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Research Article

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Interspecific Hybridization of Tilapiines in Lake Victoria, Kenya

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Abstract

Before the introduction of non-indigenous species like *Oreochromis niloticus* and *Tilapia zillii* (Gervais) in Lake Victoria, the great majority of the ichthyofauna of the lake was made up of two groups of indigenous cichlids, the haplochromines and the tilapiines. The latter, although much less diversified, represented an important part of the total fisheries catch, and were a highly-valued food resource for the local community. Two species constituted this tilapia stock: *Oreochromis variabilis* (Boulenger) and *O. esculentus* (Graham). In less than 20 years, several hundreds of species have disappeared from Lake Victoria among which are these two native tilapias. Today, these two species are no longer present except in a few satellite lakes of Lake Victoria. Most of these populations are considered either as endangered or as having suffered genetic modification by hybridization with closely related introduced species. Tilapias are well known for their hybridizing abilities in the natural environment when native species are in contact with introduced species. The hybrids between *O. niloticus* and *O. variabilis* were observed before the latter species had disappeared from the lake. It also seems likely that *O. esculentus* hybridized with *O. niloticus*. In order to protect the remaining populations of native tilapias in this region, it is important to be able to characterize the endemic species genetically to determine their degree of genetic. This will make the conservationists know how to handle these species and if at all we have pure breeds for protection of biological diversity.

Keywords: Hybridization; *Oreochromis esculentus*; Endangered; *Oreochromis variabilis; Oreochromis niloticus;* Lake Victoria

Introduction

Tilapia is a large genus in the cichlid family (*Cichlidae*). Previously regarded as members of a single genus, Tilapia, three main genera are now recognized, based on the last taxonomic revision [1]. Apart from morphological characteristics, generic distinction of tilapias is also based on the reproductive biology: *Oreochromis* (maternal mouth-brooders), *Sarotherodon* (paternal or bi-parental mouth-brooders), and *Tilapia* (sub-strata spawners). Tilapias are a diverse group. They occupy almost all available aquatic habitats, from hot springs to highly alkaline waters [2], and from fresh waters to brackish environments [3]. Since these habitats exhibit different environmental variables based on the existing geographical differences, this diversity of tilapias is desirable for biodiversity, as the tilapias adapt to prevailing conditions. Different tilapia species therefore give rise to different populations or strains, with unique traits that could be exploited for higher aquaculture production. Some tilapias are cold tolerant [4], while others are salt tolerant [3] or sensitive to a rise in environmental temperature [5].

Almost 100 species of this group of fishes are referred to by the common name tilapia but only three species feature significantly in aquaculture: the Nile tilapia, *Oreochromis niloticus* (Linnaeus 1758), *O. mossambicus*, and *O. aureus* [1]. Kenya has a total of 18 tilapia species spread throughout its inland waters [6]. The major species are highlighted in Table 1. Many of these are exotic, having been introduced for aquaculture, and often escape from aquaculture farms to wild habitats. *Oreochromis niloticus* is the most important tilapia species in aquaculture in most countries of the world, because of its fast growth rate [7], and its excellent meat quality endear0s it to many nationalities. Even the flagship strain of tilapia genetic improvement programs, the genetically improved farmed tilapia (GIFT strain), was developed using strains of *O. niloticus*, exploiting the commercially important trait of faster growth rate.

However, another major trait of tilapias, the ability to reproduce with ease even in captivity, predisposes them to hybridize among species, and this affects biodiversity. *O. niloticus*, which has a higher ability to compete for resources than other tilapias, also easily hybridizes with other tilapias, with the hybrid often resembling more of *O. niloticus* than the other species. Because this species is the most translocated across countries or regions because of its faster growth rate, the problem of interspecific hybridization could be more widespread than thought or actually documented. Furthermore, interspecific hybridization could be enhanced by weak regulations governing inter-basin transfer of fish species, or weak capacity to enforce existing regulations. Apart from lowering tilapia species biodiversity, interspecific hybridization among tilapias affects the purity of species or strains as well. The use of impure strains of tilapia as brood stock for aquaculture lowers productivity, which is expressed as lower survival and lower growth rates. Lower growth rate of farmed tilapias due to impure stocks was a serious problem in major tilapia farming countries of Asia, such as Thailand and Phillipines [8], and was the rationale underlying the international effort that developed the GIFT strain [9]. Inter-specific hybridization in tilapias in Kenya is reviewed, and the possible effects of this on species diversity and production discussed (Table 1).

