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Selective breeding of Nile tilapia, *Oreochromis niloticus*: A strategy for increased genetic diversity and sustainable development of aquaculture in Kenya

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ABSTRACT

The aquaculture subsector is important in Kenya for food and nutritional security. The rapid growth of the subsector is evident especially in the widespread culture of Nile tilapia (*Oreochromis niloticus*); however, the gains made in the industry may be curtailed by inadequate quality seed. Currently, hatcheries are plagued by inbreeding, hybridization of related stocks, and poor-quality broodstock due to lack of proper selective breeding plans or strain improvement for broodstock development. Properly designed selective breeding programs in both public and private hatcheries will be the solution to provision of quality seeds for sustained aquaculture growth. Currently, the fingerlings produced exhibit a low growth rate under culture conditions. This review discusses the significance of genetic improvement of *Oreochromis niloticus* through selective breeding with reference to current and previous global experiences and reports. Genetic improvement of tilapia is important in provision of quality seeds to farmers for growth in body weight and sustainable aquaculture development. Body weight, survival, and resistance to diseases are heritable traits that can be improved through selective breeding for a long-term genetic gain and trait improvement. A strain improvement program that encompasses establishment of breeding nuclei and programs for monitoring and evaluation of hatcheries, based on the existing standard operating procedures for tilapia seed production, should be in place to ensure adherence to the procedures for stock improvement and sustainable growth of aquaculture in Kenya.

KEYWORDS

Aquaculture; genetics; *Oreochromis niloticus*; selective breeding

Introduction

Aquaculture is the world's fastest agrifood production sector and through its value chain linkages is important for emerging economies in promoting rural development, food and nutrition security, and poverty alleviation (Chu et al. 2018).

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Aquaculture contributed 47% of the total fish produced globally in 2018 and has had an annual growth of 12% since 1990 (FAO, 2020). A vast majority of aquaculture products are derived from Asian countries, with the region producing 72.8 million tons of farmed aquatic produce out of the total 82.1 million tonnes of total production (FAO, 2020). One of the reasons that make Asia a lead aquaculture producing region is the use of improved strains of farmed fish species. These include the carps (Hulata 1995; Nguyen and Ponzoni 2008), tilapias (Nguyen 2016), salmonids (Khang et al. 2018), and shrimp (Fjalestad, Moen, and Gomez-Raya 2003), all developed mainly through traditional selective breeding. The Genetically Improved Farmed Tilapia (GIFT) strain of the Nile tilapia (*Oreochromis niloticus*), for instance, was developed in Asia to address poor growth rates of existing farmed strains (Eknath et al. 1993) and helped increase tilapia production in the Philippines by 186% (ADB 2005). Since its development in 1997, the GIFT strain has been widely distributed in Asia, and farmers have continuously improved the strain through selective breeding. It has demonstrated great performance: 30%–65% higher than nonimproved strains (Dey 2000).

Nile tilapia (*Oreochromis niloticus*) is a leading species in Kenyan aquaculture, although farmed production of the species is low, averaging 14,952 tonnes annually (Opiyo et al. 2018). The fish is reared mainly through semi-intensive culture systems and contributes more than 70% to the total aquaculture production (Obwanga et al. 2020). Although costly, intensive culture systems of tilapia have emerged, with more focus on the Recirculating Aquaculture System (RAS) being embraced and cage culture becoming an investment choice for many farmers (Orina et al. 2018; Opiyo et al. 2018). The RAS system is suitable in areas with low annual rainfall like arid and semi-arid lands, which has opened opportunities for fish farming in such areas, hence opening up rural economies and enhancing protein uptake. For instance, Kamuthanga Fish Farm has increased the efficiency of aquaculture enterprises through RAS, reducing the growout period by half, with an average fish harvest weight of 400 to 500 g, compared to 300 g in 9 months from farms not practicing RAS (Obiero, Munguti, and Ani 2019).

A recent effort at increasing production of the species, and aquaculture in general, was the Government-supported National Fish Farming Enterprise Productivity Program (FFEPP), in which farm subsidies were provided to farmers, new hatcheries were established, and existing or dilapidated ones in the country were improved from 2009 to 2012. The result of this was an instantaneous increase in the number of farmers engaged in fish farming from 4,742 to 49,050 (Nyandat and Owiti 2013). Land under aquaculture increased from 722 Ha in 2008 to 3500 Ha in

2018 (Opiyo et al. 2018). Production levels increased from 4,452 MT (in 2008) to a record high of 24,096 MT in 2014 (Figure 1). Currently, fish farming contributes 12.8% to the total fish production, with a production of 18,542 MT realized in 2019 (Kenya National Bureau of Statistics 2020).

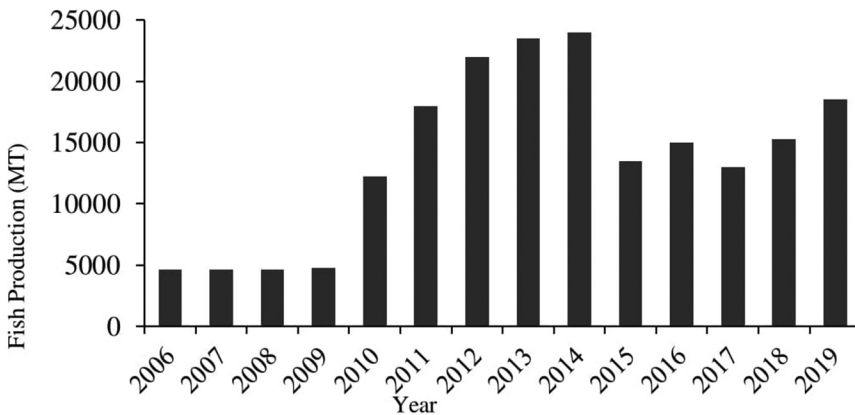


Figure 1. Trends in aquaculture production in Kenya from 2006 to 2019 (Kenya National Bureau of Statistics 2020).

Although the increase in tilapia production was modest, this national program stimulated private investments in aquaculture, and more hatcheries have since been established by farmers interested in commercial farming of tilapia. By 2013, another opportunity to upscale aquaculture production in Kenya came via establishment of devolved units of governance (county governments), following the promulgation of the Constitution of Kenya in 2010, in which aquaculture development was devolved from national to county governments. A number of these devolved units have started investments in aquaculture, with more hatcheries being established in Uasin Gishu, Vihiga, Muranga, Kirinyaga, Kiambu, Nairobi, Homabay, and Siaya counties; others such as Kisii, Murang'a, and Bungoma have renovated hatchery facilities that had been grounded. Further opportunities for higher tilapia production have also occurred in cage culture of tilapias in Lake Victoria, which provide lucrative investment opportunities for tilapia farmers and hatchery operators. Production from cages is estimated to be 40,000 MT of fish per year (Njiru, Aura, and Okechi 2019). However, these important investments and official efforts to support tilapia farmers face significant challenges along the production value chain, which could be addressed by adopting modern scientific techniques, such as selective breeding.

