the bottom of the pool. The organic matter content in the pond mud in some aging tilapia fish in southern China is much higher than that in normal soil, and it is in a sour and odorous state, and it needs to be regularly silted and changed to the bottom. In addition, intensive farming may induce heavy metal and drug residue problems. Heavy metal elements entrained in feed and water sources are enriched in fish bodies and sediments, which may ultimately affect human health through the food chain (Melo Júnior et al., 2023; Shafiujjaman et al., 2024).

7.3 Contradiction between genetic pollution and natural population protection

Large-scale breeding of tilapia and multi-line introduction of species inevitably brings genetic pollution to wild relative populations and native fish. Genetic contamination refers to the hybridization of farmed fish with wild fish, or foreign lines with local lines, resulting in dilution or alteration of the genetic purity and genetic characteristics of the original population. On the one hand, in Africa, local tilapia species exist in some natural waters (such as Mozambique tilapia, Galaria tilapia, etc.). When people introduce Nile tilapia into these waters for breeding, hybridization may occur between different species, and the hybrid offspring produced breaks the original species boundaries, which may cause the unique gene pool of certain species to disappear in the long run (Ciezarek et al., 2024). On the other hand, in foreign countries, some of the original indigenous fish in the territory may also cross with escaped tilapia. For different tilapia strains introduced from abroad, hybridization during breeding may also reduce the purity and performance stability of the breeding strains (Figure 2). Faced with the risk of genetic pollution, there is a certain contradiction between fish resource protection and breeding production: an overly strict isolation policy may limit the development of the breeding industry, but if left unchecked, it may cause irreversible damage to biodiversity.

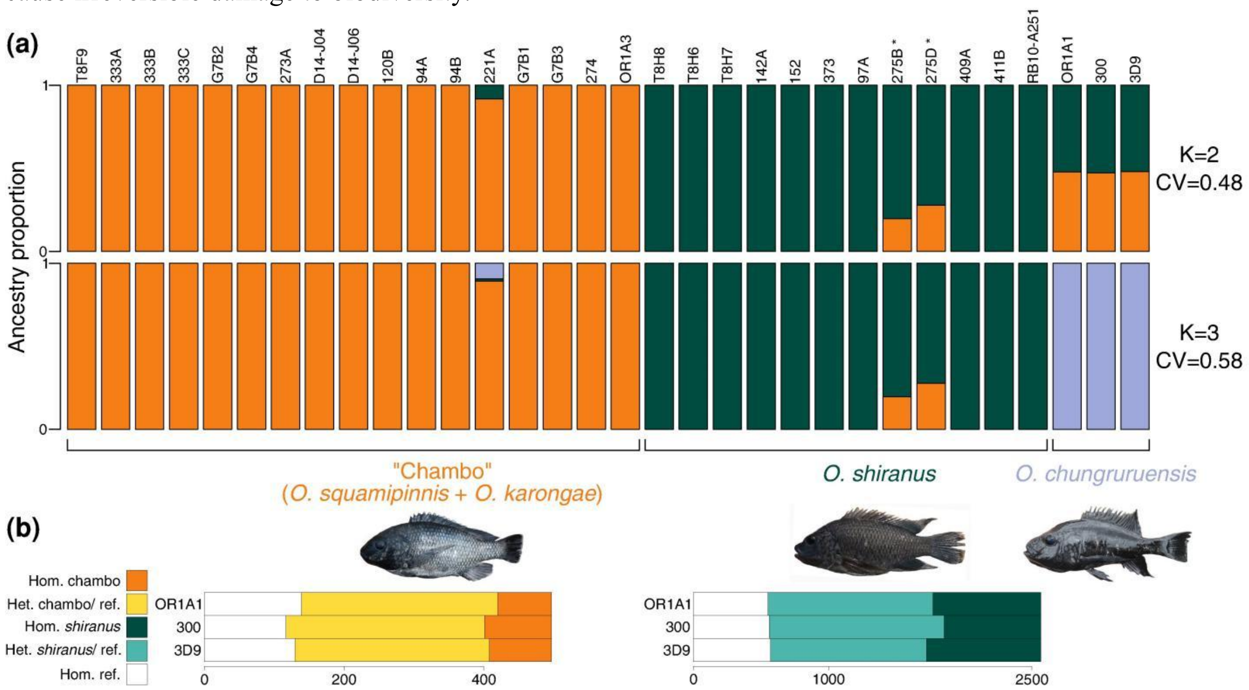

Figure 2 (a) ADMIXTURE analysis of all *O. shiranus—O. placidus*, "Chambo", and *O. chungruruensis* at K = 2 and K = 3. (b) The proportion of species-diagnostic SNPs which are either homozygous for the alternate allele (Hom.), heterozygous (Het.), or homozygous for the reference allele (ref.) in the three *O. chungruruensis* individuals (abbreviation *shi-plac—O. shiranus + O. placidus*). *indicates genetically identified *O. shiranus shiranus* × "Chambo" hybrids in Lake Itamba (Adopted from Ciezarek et al., 2024)