Introduction of Tilapias in Lake Victoria

The Lake Victoria ecosystem has been colonized by a number of fish species, and studies on the interactions in the lake began in the 1920s. By then, the ecosystem thrived on an indigenous and multi-species fishery, including indigenous tilapias, the African lungfish, catfishes,

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Species, common and local names	**Distribution in Kenya, annotations and maximum known length**
Alcolapia grahami (Boulenger, 1912) Lake Magadi tilapia	Lake Magadi. Introduced in Lake Nakuru in 1953, 1959 and 1962 (Vareschi, 1979); and possibly also introduced in Lake Elmenteita12.7 cm Standard Length (SL).
Oreochromis andersonii (Castelnau, 1861) Three-spotted tilapia	Unknown if established in natural waters; introduced in Kenya in 1980 from Botswana (Motiti Pan, an extension of the Okavango drainage) by I. Parker for aquaculture purposes in Nairobi dam; it is possible some specimens found their way from the dam to Nairobi River system; 34.4 cm SL
Oreochromis esculentus (Graham, 1928) Graham's tilapia "Ngege" (Swahili, Luhya, Luo), "Osamo" (Luo, Lake Victoria), "Dwela" (Luo, Lake Kanyaboli)	Lake Victoria drainage, Lake Kanyaboli; introduced into several dams and waters, including the Pangani system (Lake Jipe); currently the species is under threat of extinction in the Lake Victoria drainage; 25.3 cm SL
Oreochromis jipe (Lowe-McConnell, 1955) Jipe tilapia	Pangani drainage (including lake Jipe); previously also reported as *Tilapia jipe*, and *T. pangani* Lowe-McConnell, 1955 (as well as the subspecies *Oreochromis pangani pangani* and *O. pangani girigan*) are likely to be junior synonyms of O. jipe and considered as such here; 34.5 cm SL
Oreochromis leucostictus (Trewavas, 1933) Blue spotted tilapia "Odede" (Luo, Lake Kanyaboli)	Lake Victoria basin, Lake Kanyaboli, Lake Naivasha, some dams in the country (introduced). According to Welcomme (1967, 1988) and Lever (1996) this species was introduced in 1953 or 1954 from Lake Albert (Uganda) into Kenyan waters of Lake Victoria; it has also established in Lake Naivasha; also reported as *Tilapia leucosticta* (antiquated name); 32 cm TL
Oreochromis mossambicus (Peters,1852) Mozambique tilapia "Para Para" (Digo, South Coast)	In more or less brackish water of the lower course of the Ramisi River (South Coast); status uncertain, most likely introduced; 28 cm SL, 35 cm TL.
Oreochromis niloticus (Linnaeus, 1758) Nile tilapia "Ngege"(Swahili, Luhya, Luo, Lake Victoria and Lake Kanyaboli) "Nyamami" (Luo, Lake Victoria)	Lake Victoria drainage, Lake Kanyaboli (introduced); Welcomme (1967) reports introductions of this species in Kenyan waters of Lake Victoria in 1957; the introduced strain possibly belongs to the subspecies *Oreochromis niloticus eduardianus* (Boulenger, 1912); also reported as *Tilapia nilotica* ; 39.5 cm SL
Oreochromis niloticus baringoensis Trewavas, 1983 Baringo tilapia "Sopore", "Sibore" (Lake Baringo)	Endemic to Lake Baringo drainage and hot springs near Lake Bogoria (next to Lake Bogoria Lodge); 24.6 cm SL
Oreochromis niloticus sugutae Trewavas, 1983 Suguta tilapia	Endemic to Suguta River system; 17.1 cm SL
Oreochromis niloticus vulcani (Trewavas, 1933) Turkana tilapia "Kokine", "Rogene" (Turkana, Lake Turkana), "Sigir orok (El Molo, Lake Turkana)	Endemic to Lake Turkana drainage; previously also reported as *Tilapia vulcani* and *T. nilotica* (old names); used for aquaculture purposes at Sagana fish farm (upper Tana River drainage); 25.6 cm SL
Oreochromis variabilis (Boulenger, 1906)Victoria tilapia "Mbiru" (Luo, Lake Victoria)	Endemic to Lake Victoria drainage; also reported as *Tilapia variabilis* (antiquated name); this species is strongly declining or has disappeared in many areas of the Lake Victoria drainage; 26.7 cm SL