Selective breeding has the potential to improve the productivity of farmed Nile tilapia in Kenya by targeting traits of economic importance. Through this

technology, a remarkable improvement in such traits can be achieved within a few generations. Despite the significance of such technologies, little effort has been devoted to conservation and selection of the tilapia germplasm for seed improvement in Kenya (Omasaki et al. 2016). The country has made little effort in initiating a well-planned selective breeding program for Nile tilapia for sustainable and cost-effective aquaculture production. This has been coupled with weak policies and lack of regulation for authentication and monitoring of hatcheries. This article reviews the global experience and significance of genetic selection of *O. niloticus* to inform on the need to initiate policy guidelines for the management of genetic resources to optimize aquaculture production in Kenya.

Tilapia in aquaculture

As a lead species in aquaculture with fast growth rates, resistance to diseases, ability to feed on artificial diet, ability to culture in different production systems, and global market appeal (Liping and Fitzsimmons 2011; Yáñez, Joshi, and Yoshida), the Nile tilapia (*Oreochromis niloticus*) is native to Africa and the Middle East (Trewavas 1983), with its natural range encompassing the Nilo-Sudanian province, from the headwaters of the Nile in Ethiopia and Kenya, to the Nile Delta in Egypt, the Niger Basin, and lakes and streams once historically connected to these drainages (Trewavas 1983). Projected as the most important food fish on the planet (Liu and Fitzsimmons 2011), annual global production of farmed tilapia reached 6 million metric tonnes in 2020, overtaking salmonids and catfishes. Of this global production, China led the world with 1.8 million tonnes, followed by Indonesia with 900,000 tonnes in 2020 (FAO, 2020).

Apart from being a model species that allows the study of diverse traits of commercial importance (Kocher 2004), expansion of tilapia culture globally is also fueled by high genetic diversity in the available natural tilapia germplasm (Hassanien and Gilbey 2005). Additionally, a wide range of genomic resources has been developed for *O. niloticus* over the years to support the identification and mapping of traits for breeding improved and desired strains. One such commercially appealing trait of farmed tilapias is monosex male tilapias. Tilapias are sexually dimorphic for growth rate, with males having a natural ability to grow faster than females (Bhatta et al. 2013). Global production of farmed tilapia relies on all-male populations, as this eliminates prolific breeding at the expense of somatic growth (Beardmore, Mair, and Lewis 2001), common in mixed-sex cultures. All-male tilapia seeds are, for instance, in high demand by tilapia cage culture enterprises in Lake Victoria, to avoid breeding where hatchlings would easily escape through the mesh into open waters and interact with natural tilapias. In this regard, considerable research efforts have been invested in identification of loci linked to sex (Lee, Hulata, and

Kocher 2004), identification of tilapia brood stock carrying the W or Y chromosomes (Lee, Hulata, and Kocher 2004), mapping of quantitative trait loci regions for sex determination in tilapias (Shirak et al. 2006), developing physical maps for whole genome sequencing (Katagiri et al. 2005), and identification of genes that drive sex determination in tilapias (Cnaani et al. 2008).

Current status of Nile tilapia breeding in Kenya

To support and upscale the tilapia industry in Kenya, there is a need to produce and supply high-quality fingerlings all year round at affordable cost to farmers. The establishment of hatcheries in Kenya coincided with the rapid growth in aquaculture realized between 2009 and 2012 due to the prevailing demand for fingerlings. Between 2009 and 2012, Kenya recorded a rapid growth in hatcheries from 21 to 147; however, the number decreased to 125 in 2016, due to the cessation of funding of fish farming by the government (Nyonje et al. 2018). Currently the freshwater fish production hatcheries actively involved in production of tilapia, catfish, and various ornamental fish are approximated to be 40, mostly concentrated in Western Kenya, as shown in Table 1 and Figure 2. There is generally a lack of coordinated or weak regulatory policy among the relevant government entities for the establishment of tilapia hatcheries, hence compromising production and supply of quality seeds to farmers in Kenya.

Hatchery production of *O. niloticus* is typified by small-scale fingerling production in open earthen ponds measuring between 50 and 600 m². Therefore, the fry are bred and nursed in these ponds. Farmers utilizing such ponds as hatcheries also stock brood fish of nonuniform sizes, of unknown ancestry, and maintained under poor managerial regimes. These are the same conditions in which most Asian farmers kept their tilapias in backyard ponds (Eknath et al. 1993), with poor yields of small-sized tilapias, necessitating the initiation of the genetically improved farmed tilapia (GIFT) project (Eknath et al. 1993). Furthermore, without a clearly known origin of the brood stock, the fish most likely is sourced from stocks suffering from genetic founder effects, as is common among farmed tilapia sources globally (Beardmore, Mair, and Lewis 2001), a practice that is difficult to avoid under farm conditions. Consequently, the fish suffer high levels of inbreeding, which is often compounded by hybridization or introgression of genetic material from feral tilapias (Macaranas, Taniguchi, and Pante 1986), since tilapias are also prolific breeders in culture conditions. Inbreeding leads to loss of genetic variability (Brummett and Ponzoni 2009) and inbreeding depression associated with lower growth rates, low survival, and low fecundity (Ren et al. 2020). Often, these challenges are due to lack of properly trained personnel and proper framework that is important in guiding farmers.

Table 1. Major freshwater fish production hatcheries in Kenya.

County	Hatchery	Species
Siaya	Belvis Hatchery	<i>O. niloticus</i>
	Mabro Fish Farm Hatcheries	<i>O. niloticus</i>
	Cosade Hatchery	<i>O. niloticus</i>
	Agunja Hatchery	<i>O. niloticus</i> , <i>C. gariepinus</i>
	Dominion Fish Farm	<i>O. niloticus</i>
Kakamega	Maisha Fish Farm	<i>O. niloticus</i>
	SAFE Farm	<i>O. niloticus</i>
	Labeled Cash Marine Enterprise	<i>O. Niloticus</i> , <i>C. gariepinus</i> , <i>goldfish</i>
	Jafi Fish Farm	<i>O. niloticus</i>
	Lutonyi Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i>
Busia	Oketebwa Hatchery Fish Farm	<i>O. niloticus</i>
	Hydro Victoria Fish Hatchery	<i>O. niloticus</i>
	Butula Nerika Fish Hatchery	<i>O. niloticus</i>
	Wakhungu Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i>
	USUO Fish Hatchery	<i>O. niloticus</i>
Homabay	Lake View Fisheries Limited	<i>O. niloticus</i>
	Jewlet Enterprises	<i>O. Niloticus</i> , <i>C. gariepinus</i>
	Muga Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i>
	Victory Fish Farm	<i>O. niloticus</i>
Kisumu	Lake Basin Kisumu	<i>O. niloticus</i> , <i>C. gariepinus</i>
	Victolapia Fish Farm	<i>O. niloticus</i>
	Pioneer Fish Farm	<i>O. niloticus</i>
	Sangoro Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i>
Kirinyaga	Green Algae Highlands	<i>O. niloticus</i> , <i>C. gariepinus</i> , <i>ornamental fish</i>
	Sagana Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i> , <i>ornamental fish</i>
	Karunditu Fish Farm	<i>C. gariepinus</i> , <i>ornamental fish</i>
	Mwea Aquafish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i> , <i>ornamental fish</i>
	Kutus Fish Farm and Hatchery	<i>O. niloticus</i> , <i>C. gariepinus</i>
	Emmick Enterprises	<i>O. niloticus</i>
Kisii	Kegati Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i> , <i>goldfish</i>
	Kisii Multiplication Center	<i>O. niloticus</i> , <i>C. gariepinus</i>
Machakos Muranga	Kamuthanga	<i>O. niloticus</i>
	Makindi Fish Farm	<i>O. niloticus</i>
Vihiga	Tigoi Fish Farm	<i>O. Niloticus</i> , <i>C. gariepinus</i>
	Mwitoko Fish Hatchery	<i>O. niloticus</i> , <i>C. gariepinus</i>
Uasin Gishu	University of Eldoret Fish Farm	<i>O. niloticus</i> , <i>C. gariepinus</i>
Baringo	Omega Farm	<i>O. niloticus baringoensis</i>
Nairobi	Paradise Fish Farm	<i>C. gariepinus</i>