8 Technical Innovation and Future Paths

8.1 The application potential of precision breeding and gene editing in tilapia

Since the 21st century, cutting-edge advances in life sciences have brought revolutionary opportunities for tilapia breeding. Among them, genome selection and gene editing are highly expected to significantly improve breeding efficiency and break through target trait improvements that are difficult to achieve in traditional technologies. Genome selection (GS) uses genome-wide marker information for breeding value evaluation, has been successful in varieties such as Atlantic salmon and has also begun to be used in tilapia. A review pointed out that the growth genetic progress of tilapia in each generation through GS can reach more than 10%, which is far higher than that of traditional methods. Some leading institutions (such as WorldFish) have established SNP chips and breeding databases for tilapia to lay the foundation for precise breeding. In the future, as sequencing costs further reduce, large-scale genome-wide selection will be more feasible. Gene editing (GE) provides tools for directly modifying the tilapia genome. CRISPR/Cas9 technology can perform "site-point knockout" or "site-point insertion" of specific genes in the tilapia genome, thus giving them new traits. Cases that have been successfully implemented in tilapia include: knocking out the *DMRT1* gene to turn genetic males into functional females to achieve the purpose of breeding supermale; knocking out the *myostatin* gene (muscle growth inhibitor) to relieve the restrictions on muscle growth and obtaining individuals with tilapia whose muscle yield is increased by about 20%. These experimental results prove that gene editing has the potential to target the improvement of important economic traits of tilapia. Especially in disease-resistant breeding, gene editing can play a unique role.

8.2 Intelligent aquaculture system and data-driven management

The deep integration of information technology and aquaculture is promoting the development of tilapia farming in the direction of intelligence. The application of technologies such as the Internet of Things (IoT), big data and artificial intelligence (AI) is expected to significantly improve the efficiency of breeding management, reduce labor costs and optimize production decisions. At present, in tilapia farming, intelligent exploration focuses on the following aspects: first, online monitoring and regulation of water quality. The Internet of Things-based water quality monitoring system can collect key parameters such as dissolved oxygen, temperature, pH, ammonia nitrogen in real time, and transmit it to the breeder's mobile phone or control center through wireless network. The second is intelligent feeding and image recognition. The feed cost of tilapia accounts for about 70% of the total cost, and traditional manual feeding can easily lead to feed waste and deterioration of water quality. The intelligent feeding machine realizes timing, quantitative and on-demand feeding through pre-set programs combined with monitoring of fish feeding behavior. The third is big data analysis of the breeding environment and diseases. By collecting long-term environmental and production data, data mining can be used to identify key factors that affect tilapia growth and health, and to predict potential risks. In a pilot project in Malaysia, applied machine learning models successfully predicted more than 90% of streptococcal disease outbreaks, winning time for farmers to prevent and control (Abid et al., 2024). The fourth is unmanned and automation. In future smart fishing grounds, pond patrol robots, underwater drones, etc. will undertake routine inspection tasks, and can monitor the status of fish schools and the operation of facilities 24 hours a day, and detect abnormalities in a timely manner (Figure 3).