Table 1: Annotated checklist of the Tilapias of Kenya.

the native cyprinid *Rastrineobola argentea* and haplochromines [10]. In the late 1950s and early 1960s, four tilapiine species, *Oreochromis niloticus* (L), *Oreochromis leucostictus* (Trewavas), *Tilapia zillii* (Gervais) and *Tilapia rendalii* (Boulenger) were introduced into the lake to increase catches, which had declined due to overfishing [11]. The introduced tilapias quickly established themselves in the lake and began to appear in commercial landings from 1959 onwards [12]. However, the interactions between native and exotic tilapias in Lake Victoria were considerably more complex than had been originally anticipated [13,14]. There was clearly no overlap between the diet of adult *O. esculentus* and any of the exotic species, but significant overlap was found between the diet of adult *O. leucostictus* (introduced) and *O. variabilis*. Moreover, examination of the diets of juveniles revealed extensive overlap between the diets of *O. esculentus* and all three exotics [15]. Changes in the fish assemblage structure led to changes in the food webs and the functional roles of species in the lake ecosystem.

Exotic tilapiines impacted on the endemic populations of *O. esculentus* and *O. variabilis*. *O. niloticus* and *O. leucostictus* hybridized with the native species, with the resultant hybrids being more of exotic tilapias leading to the disappearance of native species and lose of biodiversity. The exotic tilapias also successfully competed against the native tilapias for food, spawning sites and nursery grounds [11,14].

Hybridization in tilapias

Hybridization is the interbreeding of individuals from what are believed to be genetically distinct populations, regardless of the taxonomic status of such populations [16]. "Hybridization" most commonly refers to mating by heterospecific individuals but has been applied to mating by individuals of different subspecies and even of populations that, though not taxonomically distinguished, differ genetically (Figure 1).

Introgression is gene flow between populations whose individuals hybridize, achieved when hybrids backcross to one or both parental populations [17]. Beyond F1 hybrids, the point at which an individual is no longer viewed as a hybrid but rather as a member of one of the parental populations that has undergone introgression is arbitrary [18].

Natural introgressive hybridization between species has been described in all major groups of organisms, including plants [19,20]. It provides favorable conditions for major and rapid evolution and has a significant contribution in the within species gene diversity [21-24]. With regard to the other groups of vertebrates, teleosts (mainly freshwater species) show a higher aptitude to hybridize [23,25]. This could result from the combination of intrinsic characteristics such as external fertilization and weakness of ethological reproductive barriers or gametic specificity, and high susceptibility to secondary contacts between recently evolved forms [25]. Furthermore, viable hybrids are often fertile and gene introgression could frequently occur after natural or human-induced secondary contacts [26,27].

For instance, when *O. niloticus* hybridizes with *O. urolepis hornorum*, the first generation progeny is all-male [17]. On the other hand, *O. niloticus* hybridizes with *O. mossambicus* to give a normal, 1:1 sex ratio. This strategy has been applied to create monosex male tilapia for higher aquaculture production, since male tilapias grow faster than females. Global economic production of tilapias relies on the use of monosex male populations. The development of the YY super male tilapia (YY super male tilapia technology) in the 1990s was based on the principle of skewed sex ratios of progeny from crosses of *O. niloticus* and certain *Oreochromis* species. The YY super male tilapia had a higher growth rate, and could therefore contribute to higher aquaculture production [17]. However, the adoption of this technology was limited by a laborious progeny testing for phenotypic sex, to choose suitable combinations that would cross to give all male tilapia populations. While the super male tilapia technology faced these challenges, it has been improved upon, especially with the advent of molecular marker technology, and now marker assisted selection or breeding is being