Source of broodstock for the hatcheries in Kenya

The main source of broodstock, as recorded in the recent survey by Nyonje et al. (2018), is Lake Victoria, which provides 80% of the broodstock to the Kenyan hatcheries. Others include Lakes Baringo and Kyoga. Recently, there has been interest in the Lake Turkana *O. niloticus* strain due to the observed high genetic diversity and the high number of private alleles, which is

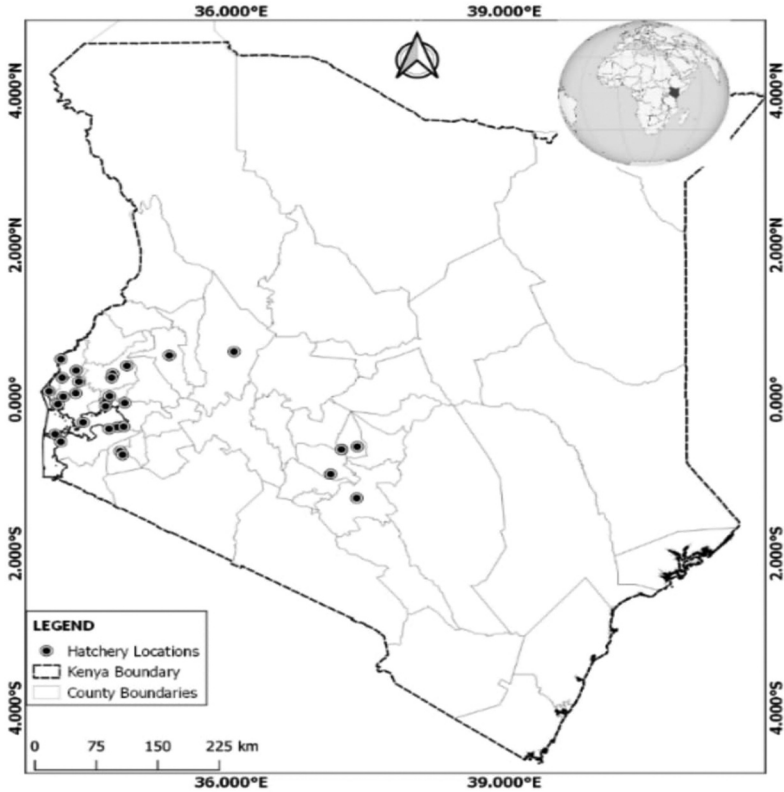


Figure 2. Current distribution of major fresh water fish production hatcheries in Kenya.

important in maintenance of a vibrant breeding stock (Tibihika et al. 2020). This population will be important in stock improvement in the local breeding programs. In other hatcheries, broodstock are obtained from more established hatcheries like the National Aquaculture development training and Research Center (NARDTC), Sagana. Other hatcheries have illegally imported improved broodstock from Asian countries and Uganda due to the emerging demand for high-performing strains. However, the genetic quality of the imported populations is not known, and the consequences on the feral population may be negative, considering the chances of fish escaping from aquaculture facilities into the natural ecosystems.

The concept and history of selective breeding

Selective breeding is the process where the genetic variation present in desirable traits within a population is used to improve production quality, efficiency, and sustainability of the target species (Brummett and Ponzoni 2009). It has very high potential for improving genetic makeup of fish in aquaculture

production, which is important in realizing high fish production and profitability of the culture enterprise (Murphy et al. 2020). Though relatively limited in application in aquaculture species, this technology has an advantage of producing permanent genetic gains that are cumulative compared to other genetic improvement methods such as hybridization, chromosomal manipulation, cross-breeding, transgenesis, etc. (Chavanne et al. 2016). For example, a genetic gain of 2% per annum will impart to commercial fish 20% superiority in productivity compared to the current production for the next 10 years (Gjedrem, Robinson, and Rye 2012). A simple genetic improvement protocol would involve selection of the best-performing parents of generation one, which are then paired to produce generation two progeny. The resulting population will demonstrate a genetic improvement with a higher phenotypic mean of the trait targeted compared to the founder population.

The most significant selective breeding program where a high-performing strain for fresh water aquaculture was developed is the GIFT, which was established in 1988 through a collaborative research approach involving the Asian Development Bank (ADB) and other institutions in Asia and executed by the International Center for Living Aquatic Resources Management (ICLARM)—currently, World Fish and AKVAFORSK in Norway (Eknath et al. 1993; Yáñez, Joshi, and Yoshida). The GIFT strain was generated by crossing four wild strains from Africa and four farmed strains from the Philippines (Murphy et al. 2020). The base population was established in early 1990 in the Philippines, and by 1996, six generations of selection for growth had been produced (Nguyen 2016), with an average genetic response of 13% higher than the local strains. The improved strain has been transferred to several countries globally, where selection has been continuing. By 2013, sixteen generations of selection had been developed. The countries in Asia where the GIFT strain has had a remarkable impact on aquaculture productivity include China, the Philippines, Malaysia, Bangladesh, Thailand, Vietnam, and Sri Lanka (Hamzah, Ponzoni, Nguyen, and Khaw 2014). For example, in the Philippines, tilapia production increased by 186% over a period from 1990 to 2007. The cost of production was also reduced by 32%–35% in the same period, signifying the impact of selective breeding for aquaculture productivity (ADB 2005). The superiority of the GIFT strain over the non-GIFT tilapia across different countries and production systems is illustrated in Table 2. Pond and cage systems used in the evaluation of the performance of the GIFT strain in Asia mirror the production systems in Kenya, demonstrating that the application of selective breeding will yield similar results and therefore should be adopted.

Table 2. Comparative yields of F3 GIFT and non-GIFT strains in selected Asian countries, adopted from Dey et al. (2008).

Country	Production system	Non-GIFT yield (Kgs/ha)	GIFT yield Kgs/ha	Yield gain (%)
Bangladesh	Pond	896	1593	78
China	Pond	310,967	389,346	25
	Cage	4275	4645	9
Philippines	Pond	15,285	23,551	54
	Cage	912	1361	49
Thailand	Pond	2044	2829	38
Vietnam	Pond	558	743	33

The most popular and preferred genetic improvement of tilapia is mass selection and pedigree-based selection, although recently genome-wide single nucleotide polymorphism (SNP) has been embraced by top global breeders as standard and more robust for stock improvement (Gratacap et al. 2019; Houston et al. 2020; Lu et al. 2020; Zenger et al.). Furthermore, due to increasing sophistication of tools for genomics research, as well as decreasing costs of sequencing, it should be possible to study quantitative trait loci for other economically important traits yet impossible to measure such as disease resistance, fillet quality, maturation, and feed efficiency (Chen et al. 2019) to hasten the process of selecting desirable genotypes for use in breeding.