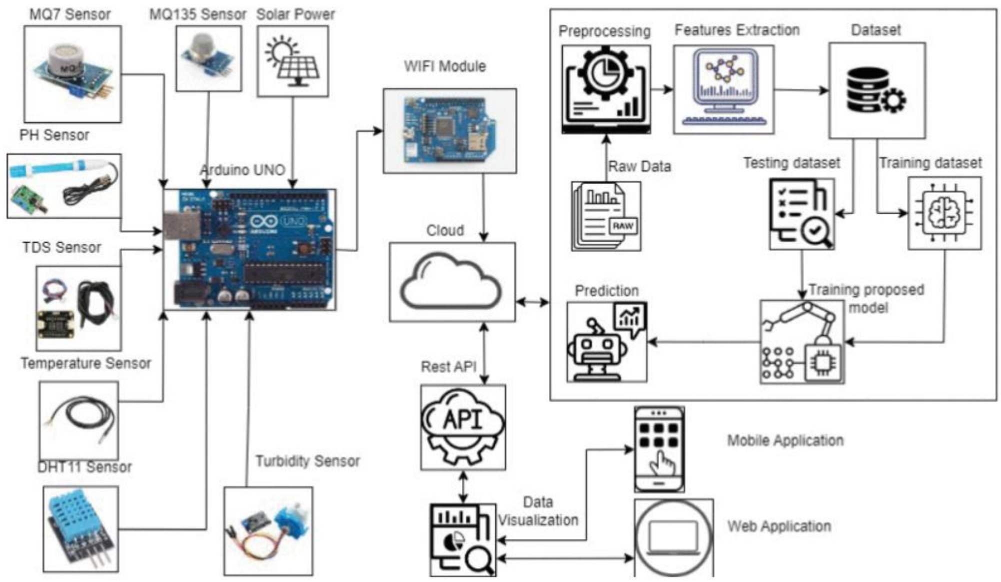

Figure 3 Smart biofloc monitoring system (Adopted from Abid et al., 2024)

8.3 Application of comprehensive environment-genetic model in industrial layout

In order to guide the sustainable layout of the tilapia industry at a more macro level, scholars have proposed to build a comprehensive environmental-genetic model, combining environmental factors with strain genetic characteristics for analysis and simulation. The concept of this model is that different tilapia strains (or species) have different environmental adaptability and production performance, and the most matching strain and breeding model should be selected according to local environmental conditions to achieve the unity of maximization of yield and minimize risk. The comprehensive model can also evaluate the effect of environmental changes on genetic improvement effects. In some areas with significant warming climates, the originally selected strains may experience "ecological deviations" such as rapid growth and early sexual maturity. The model can simulate the results of different breeding strategies in new environments, thereby guiding the adjustment of breeding targets (such as increasing the weight of thermal traits). Comprehensive environmental-genetic models can also provide scientific basis for aquaculture risk management. By incorporating the probability of extreme weather events, biological invasion risks, biosecurity measures, etc. into the model, the comprehensive risk score for the development of tilapia farming in a certain area can be used. If the score is too high, you should be cautious in launching or take strengthening measures to reduce risks. Finally, such models can also be used for industrial policy formulation and international cooperation. For example, predict the possible changes in the tilapia production capacity pattern of various countries under the background of global climate change, so as to layout market and trade strategies in advance; for emerging regions suitable for breeding, they can help them develop the tilapia industry through assistance or technical cooperation to achieve mutual benefit and win-win results.

Acknowledgments

Authors would like to thank all teachers and colleagues who provided guidance and assistance during this research, and for the peer review's revision suggestions.

Conflict of Interest Disclosure

The authors confirm that the study was conducted without any commercial or financial relationships and could be interpreted as a potential conflict of interest.

References

Abid M., Amjad M., Munir K., Siddique H., and Jurcut A., 2024, IoT-based smart biofloc monitoring system for fish farming using machine learning, IEEE Access, 12: 86333-86345.
https://doi.org/10.1109/ACCESS.2024.3384263

Acosta-Pérez V.J., Vega-Sánchez V., Fernández-Martínez T.E., Zepeda-Velázquez A.P., Reyes-Rodríguez N., Ponce-Noguez J., Peláez-Acero A., De-La-Rosa-Arana J., and Gómez-De-Anda F., 2022, Physicochemical water quality influence on the parasite biodiversity in juvenile tilapia (*Oreochromis* spp.) farmed at valle del mezquital in the central-eastern socioeconomic region of Mexico, Pathogens, 11(10): 1076.
https://doi.org/10.3390/pathogens11101076

Ansah Y., Frimpong E., and Hallerman E., 2014, Genetically-improved tilapia strains in Africa: potential benefits and negative impacts, Sustainability, 6: 3697-3721.
https://doi.org/10.3390/SU6063697

Barroso R.M., Muñoz A.E.P., and Cai J., 2019, Social and economic performance of tilapia farming in Brazil, FAO, 2019.
https://doi.org/10.4060/ca5304en

Bentsen H., Gjerde B., Eknath A., Vera M., Velasco R., Danting J., Dionisio E., Longalong F., Reyes R., Abella T., Tayamen M., and Ponzoni R., 2017, Genetic improvement of farmed tilapias: Response to five generations of selection for increased body weight at harvest in *Oreochromis niloticus* and the further impact of the project, Aquaculture, 468: 206-217.
https://doi.org/10.1016/J.AQUACULTURE.2016.10.018