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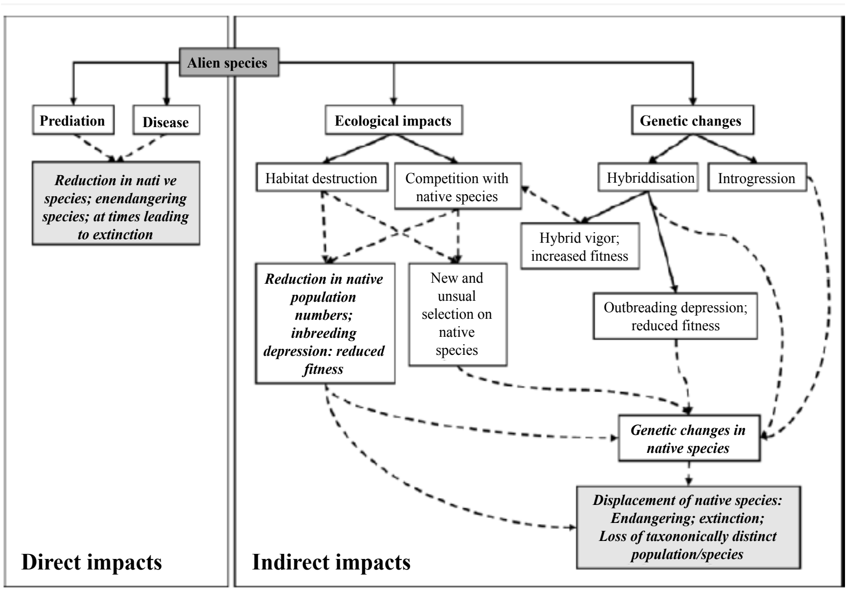

Figure 1: Schematic diagram of the potential direct and indirect effects on biodiversity impacts from alien species.

applied to create populations from strains of *O. niloticus* and *O. aureus* that yield all-male fingerlings when crossed.

Interspecific hybridization in tilapias in Kenya is probably widespread, since *O. niloticus* is widely translocated across regions for aquaculture. Between the year 2009 and 2012, for instance, the Government through the Ministry of Fisheries Development implemented the National Fish Farming Enterprise productivity program, in which farmers were supported to start aquaculture enterprises across the country. New hatcheries were also established, and the capacity of existing ones boosted, in order to supply tilapia seeds to the farmers. Mwanja and Kaufman [28] studied hybridization between O. *niloticus* and *O. esculentus* from different water bodies in the Lake Victoria basin, using random amplified polymorphic DNA markers, and concluded that both species hybridized and that no pure stocks of *O. esculentus* should exist. This led Agnese et al. [29] to genetically characterize a relict population of *O. esculentus* from Lake Kanyaboli, Kenya, using allozymes and microsatellite DNA loci, and reported the population to be genetically pure. More recently, almost a decade later, Angienda et al. [30] reported low levels of nuclear admixture from *O. niloticus* to *O. esculentus* in Lake Kanyaboli. Similarly, the study reported the presence of *O. esculentus* alleles in *O. niloticus* population of Lake Sare, which currently lacks *O. esculentus* [31]. L. Sare is historically connected to L. Victoria, and exchange fish fauna, leading to invasion of the satellite lake by both *O. niloticus* and *L. niloticus* from L. Victoria. The presence of *O. esculentus* alleles in *O. niloticus* was therefore explained by the fact that historically, L. Sare had *O. esculentus*, but was extirpated by both *O. niloticus* and *L. niloticus*. Therefore, introgression of *O. esculentus* alleles into *O. niloticus* occurred prior to its extinction from the satellite lake. Since these studies show that *O. esculentus* in L. Kanyaboli was genetically pure by 1999, but introgressed with *O. niloticus* alleles almost a decade later, it appears that ecological factors could be playing an important role in preventing contact between the two species, or predisposing the two species to hybridize. Since L. Kanyaboli lacks the invasive *L. niloticus*, it is suspected that distribution of food materials for the two tilapias could lead to contact of the species, leading to hybridization. However, these studies reflect the complex nature of the interaction between the invasive *O. niloticus* and the native tilapia species, and underscores the need for more studies, especially on the role of the prevailing ecological conditions in particular habitats, and the ecological competitiveness and physiological tolerance of the invasive species.