In Africa, the need to improve strains and to benefit from the GIFT project without ecological risks led to the development of the Akosombo and Abbassa strains in Ghana and Egypt respectively. The Akosombo strain was developed from the year 2000 at the Aquaculture Research and Development Center (ARDC) of the Water Research Institute (WRI) in Ghana (Anane-Taabeah and Hallerman 2019). This strain was developed from a founder population of wild germplasm from different ecological zones and a farmed stock in 4 × 4 diallel cross. This has since become the nucleus of the breeding program in Ghana and the West African region due to its comparatively high performance in growth. A recent evaluation of the performance of the improved strains in Ghana demonstrated that the Akosombo strain grew 16.6 g larger than the nonimproved strains (Trinh et al. 2021), and the Abbassa strain has demonstrated a growth performance 28% better than a commercial strain and a comparatively lower recorded food conversion ratio (FCR) of 1.5 (Ibrahim, Mohamed Nasr-Allah, and Charo-Karisa 2019). All these programs clearly demonstrate great opportunities for tilapia aquaculture in Africa and particularly Kenya through adoption of selective breeding for stock improvement.

Genetic improvement of Nile tilapia in Kenya

Genetic improvement through selective breeding involves heavy capital and human resource investment, and these factors have constrained its adoption in Kenya. The first attempt at selective breeding of tilapias in Kenya was initiated at the National Aquaculture Research Development and Training Center

(NARDTC), Sagana, in 2010 through a project funded by the Kenya Productivity and Agribusiness Project (KAPAP). The founder population was comprised of locally available *O. niloticus* strains from private and government hatcheries and the wild population from Lakes Victoria and Turkana. The main goal for selection in this program was improving harvest weight in semi-intensive systems. This was important because the culture systems in Kenya are at a semi-intensive level, exploiting both primary productivity of the water and supplementary feeding of the fish. The program at NARDTC set a model in which the station would act as the breeding nucleus that would supply improved tilapia broodstock to other hatcheries, as shown in [Figure 3](#). The proposed model for stock improvement never achieved expected objectives due to lack of funding and goodwill from the government after the KAPAP project ended. However, Omasaki et al. (2016), with funding from the Koepon Foundation and Wageningen University estimated the genetic parameters of the nucleus population at NARDTC through genotype by environmental interaction ($G \times E$), which generated the seventh-generation (F7) population. Ongoing research at the same station, funded by the Kenya Climate Smart Agriculture project (KCSAP) and the AgriFI-Kenya Climate Smart Agricultural Productivity Project (AgriFI Kenya CSAPP), still focuses on improving traits of economic importance for distribution of improved broodstock and seeds to hatcheries and farms in the country.

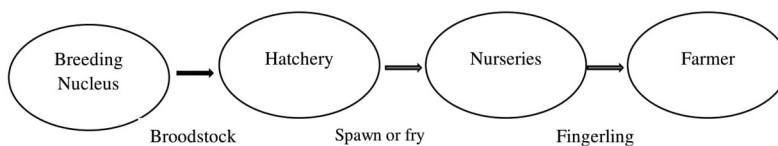


Figure 3. Proposed genetic improvement model for *O. niloticus* in Kenya.

Significance of stock improvement

Increased farm production

Fish farmers in Kenya rank growth as the most important trait for choice of culture species since it influences the final harvest weight and the growout period (Omasaki, Charo-Karisa, and Kosgey 2013; Oyieng and Kahi 2013), two factors that impact the profitability of the aquaculture venture. For example, most tilapia farmers in Kenya use all-male tilapia brooders for aquaculture ventures (Githukia et al. 2015), just like the practice globally where economic production of tilapias exploits monosex populations (Wohlfarth 1994). This is because prolific breeding in mixed-sex tilapia culture diverts energy from somatic growth to reproduction, producing many small-sized fish of low market value (Opiyo et al. 2020). Due to sexual dimorphism,

male tilapias grow faster than females (El-Greisy and El-Gamal 2012). For mouth brooding species like *O. niloticus*, females further forego feeding for up to 21 days as they incubate eggs and nurse fry, which further impedes their growth (Ajiboye et al., 2015). In a selective breeding program, it is still possible for farmers using all-male tilapias to select the faster-growing individuals from the pool of all-male fish for stocking in ponds to begin the enterprise.

Using genetically improved tilapia in breeding programs in Kenya will dramatically increase aquaculture production twofold, thus enhancing aquaculture sustainability in the country. This is also supported by a review by Gjedrem, Robinson, and Rye (2012), who predicted double production by the year 2020 globally under the application of genetically improved organisms and estimated that genetic gain of 5.4% would result to 53.2 million tonnes of fish when improved material is used in aquaculture systems. In other studies on *O. niloticus* reared in brackish water and selected for improved growth over four generations, Ninh et al. (2014) realized a positive genetic correlation between body weight and length (0.97); the study by Rye et al. (2015) on determination of growth parameters, selection response, and fillet yield of *O. niloticus* after six generations of multitrait selection revealed a considerable improvement of growth of between 60% and 90% with selection response of 8% per generation. Selection for growth of the GIFT strain in Malaysia revealed a progressive trait improvement through eight generations, as shown in Figure 4 while in Sri Lanka, the GIFT strain exhibited a remarkably improved genetic gain of 112% compared to local varieties across three different culture systems (Nguyen 2016). A higher survival of between 8% and 23% was also registered compared to the local stock.

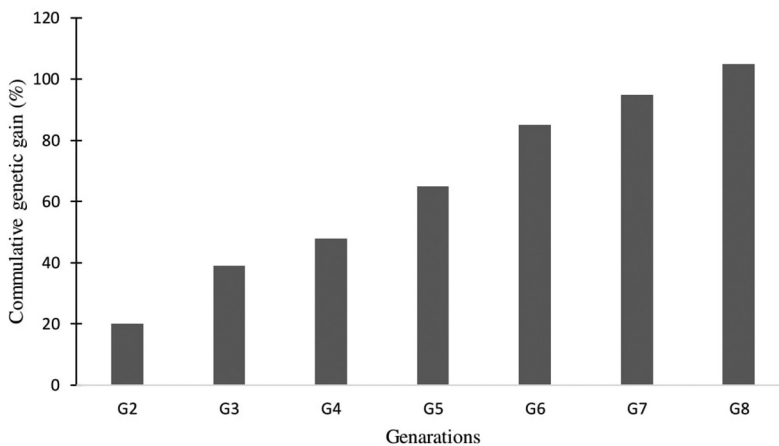


Figure 4. Genetic gain of body weight of GIFT strain over eight generations in Malaysia (adopted from Hamzah et al. 2014).