Burggren W., Mendez-Sanchez J., Bautista G., Peña E., Garcia R., and González C., 2019, Developmental changes in oxygen consumption and hypoxia tolerance in the heat and hypoxia-adapted tabasco line of the Nile tilapia *Oreochromis niloticus* with a survey of the metabolic literature for the genus *Oreochromis*, Journal of Fish Biology, 94(5): 732-744.
https://doi.org/10.1111/jfb.13945

Camargo A.F.M., and Amorim R.V., 2020, Fish farming in cages: a practice to be restricted in Brazil, Acta Limnologica Brasiliensia, 32: e101.
https://doi.org/10.1590/s2179-975x5519

Cassemiro F., Bailly D., Da Graça W., and Agostinho A., 2017, The invasive potential of tilapias (*Osteichthyes Cichlidae*) in the Americas, Hydrobiologia, 817: 133-154.
https://doi.org/10.1007/s10750-017-3471-1

Chen C., Li B., Gu X., Lin H., and Xia J., 2018, Marker-assisted selection of YY supermales from a genetically improved farmed tilapia-derived strain, Zoological Research, 40: 108-112.
https://doi.org/10.24272/j.issn.2095-8137.2018.071

Ciezarek A.G., Mehta T.K., Man A., Ford A.G.P., Kavembe G.D., Kasozi N., Ngatunga B.P., Shechonge A., Tamatamah R., Nyingi D., Cnaani A., Ndiwa T., Di Palma F., Turner G., Genner M., and Haerty W., 2024, Ancient and recent hybridization in the *Oreochromis Cichlid* fishes, Molecular Biology and Evolution, 41(7): msae116.
https://doi.org/10.1093/molbev/msae116

Esmaeili H.R., and Barzoki Z., 2023, Climate change may impact Nile tilapia *Oreochromis niloticus* (Linnaeus 1758) distribution in the southeastern arabian peninsula through range contraction under various climate scenarios, Fishes, 8(10): 481.
https://doi.org/10.3390/fishes8100481

Gao F., Zhang D., Lu M., Cao J., Liu Z., Ke X., Wang M., and Zhang D., 2019, MHC class *IIB* gene polymorphisms associated with resistance/susceptibility to Streptococcus agalactiae in Nile tilapia *Oreochromis niloticus*, Diseases of Aquatic Organisms, 133(3): 253-261.
https://doi.org/10.3354/DAO03349

Huang R., Tao Y., Jiang B., Badran M.F., Zhu J., Hua J., Wang Q., Lu S., Saleh M., Aboueleila R., Xu P., and Qiang J., 2025, Integrated gill transcriptome and biochemical indices analyses reveal that acute salinity stress induces oxidative stress and immune and metabolic disorders in Red Tilapia (*Oreochromis* spp.), Aquaculture, 599: 742108.
https://doi.org/10.1016/j.aquaculture.2024.742108

Joshi R., Skaaurd A., and Alvarez A., 2020, Experimental validation of genetic selection for resistance against Streptococcus agalactiae via different routes of infection in the commercial Nile tilapia breeding programme, Journal of Animal Breeding and Genetics, 138(3): 338-348.
https://doi.org/10.1111/jbg.12516

Júnior H.N., De Paula Filho F.J., Menezes J.M.C., De Araújo J.A.C., Santana J.E., Melo H., De Sales Vieira R., De Morais Oliveira-Tintino C., Tintino S., Coutinho H., and Teixeira R., 2023, Impacts of the residual trace metals of aquaculture in net cages on the quality of sediment, Life, 13(2): 338.
https://doi.org/10.3390/life13020338

Liang C., Lu Y., and Mai R.D., 2024 CRISPR-Cas9 mediated gene editing in tilapia: enhancing growth rates and disease resistance, Genomics and Applied Biology, 15(2): 99-106.

Liu R., Liu R., Song G., Li Q., Cui Z., and Long Y., 2022, Mitochondria dysfunction and cell apoptosis limit resistance of Nile Tilapia (*Oreochromis niloticus*) to lethal cold stress, Animals, 12(18): 2382.
https://doi.org/10.3390/ani12182382

Ma J.L., Xu D.P., Tao Y.F., Zheng T., Xu P., and Qiang J., 2023, Integrated transcriptome and miRNA sequencing analyses reveal that hypoxia stress induces immune and metabolic disorders in gill of genetically improved farmed tilapia (GIFT *Oreochromis niloticus*), Fish and Shellfish Immunology, 139: 108909.
https://doi.org/10.1016/j.fsi.2023.108909

Malik A., Shah S., Kalhoro I.B., and Kalhoro H., 2014, Growth performance and adaptation of imported strain of Nile tilapia *Oreochromis niloticus* (Linnaeus 1758) culture at fish hatchery *Chilya thatta* (Sindh-Pakistan), J. Sci. Tech., 3: 5-9.