According to Aloo [31], *O. niloticus baringoensis* was introgressed with *O. leucostictus* mitochondrial DNA haplotypes, and attributed this to possible introduction of *O. leucostictus* into L. Baringo, to boost declining catches of *O. niloticus*. Since L. Baringo only harbours the indigenous *O. niloticus baringoensis*, the presence of *O. leucostictus* haplotypes in this lake shows that *O. leucostictus* has been introduced in the lake. While there is no gazetted stocking of *O. leucostictus* in the lake, the watermass has suffered frequent drying, leading to two closures over the last decade, meant to boost catches. During these closures, it is possible that *O. leucostictus* could have been introduced, without knowing that the species being stocked was *O. leucostictus* and not *O. niloticus*. This scenario represents the difficulties in managing tilapia resources, especially if proper identification of species is limited among fishery managers. Furthermore, the capacity by authorities or managers to enforce regulations governing fish species transfers and introductions in the country is limited (Figure 2).

Interspecific hybridization in tilapias is reported in many countries on the African continent. Agnese et al. [28] reported a mitochondrial DNA (mtDNA) haplotype of *Oreochromis aureus* in natural populations of *O. niloticus* of West Africa. A similar finding was reported by Rognon and Guyomard [32], who worked on different West African populations of both species. Hybrids of *O. niloticus* and *O. variabilis* were reported in L. Victoria prior to the decline of *O. variabilis* in the lake [14].

Fishes are generally more plastic in their potential for interbreeding than other animals. In Lake Victoria, the introduction of *O. niloticus, O. leucostictus* and *T. zillii* resulted in hybridization between *O. variabilis* and the introduced *O. niloticus* [33,14]. The phenomenon might also have contributed to the disappearance of *O. variabilis* from the lake. Welcomme [34,14] documented the presence of *O. niloticus* hybrid fry in the lake within the first decade of introduction. As *O. variabilis* numbers declined and *O. niloticus* numbers increased, the likelihood of the less abundant of the two species being able to find a co-specific spawning partner likewise diminished. Such a situation

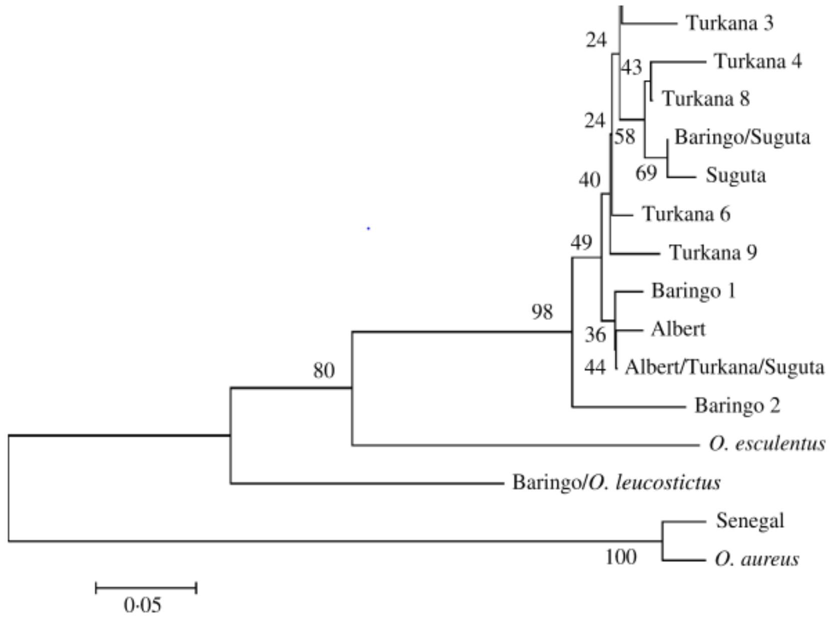

Figure 2: Neighbor joining consensus tree of mitochondrial DNA haplotypes based on kimura's two parameter sequence divergence between DNA sequences of *Oreochromis*.

favors hybridization which, in the absence of significant immigration of representatives of the less abundant species, leads to its eventual disappearance. Data from tagging experiments [33] suggest that adult *O. variabilis* tend to remain within a relatively restricted area. Such subpopulations would clearly be at risk from the consequences of this sort of genetic introgression. The successful naturalization of *O. niloticus*, *O. leucostictus*, and *T. zillii* to the lake resulted in *O. variabilis* moving to the edge of extinction.