Increased economic value

Improved economic value of an aquaculture enterprise is another important goal for a selective breeding program. Profitability is a key parameter in adoption of breeding technology. In Kenya and sub-Saharan African countries, feed cost is the greatest challenge and may stymie the realization of profitable aquaculture as it constitutes between 50% and 70% of production cost (Chan et al. 2019; Munguti, Kim, and Ogello 2014). Stock improvement programs should therefore target selection for improved food efficiency of tilapia; that will result in reduced feed consumption at a targeted production level to achieve economic sustainability of fish farming (de Verdal et al. 2018). Kenya's aquaculture industry will be more economically sustainable with a well-designed stock improvement program for tilapia, as has been experienced in countries that continue to invest in selective breeding. For example, the second generation of genetically improved farmed tilapia (GIFT) tested in Bangladesh, China, Thailand, and Vietnam revealed a lowered production cost by 20%–30%, partly due to the efficiency of the improved strain in utilization of feed resources (Dvergedal et al. 2019). Additionally, in the Philippines, 84% profitability was estimated for a 40% increase in productivity due to the adoption of the improved GIFT strain in the Philippines (Gupta et al. 2010).

Fish appearance, such as color and body shape, plays an important role in consumer preference; at the same time, large variation in cohort weight and size at harvest reduces the market value and fish farm profitability. Selective breeding technology can be used to mitigate such challenges for increased hatchery and farm returns (Marjanovic et al. 2016). Under the standard operating procedures for tilapia seed production in Kenya and the manual for good aquaculture management practices for hatcheries in Kenya, there is a need to produce and supply uniform-sized fingerlings to farmers. Genetic selection for uniformity within a population will mitigate against the effects of environmental fluctuations on some individuals, hence enhancing their performance. The study of the estimation of genetic parameters of uniformity of harvest weight and body size of the GIFT strain of tilapia revealed a 13% genetic variance as a result of the group effect (Marjanovic et al. 2016). This implies that individuals in the same group are more uniform than in a different group. This still justifies that application of selective breeding in the culture of tilapia is important in producing uniform individuals for both local and international markets, a factor that can be exploited by Kenyan fish traders.

Disease resistance

With the rapid growth of the aquaculture industry in Kenya, sustainable growth hinges on intensification of the systems. Disease outbreaks are associated with such systems and are very problematic, hence the need for

mitigation measures. Currently, there is no information on regulation of the use of antibiotics, probiotics, and vaccines for aquaculture in Kenya (Opiyo et al. 2018). Disease transmission vectors are common in farmed fish in Kenya (Mukwabi et al. 2019), with *Philometroides spp.*, *Acanthocephalus spp.*, and *Procamallanus spp.* being common in farmed tilapia. The disease occurrences are caused by poor water quality coupled with poor fish husbandry. Furthermore, biosecurity measures are inadequate and at times not adhered to, resulting in mass mortalities due to infectious diseases.

Selective breeding has been proposed as a promising option for disease management in culture systems (Leeds and Wiens 2019; Megahed 2019). A recent report by Barriá et al. (2020) on the genetic parameters to resistance against the Tilapia lake virus (TiLV) revealed that selective breeding of *O. niloticus* with GIFT origin increased resistance and reduced mortality. A significant additive genetic variation was detected in the different models applied to the population, and a heritability value of 0.23 was estimated, signifying the potential of selective breeding to improve resistance to diseases. Similar responses were observed in another selection for resistance to *Streptococcus agalactiae* in Thailand where the risks of death of fish remarkably decreased by 54%, the survival rate increased by 21%, and heritability was estimated at 0.22 (Suebsong et al. 2019). columnaris disease (*Flavobacterium columnare*) is a major cause of tilapia mortality in Thailand, and selective breeding has been demonstrated to increase resistance to the disease. Another study by Wonmongkol et al. estimated quantitative genetic parameters in the Chitralada tilapia strain on resistance against columnaris disease, which demonstrated a heritability estimate of 0.33 under the threshold sire–dam model and a mean survival of 32%.

Adaptability to various culture conditions

The semi-intensive culture systems of tilapia culture practiced in Kenya are characterized by low input and diverse culture conditions dictated by level of income and market objectives (Omasaki et al. 2017). The systems are also associated with poor water quality due to poor husbandry practices. Water quality is the most limiting factor in aquaculture and affects feed efficiency, fish growth rate, survival, and fish health (Wanja et al. 2020). Other external stressors that might compromise fish welfare include high stocking densities, poor nutrition, and transportation stress, among others.

Understanding genetic and environment interaction ($G \times E$) is very important in the design of a selective breeding program that suits different culture environments. According to Thoa et al. (2016), selection for traits under vulnerable conditions may produce genotypes that excel in a wide range of culture environments. Selection for faster growth, FCR, sexual maturity, and gill condition of tilapia revealed a heritability for body weight of 0.6–0.7 (Thoa

et al. 2016), indicating a positive chance for future genetic response to further selection by the population. A genetically improved tilapia strain has been demonstrated to adapt to various culture systems; both controlled and open. Studies by Rowena, Ikeda, and Basiao (2010) indicated the superiority of the GIFT strain compared to the unselected red tilapia in growth in all the culture systems, where the GIFT strain exhibited a specific growth rate (SGR) of 1.358%/day in a controlled environment in tanks; the unselected strain was 1.257% in the tanks. The same trend was demonstrated in the open system in cages, where the SGR in the GIFT and unselected strains was 1.57% per day and 1.456% per day respectively. It is therefore possible for Kenyan fish farmers to grow tilapia profitably using improved strains that adapt to a wide range of culture conditions.

Conclusions and recommendations

The growing demand for food and nutritional security will require strengthening of strategies of boosting aquaculture production. Clearly, adoption of genetically improved breeding of tilapia is still not popular in Kenya, yet it is one of the best approaches that can enhance the productivity of tilapia significantly, increase profitability of farmed tilapia for economic empowerment of the rural and peri-urban populations, and improve nutritional and food security due to increase per capita fish consumption. Kenya plans to increase per capita fish consumption from 4.5 kg to 10 kg in the next 10 years, with a target production of 350,000 MT fish under aquaculture. This targeted production and economic sustainability will only be realized under a well-planned breeding program. Such strategies should focus on traits of economic value such as improved fish growth, feed efficiency, improved food conversion ratio (FCR), tolerance to disease as production intensifies, and tolerance to environmental and climate changes.

Cage culture technology is emerging as an alternative system embraced by fish farmers in Kenya due to the relatively high income associated with a high production of fish (Njiru, Aura, and Okechi 2019). However, there are challenges experienced, such as fish death from anoxic conditions, poor feeds, and lake upwelling. Development of a tilapia strain that withstands poor culture conditions is critical for the successful development and implementation of cage culture in freshwater lakes, dams, and rivers. The genetic impact of improved stock on the recipient wild population is a contested debate that cannot be overlooked, and the potential ecological ramifications can negatively affect both capture fisheries and aquaculture in Kenya. Currently the cage establishments, especially in Lake Victoria, cannot prevent fish from escaping into open waters. The government, through extension officers, should monitor and provide awareness of proper cage construction, stocking, and good

harvesting to avoid farmed fish escaping into the water. In consultation with the stakeholders, the national and county governments should formulate evidence-based policies to protect and mitigate against genetic pollution of the wild tilapia germplasm. Regulatory measures also need to be put in place to ensure inspection and monitoring of the hatcheries and evaluation of the hatcheries' performance to ensure maintenance of high-quality fish seed for Nile tilapia culture in Kenya.