Mirera D.O., and Okemwa D., 2023, Salinity tolerance of Nile tilapia (*Oreochromis niloticus*) to seawater and growth responses to different feeds and culture systems, Western Indian Ocean Journal of Marine Science, 22(2): 75-85.
https://doi.org/10.4314/wiojms.v22i2.6

Mohamad S.N., Noordin W.V.M., Ismail N.F., and Hamzah A., 2021, Red hybrid tilapia (*Oreochromis* spp.) broodstock development programme in Malaysia: status challenges and prospects for future development, Asian Fisheries Science, 34(1): 73-81.
https://doi.org/10.33997/J.AFS.2021.34.1.008

Obirikorang K.A., Appiah-Kubi R., Adjei-Boateng D., Sekey W., and Duodu C., 2023, Acute hyperthermia and hypoxia tolerance of two improved strains of nile tilapia (*Oreochromis niloticus*), Stress Biology, 3(1): 21.
https://doi.org/10.1007/s44154-023-00099-w

Radwan I., 2020, Case study on developing financially viable recirculation aquaculture systems (RAS) for tilapia production in Egypt: technology transfer from the Netherlands, Alexandria: Egyptian Aquaculture Centre and Institute of Aquaculture, University of Stirling, 2011.
https://doi.org/10.1079/ac.118016.20203483082

Shaalan M., El-Mahdy M., Saleh M., and El-Matbouli M., 2018, Aquaculture in Egypt: insights on the current trends and future perspectives for sustainable development, Reviews in Fisheries Science and Aquaculture, 26(1): 99-110.
https://doi.org/10.1080/23308249.2017.1358696

Shafiujjaman M., Mandal S.C., Moniruzzaman M., Habibullah-Al-Mamun M., Shaikh M.A.A., Watanabe K., and Hossain A., 2024, Environmental and human health risk of potentially toxic metals in freshwater and brackish water Nile tilapia (*Oreochromis niloticus*) aquaculture, Environmental Geochemistry and Health, 46(11): 477.
https://doi.org/10.1007/s10653-024-02249-z

Shuai F., and Li J., 2022, Nile tilapia (*Oreochromis niloticus* Linnaeus 1758) invasion caused trophic structure disruptions of fish communities in the south china river-Pearl River, Biology, 11(11): 1665.
https://doi.org/10.3390/biology11111665

Li S.F., Cai W.Q., Elghobashy H., Fitzsimmons K., and Diab A., 2008, Contribution of genetic improved strains to Chinese tilapia industry, International Symposium on Tilapia in Aquaclture, 2008: 213-218.

Vicente I., and Fonseca-Alves C., 2013, Impact of introduced Nile tilapia (*Oreochromis niloticus*) on non-native aquatic ecosystems, Pakistan Journal of Biological Sciences, 16(3): 121-126.
https://doi.org/10.3923/PJBS.2013.121.126

Yan T., Guo Y., Wang Z., Liu L., and Liu C., 2014, Genetic diversity of GIFT tilapia populations by AFLP analysis, The International Journal of Marine Science, 2014: 4.
https://doi.org/10.5376/IJMS.2014.04.0060

Yáñez J., Yoshida G., Barría A., Palma-Vejares R., Travisany D., Díaz D., Cáceres G., Cádiz M., López M., Lhorente J., Jedlicki A., Soto J., Salas D., and Maass A., 2020, High-throughput single nucleotide polymorphism (SNP) discovery and validation through whole-genome resequencing in Nile tilapia (*Oreochromis niloticus*), Marine Biotechnology, 22: 109-117.
https://doi.org/10.1007/s10126-019-09935-5

Yuan Y., Yuan Y., Dai Y., and Gong Y., 2017, Economic profitability of tilapia farming in China, Aquaculture International, 25: 1253-1264.
https://doi.org/10.1007/s10499-017-0111-8

Zhou Y., Zhang Y.J., Wei S., Li W., Li W.H., Wu Z.C., Jiang S.W., Lu Y., Xu Q.H., and Chen L.B., 2022, Reduced hypoxia tolerance and altered gill morphology at elevated temperatures may limit the survival of tilapia (GIFT *Oreochromis niloticus*) under global warming, Fishes, 7(5): 216.
https://doi.org/10.3390/fishes7050216