Satellite lakes

Satellite lakes are fragments of the main lake, and therefore smaller than the main lake. For instance, the Lake Victoria basin has a number of smaller lakes, which are fragments of L. Victoria. Most of these satellites are separated from L. Victoria by varying ecological conditions, like sand spits, dense papyrus vegetation and swamps of low dissolved oxygen. Since satellite lakes are fragments of the main lake, both the satellite and main lake initially held similar fish fauna, and should continue holding the same fauna, and therefore current variations from this expectation are used to infer historical patterns and insights, especially with regard to introduction of exotic species and ecological changes to the water masses. Lake Victoria has a number of satellites: Kanyaboli, Namboyo and Sare, on the Kenyan side and Nabugabo on the Ugandan side. Satellite lakes have been recognized as important functional refugia for fish fauna, since they are connected to main lakes by extensive papyrus swamps that are anoxic to invasive predators like *L. niloticus* [29,31,35-37]. Anoxic conditions prevent the natural entry of *L. niloticus* to these habitats, which are inhabited by indigenous fish fauna tolerant to low dissolved oxygen conditions, and this helps to conserve indigenous fish stocks (a valuable food resource for the local communities) from predation pressure, unless the invasive predator is introduced there by man.

The three satellite lakes of L. Victoria in Kenya are housed by Yala swamp, the largest fresh water swamp in the Lake Victoria basin, covering 175 km^2 [31,38]. The swamp was formed in the Pleistocene by changes in water levels and reversal of river flows, leading to deposition of silt, infilling of former lakes and colonization by rooted plants. Apart from dense papyrus, the swamp is also separated from L. Victoria by sand bars or spits [31]. Of the three satellites, L. Kanyaboli is the largest (10.5 km^2) and most remote from L. Victoria [39], with a depth of 2.5-4.5 m [40]. Indigenous tilapias, *O. esculentus*, *O. variabilis* and *O. leucostictus*, which have been extirpated from L. Victoria, form the main fishery of L. Kanyaboli [31,36,41]. However, the invasion of the lake by exotic *O. niloticus* could threaten the survival of the indigenous tilapias, and negatively affect the fishery and livelihoods of the local community. Lake Namboyo is a small lake (0.01 km^2 surface area) with a depth of between 15 and 20 m. It is surrounded by rooted as well as floating papyrus swamps, mainly *Papyrus latifolia*, and inhabited by *O. esculentus*, *O. leucostictus* and *O. niloticus* in lower numbers [31] (Table 2).

Case study

The effect of hybridization of exotic *O. Niloticus* and the endemic tilapias *O. Esculentus* and *O. Variabilis* in lake victoria and its staellite lakes.

Between 1931 and 1961, six exotic species of tilapia *Oreochromis niloticus vulcani* (Trewavas), *Oreochromis niloticus eduardianus* (Boulenger), *Oreochromis leucostictus* (Trewavas), *Tilapia zillii* (Gervais), *Tilapia rendalii* (Boulenger) and *O. mossambicus* (Peters) were introduced into Lake Victoria and its catchment waters. *O. niloticus* has over time displaced indigenous stocks of *O. esculentus* and *O. variabilis*, which are no longer landed from L. Victoria. The effect of *O. niloticus* on the two species is thought to have occurred by interspecific breeding with the resultant hybrids resembling more of *O. niloticus* than either of the indigenous species. Similarly, *O. nioticus* is believed to have out-competed the indigenous tilapia species for breeding, feeding and nursery grounds there by affecting the feeding and reproductive behavior of the indigenous tilapias, leading to their decline. In addition, the decline in water quality due to pollution of L. Victoria replaced diatoms (the major food material for indigenous tilapias) by cyanobacteria which are less palatable, and this also affected the survival of the two species [11,14,42,43]. These factors, together with predation pressure from *L. niloticus* led to the dramatic decline of *O. esculentus* and *O. variabilis* from in the lake [11,39] (Tables 3 and 4).