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References

- ADB. 2005. *An impact evaluation study on the development of genetically improved farmed tilapia and their dissemination in selected countries*. 77th. Manila, Philippines: Asian Development Bank.
- Ajiboye, O. O., A. O. Victor, F. Adams, A. O. Victor, F. Adams, and F. Adams. 2015. Effect of testosterone-induced sex reversal on the sex ratio, growth enhancement and survival of Nile Tilapia (*Oreochromis niloticus*) fed coppers and farm produced feed in a semi flow-through culture system. *Fisheries and Aquaculture Journal* 06 (2):02. doi:10.4172/2150-3508.1000123.
- Anane-Taabeah, F., and Hallerman. 2019. Aquaculture-mediated invasion of the genetically improved farmed Tilapia (gift) into the lower volta basin of Ghana. *Diversity* 11 (10):188. doi:10.3390/d11100188.
- Barria, A., T. Q. Trinh, M. Mahmuddin, J. A. H. Benzie, V. M. Chadag, and R. D. Houston. 2020. Genetic parameters for resistance to Tilapia Lake Virus (TiLV) in Nile tilapia (*Oreochromis niloticus*). *Aquaculture* 522 (May):1–7. doi:10.1016/j.aquaculture.2020.735126.
- Beardmore, J. A., G. C. Mair, and R. I. Lewis. 2001. Monosex male production in finfish as exemplified by tilapia: Applications, problems, and prospects. *Aquaculture* 197 (1–4):283–301. doi:10.1016/S0044-8486(01)00590-7.

- Bhatta, S., T. Iwai, T. Miura, M. Higuchi, G. Maugars, and C. Miura. 2013. Differences between male and female growth and sexual maturation in tilapia (*Oreochromis mossambicus*). *Kathmandu University Journal of Science, Engineering and Technology* 8 (2):57–65. doi:10.3126/kuset.v8i2.7326.
- Brummett, R. E., and R. W. Ponzoni. 2009. Concepts, alternatives, and environmental considerations in the development and use of improved strains of Tilapia in African Aquaculture. *Reviews in Fisheries Science* 17 (1):70–77. doi:10.1080/10641260802083174.
- Chan, C. Y., N. Tran, S. Pethiyagoda, C. C. Crissman, T. B. Sulser, and M. J. Phillips. 2019. Global food security. *Prospects and Challenges of Fish for Food Security in Africa* 20 (November 2018):17–25. doi:10.1016/j.gfs.2018.12.002.
- Chavanne, H., K. Janssen, J. Hofherr, F. Contini, P. Haffray, A. Consortium, . . . L. Bargelloni. 2016. A comprehensive survey on selective breeding programs and seed market in the European aquaculture fish industry. *Aquaculture International* 24 (5):1287–307. doi:10.1007/s10499-016-9985-0.
- Chen, C. H., B. J. Li, X. H. Gu, H. R. Lin, and J. H. Xia. 2019. Marker-assisted selection of YY supermales from a genetically improved farmed tilapia-derived strain. *Zoological Research* 40 (2):108–12. doi:10.24272/j..2095-8137.2018.071.
- Chu, L., M. J. Phillips, C. Y. Chan, N. Tran, A. S. Kefi, and S. Genschick. 2018. Fish supply and demand for food security in Sub-Saharan Africa: An analysis of the Zambian fish sector. *Marine Policy* 99 (November):343–50. doi:10.1016/j.marpol.2018.11.009.
- Cnaani, A., B. Y. Lee, N. Zilberman, C. Ozouf-Costaz, G. Hulata, M. Ron, . . . T. D. Kocher. 2008. Genetics of sex determination in tilapiine species. *Sexual Development* 2 (1):43–54. doi:10.1159/000117718.
- de Verdal, H., M. Vandeputte, W. Mekki, B. Chatain, and J. A. H. Benzie. 2018. Quantifying the genetic parameters of feed efficiency in juvenile Nile tilapia *Oreochromis niloticus*. *BMC Genetics* 19 (1):105. doi:10.1186/s12863-018-0691-y.
- Dey, M. M. 2000. The impact of genetically improved farmed Nile tilapia in Asia. *Aquaculture Economics and Management* 4 (1–2):107–24. doi:10.1080/13657300009380263.
- Dey, M. M., A. E. Eknath, L. Sifa, M. G. Hussain, T. M. Thien, H. N. Van, . . . N. Pongthana. 2008. Performance and nature of genetically improved farmed tilapia : A bioeconomic analysis. *Aquaculture Economics & Management* 4 (1–2):83–106. doi:10.1080/13657300009380262.
- Dvergedal, H., J. Ødegård, M. Øverland, L. T. Mydland, and G. Klemetsdal. 2019. Selection for feed efficiency in Atlantic salmon using individual indicator traits based on stable isotope profiling. *Genetics Selection Evolution* 51 (1):1–14. doi:10.1186/s12711-019-0455-9.
- Eknath, A. E., M. M. Tayamenb, M. S. P. Vera, J. C. Dantingb, R. A. Reyesb, E. E. Dionisiob, . . . R. S. V. Pullin. 1993. Genetic improvement of farmed tilapias : The growth performance of eight strains of *Oreochromis niloticus* tested in different farm environments *. *Aquaculture* 111 (709):171–88. doi:10.1016/0044-8486(93)90035-W.
- El-Greisy, Z. A., and A. E. El-Gamal. 2012. Monosex production of tilapia, *Oreochromis niloticus* using different doses of 17 α -methyltestosterone with respect to the degree of sex stability after one year of treatment. *Egyptian Journal of Aquatic Research* 38 (1):59–66. doi:10.1016/j.ejar.2012.08.005.
- FAO. 2020. *The State of World Fisheries and Aquaculture 2020. Sustainability in Action*. Rome. doi:10.4060/ca9229en.
- Fjalestad, K. T., T. Moen, and L. Gomez-Raya. 2003. Prospects for genetic technology in salmon breeding programmes. *Aquaculture Research* 34 (5):397–406. doi:10.1046/j.1365-2109.2003.00823.x.
- Githukia, C. M., E. O. Ogello, E. M. Kembanya, A. O. Achieng, K. O. Obiero, and J. M. Munguti. 2015. Comparative growth performance of male monosex and mixed sex

- Nile tilapia (*Oreochromis niloticus* L.) reared in earthen ponds. *Croatian Journal of Fisheries* 73 (1):20–25. doi:10.14798/73.1.788.
- Gjedrem, T., N. Robinson, and M. Rye. 2012. The importance of selective breeding in aquaculture to meet future demands for animal protein. *A Review. Aquaculture* 350–353:117–29. doi:10.1016/j.aquaculture.2012.04.008.
- Gratacap, R. L., A. Wargelius, R. B. Edvardsen, and R. D. Houston. 2019. Potential of genome editing to improve aquaculture breeding and production. *Trends in Genetics* 35 (9):672–84. doi:10.1016/j.tig.2019.06.006.
- Gupta, M. V., B. O. Acosta, A. E. Eknath, and M. M. Dey. 2010. Breakthrough in genetic improvement of tropical finfish through partnership between Iclarm, Asi and developing country Nars. *Genetic Resource Management and Biotechnology* 3 (8):1–8.
- Hamzah, A., R. Ponzoni, and N. H. Nguyen. 2014. Genetic evaluation of the Genetically Improved Farmed Tilapia (GIFT) strain over ten generations of selection in Malaysia. *Pertanika Journal of Tropical Agricultural Science* 37 (4):411–29.
- Hamzah, A., R. W. Ponzoni, N. H. Nguyen, and H. L. Khaw. 2014. Performance of the Genetically Improved Farmed Tilapia (GIFT) Strain over Ten Generations of Selection in Malaysia. *Tropical Agricultural Science* 37 (4):411–29.
- Hassanien, H. A., and J. Gilbey. 2005. Genetic diversity and differentiation of Nile tilapia (*Oreochromis niloticus*) revealed by DNA microsatellites. *Aquaculture Research* (36) 1450–57. doi:10.1111/j.1365-2109.2005.01368.x
- Houston, R. D., T. P. Bean, D. J. Macqueen, M. K. Gundappa, Y. H. Jin, T. L. Jenkins, . . . D. Robledo. 2020. Harnessing genomics to fast-track genetic improvement in aquaculture. *Nature Reviews. Genetics* 21 (7):389–409. doi:10.1038/s41576-020-0227-y.
- Hulata, G. 1995. A review of genetic improvement of the common carp (*Cyprinus carpio* L.) and other cyprinids by crossbreeding, hybridization and selection. *Aquaculture* 129 (1–4):143–55. doi:10.1016/0044-8486(94)00244-I.
- Ibrahim, N. A., A. Mohamed Nasr-Allah, and H. Charo-Karisa. 2019. Assessment of the impact of dissemination of genetically improved Abbassa Nile tilapia strain (GIANT-G9) versus commercial strains in some Egyptian governorates. *Aquaculture Research* 50 (10):2951–59. doi:10.1111/are.14249.
- Katagiri, T., C. Kidd, E. Tomasino, J. T. Davis, C. Wishon, J. E. Stern, and T. D. Kocher. 2005. A BAC-based physical map of the Nile tilapia genome. *BMC Genomics* 6 (1):1–6. doi:10.1186/1471-2164-6-89.
- Kenya National Bureau of Statistics. 2020. Economic survey 2020. *Economic survey 2020*. 10.4324/9781315016702
- Khang, P., T. H. Van, Phuong, N. K. Dat, W. Knibb, and N. H. Nguyen. 2018. An 8-year breeding program for Asian Seabass Lates calcarifer: Genetic evaluation, experiences, and challenges. *Frontiers in Genetics* 9 (May):1–12. doi:10.3389/fgene.2018.00191.
- Kocher, T. D. 2004. Adaptive evolution and explosive speciation: The cichlid fish model. *Nature Reviews. Genetics* 5 (4):288–98. doi:10.1038/nrg1316.
- Lee, B. Y., G. Hulata, and T. D. Kocher. 2004. Two unlinked loci controlling the sex of blue tilapia (*Oreochromis aureus*). *Heredity* 92 (6):543–49. doi:10.1038/sj.hdy.6800453.
- Leeds, T. D., and G. D. Wiens (2019). Genetic improvement of disease resistance through selective breeding. *Global aquaculture advocate*, (February 26). Retrieved from <https://www.aquaculturealliance.org/advocate/genetic->
- Liping, L., and K. Fitzsimmons (2011). Impacts of the introduction of alien tilapias (fisheries and biodiversity of indigenous species in tri an reservoir, *Oreochromis* spp.) on the Vietnam. *Proceedings of the Ninth International Symposium on Tilapia in Aquaculture*, (April), 88–295. Retrieved from <http://ag.arizona.edu/azaqua/ista/ISTA9/>

- Liu, L., and K. M. Fitzsimmons (2011). *Proceedings of the ninth international symposium on tilapia in life international symposium on editors Liu Liping and Kevin Fitzsimmons Shanghai Ocean University, Shanghai, China.* (April).
- Lu, S., Y. Liu, X. Yu, Y. Li, Y. Yang, M. Wei, . . . S. Chen. 2020. Prediction of genomic breeding values based on pre-selected SNPs using ssGBLUP, WssGBLUP and BayesB for Edwardsiellosis resistance in Japanese flounder. *Genetics, Selection, Evolution : GSE* 52 (1):49. doi:10.1186/s12711-020-00566-2.
- Macaranas, J. M., N. Taniguchi, and M. Pante. 1986. Electrophoretic evidence for extensive hybrid gene introgression into commercial *Oreochromis niloticus* (L .) stocks in the Philippines *. *Aquaculture and Fisheries Management* 17 (233):249–58.
- Marjanovic, J., H. A. Mulder, H. L. Khaw, and P. Bijma. 2016. Genetic parameters for uniformity of harvest weight and body size traits in the GIFT strain of Nile tilapia. *Genetics Selection Evolution* 1–10. doi:10.1186/s12711-016-0218-9.
- Megahed, M. E. 2019. Genetic selection for improved disease resistance in aquaculture with special reference to shrimp and tilapia breeding programs in Egypt. *Journal of Applied Aquaculture* 00:1–50. doi:10.1080/10454438.2019.1697783.
- Mukwabi, D. M., S. O. Otieno, P. O. Okemo, R. O. Odour, and B. Agwanda. 2019. Parasites infesting Nile tilapia grown in aquaculture systems in Kenya. *Livestock Research for Rural Development* 31 (2):2–7.
- Munguti, J. M., J.-D. Kim, and E. O. Ogello. 2014. An overview of Kenyan Aquaculture: Current status, challenges, and opportunities for future development. *Fisheries and Aquatic Sciences* 17 (1):1–11. doi:10.5657/FAS.2014.0001.
- Murphy, S., H. Charo-Karisa, S. Rajaratnam, S. M. Cole, C. McDougall, A. M. Nasr-Allah, . . . L. K. Banks. 2020. Selective breeding trait preferences for farmed tilapia among low-income women and men consumers in Egypt: Implications for pro-poor and gender-responsive fish breeding programmes. *Aquaculture* 525 (April2019):735042. doi:10.1016/j.aquaculture.2020.735042.
- Nguyen, H., and R. Ponzoni (2008). Genetic improvement of carp reduces poverty, hunger in Asia. *Global Aquaculture*, (June). Retrieved from http://pubs.iclarm.net/resource_centre/WF_1038.pdf
- Nguyen, N. H. 2016. Genetic improvement for important farmed aquaculture species with a reference to carp, tilapia and prawns in Asia : Achievements, lessons and challenges. *Fish And Fisheries* 17 (2):483–506. doi:10.1111/faf.12122.
- Ninh, N. H., N. P. Thoa, W. Knibb, and N. H. Nguyen. 2014. Selection for enhanced growth performance of Nile tilapia (*Oreochromis niloticus*) in brackish water (1520ppt) in Vietnam. *Aquaculture* 428–429:1–6. doi:10.1016/j.aquaculture.2014.02.024.
- Njiru, J. M., C. M. Aura, and J. K. Okechi. 2019. Cage fish culture in Lake Victoria: A boon or a disaster in waiting? *Fisheries Management and Ecology* 26 (5):426–34. doi:10.1111/fme.12283.
- Nyandat, B., and G. O. Owiti (2013). *Aquaculture needs assessment mission report: Kenya*. SF-FAO/2013/24. Retrieved from <http://www.fao.org/3/a-az041e.pdf>
- Nyonje, B. M., M. A. Opiyo, P. S. Orina, J. Abwao, and M. Wainaina. 2018. Current status of freshwater fish hatcheries, broodstock management and fingerling production in the Kenya aquaculture sector. *Livestock Research for Rural Development* 30:1.
- Obiero, K., J. Munguti, and J. Ani (2019). *Inventory of climate smart agriculture Technologies, Innovations And Management Practices (TIMPs) for aquaculture value chain*. Retrieved from <http://www.kalro.org/sites/timps/KCSAPTIMPs-AquacultureAug2019.pdf>
- Obwanga, B., K. Soma, O. Ingasia Ayuya, E. Rurangwa, D. Wonderen, G. van, Beekman, and C. Kilelu (2020). *Exploring enabling factors for commercializing the aquaculture sector in Kenya*. Retrieved from <https://edepot.wur.nl/519215>

- Omasaki, S. K., H. Charo-Karisa, A. K. Kahi, and H. Komen. 2016. Genotype by environment interaction for harvest weight, growth rate and shape between monosex and mixed sex Nile tilapia (*Oreochromis niloticus*). *Aquaculture* 458:75–81. doi:10.1016/j.aquaculture.2016.02.033.
- Omasaki, S. K., H. Charo-Karisa, and I. S. Kosgey. 2013. Fish production practices of small-holder farmers in western Kenya. *Livestock Research for Rural Development* 25 (3):1–16.
- Omasaki, S. K., K. Janssen, M. Besson, and H. Komen. 2017. Economic values of growth rate, feed intake, feed conversion ratio, mortality and uniformity for Nile tilapia. *Aquaculture* 481:124–32. doi:10.1016/j.aquaculture.2017.04.013.
- Opiyo, M. A., E. Marijani, P. Muendo, R. Odede, W. Leschen, and H. Charo-Karisa. 2018. A review of aquaculture production and health management practices of farmed fish in Kenya. *International Journal of Veterinary Science and Medicine* 6 (2):141–48. doi:10.1016/j.ijvsm.2018.07.001.
- Opiyo, M. A., K. O. Obiero, J. Abwao, F. J. Awuor, and J. Munguti. 2020. Comparative Growth Performance of Genetically Male, Sex- Reversed, and Mixed-Sex Nile Tilapia (*Oreochromis niloticus*) Reared in Earthen Ponds in Sagana, Kenya. 21 (1):23–30.
- Orina, S., E. O. Ogello, E. M. Kembenya, and C. Muthoni. 2018. *State of cage culture in Lake Victoria, Kenya*.
- Oyieng, E., and A. K. Kahi. 2013. *Characterization of fish production and marketing practices under small-holder fish farming systems of Eastern Kenya*. February.
- Ren, S., P. B. Mat, P. Prentis, Y. Li, B. Tan, and D. A. Hurwood. 2020. *Quantitative genetic assessment of female reproductive traits in a domesticated Pacific White Shrimp (Penaeus vannamei) line in China*. 1–10. doi: 10.1038/s41598-020-64597-x.
- Rowena, M., R. R. M. Ikeda, and Z. U. Basiao. 2010. *Growth comparison of Asian Nile and red tilapia strains in controlled and uncontrolled farm conditions*. 1205–21. doi: 10.1007/s10499-010-9334-7.
- Rye, M., J. Thodesen, D. Ma, M. Rye, Y. Wang, and K. Yang. 2015. Genetic improvement of tilapias in China: Genetic parameters and selection responses in growth of Nile tilapia (*Oreochromis niloticus*) after six generations of multi-trait selectio. *Aquaculture* 322–323 (December 2011):51–64. doi:10.1016/j.aquaculture.2011.10.010.
- Shirak, A., E. Seroussi, A. Cnaani, A. E. Howe, R. Domokhovskiy, N. Zilberman, . . . M. Ron. 2006. Amh and Dmrta2 genes map to tilapia (*Oreochromis* spp.) linkage group 23 within quantitative trait locus regions for sex determination. *Genetics* 174 (3):1573–81. doi:10.1534/genetics.106.059030.
- Suebsong, W., S. Poompuang, P. Srisapoom, S. Koonawootrittriron, A. Luengnaruemitchai, H. Johansen, and M. Rye. 2019. Selection response for *Streptococcus agalactiae* resistance in Nile tilapia *Oreochromis niloticus*. *Journal of Fish Diseases* 42 (11):1553–62. doi:10.1111/jfd.13074.
- Toha, N. P., N. H. Ninh, W. Knibb, and N. H. Nguyen. 2016. Does selection in a challenging environment produce Nile tilapia genotypes that can thrive in a range of production systems? *Scientific Reports* 6 (1):1–11. doi:10.1038/srep21486.
- Tibihika, P. D., M. Curto, E. Alemayehu, H. Waidbacher, C. Masembe, P. Akoll, and H. Meimberg. 2020. Molecular genetic diversity and differentiation of Nile tilapia (*Oreochromis niloticus*, L. 1758) in East African natural and stocked populations. *BMC Evolutionary Biology* 20 (1):16. doi:10.1186/s12862-020-1583-0.
- Trewavas, E. 1983. Tilapiine fishes. In *Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakila*. London: British Museum (Natural History).
- Trinh, T. Q., S. K. Agyakwah, H. L. Khaw, J. A. H. Benzie, and F. K. Y. Attipoe. 2021. Performance evaluation of Nile tilapia (*Oreochromis niloticus*) improved strains in Ghana. *Aquaculture* 530 (September2020):735938. doi:10.1016/j.aquaculture.2020.735938.

- Wanja, D. W., P. G. Mbuthia, R. M. Waruiru, J. M. Mwadime, L. C. Bebora, P. N. Nyaga, and H. A. Ngowi. 2020. Fish husbandry practices and water quality in central Kenya: Potential risk factors for fish mortality and infectious diseases. *Veterinary Medicine International* 2020:1–10. doi:[10.1155/2020/6839354](https://doi.org/10.1155/2020/6839354).
- Wohlfarth, G. W. 1994. The unexploited potential of tilapia hybrids in aquaculture. *Aquaculture Research* 25 (8):781–88. doi:[10.1111/j.1365-2109.1994.tb00743.x](https://doi.org/10.1111/j.1365-2109.1994.tb00743.x).
- Wonmongkol, P., S. Sukhavachana, K. Ampolsak, P. Srisapoom, T. Suwanasopee, and S. Poompuang. 2018. Genetic parameters for resistance against *Flavobacterium columnare* in Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758). *Journal of Fish Diseases* 41 (2):321–28. doi:[10.1111/jfd.12728](https://doi.org/10.1111/jfd.12728).
- Yáñez, J. M., R. Joshi, and G. M. Yoshida. 2020. Genomics to accelerate genetic improvement in tilapia. *Animal Genetics* 51 (5):658–74. doi:[10.1111/age.12989](https://doi.org/10.1111/age.12989).
- Zenger, K. R., M. S. Khatkar, D. B. Jones, N. Khalilisamani, D. R. Jerry, and H. W. Raadsma. 2019. Genomic selection in aquaculture: Application, limitations and opportunities with special reference to marine shrimp and pearl oysters. *Frontiers in Genetics* 10 (JAN). doi:[10.3389/fgene.2018.00693](https://doi.org/10.3389/fgene.2018.00693).