Lake	Surface area (km²)	Average Depth (m)	D.O content (mg/L)	Indigenous Fish species	Exotic Fish Species
Kanyaboli	10.5	3	7.3	*O. esculentus*	*O.leucostictus O. niloticus.*
				O. variabilis	
				Six species of *Haplochromines*	
				P. aethiopicus	
				C. gariepinus	
Namboyo	0.01	20	4.8	*Haplochromis* spp. (9–10)	*O. niloticus*
				P. aethiopicus,	
				S. victoriae,	
				S. afrofischeri,	
				Barbus spp.	
				C. gariepinus	
Sare	5	5	8.1	*Oreochromis esculentus*	*O. leucostictus*
				Haplochromis spp.	
				Clarias gariepinus	

Table 2: Average readings of physico-chemical parameters and summary of the ichthyofauna of the three satellite lakes.

Date	*O. niloticus*		*O. esculentus*		Other tilapias		Total
	T	%	t	%	t	%	t
1971	591	18.8	1 934	61.6	617	19.6	3 142
1972	580	24.5	967	40.8	822	34.7	2 369
1973	488	28.8	304	18	900	53.2	1 692
1974	411	43	57	6	488	51	956
1975	202	31.5	28	4.4	412	64.2	642
1976	421	41.8	49	4.9	537	53.3	1 007
1977	465	32.4	42	2.9	928	64.7	1 435
1978	972	37.3	180	6.9	1 454	55.8	2 606
1979	962	35.1	94	3.4	1 683	61.4	2 739
1980	1 184	23.6	90	1.8	3 739	74.6	5 013
1981	2 213	47.4	166	3.6	2 289	49	4 668

Table 3: Species composition of the tilapia catch in Lake Victoria, 1971-81 (Fisheries Department Statistics, 1971-81).

Species	2009		2010		2011	
	M. tons	% Comp	M. tons	% Comp	M. tons	% Comp
O. niloticus	13,850	12.71	15,457	13.62	8,240	6.16
Others Tilapia	301	0.28	2,487	2.22	2,405	1.8

Table 4: Lake Victoria Tilapia landings by Species, Weight and Value 2009.

Lake victoria

Lake Victoria (0°20′N to 3°00′S and 31°39′E to 34°53′E and altitude of 1134 m) is one of the African Great Lakes. With a surface area of 68,800 square kilometres Lake Victoria is the second largest freshwater lake in the world and its fishery, one of the largest fisheries in the world, supports more than 3 million people [44,45].

However, the indigenous tilapias that disappeared from L. Victoria exist in satellite lakes as remnant populations, since these satellite lakes act as refugium for indigenous fish fauna [31,29]. Satellite lakes like L. Kanyaboli and Namboyo are separated from the main lake by dense papyrus swamps of low dissolved oxygen, and the anoxic conditions restrict the natural invasion of the predatory *L. niloticus* [31,46]. Similarly, these satellite lakes are less polluted, hence are still dominated by diatoms, which are suitable food materials for indigenous tilapias. On other hand, even in some of these refugial habitats, *O. niloticus* has been introduced, and the indigenous tilapias which dominate catches are currently under threat from hybridization [29] (Figure 3).

Discussions

The cichlid fish species flock in Lake Victoria experienced one of the worst mass extinctions of the 20th century [47]. Mainly due to anthropogenic influences, particularly the introduction of exotic species such as L. *niloticus* and *O. niloticus*, hundreds of endemic species, including the native tilapia *O. esculentus*, went extinct [35,48]. Recent studies on satellite lakes in the Lake Victoria region have led to the discovery of fish species richness and genetic diversity previously not sampled from Lake Victoria [41,49,50]. This demonstrates that satellite lakes and other small water reservoirs surrounding Lake Victoria are playing a critical role in the evolution and conservation of the region's ichthyofauna in this era of anthropogenically induced extinction. Primarily this occurs by isolated habitats with ecological conditions different from Lake Victoria and that are not yet invaded by aggressive introduced species. Invasive species are generally viewed as having a broader range of tolerances (i.e., a bigger bioclimatic envelope) than natives, thereby providing invaders with a wider array of suitable habitats [31,49,51]. A shift in temperature, for example, might have significant impacts on a native species, but little impact on an introduced species, thereby altering the competitive dynamics between them. In some cases, temperature alone may not be a determining factor. It is therefore necessary to look at the full suite of variables relevant to a particular species' bioclimatic envelope, as well as its broader symbiotic relationships and trophic webs. The fishing pressure also has increased, and the introduction of *O. niloticus* and predatory Nile perch have changed the trophic dynamics of the lake [11,39,52]. Similar tactical

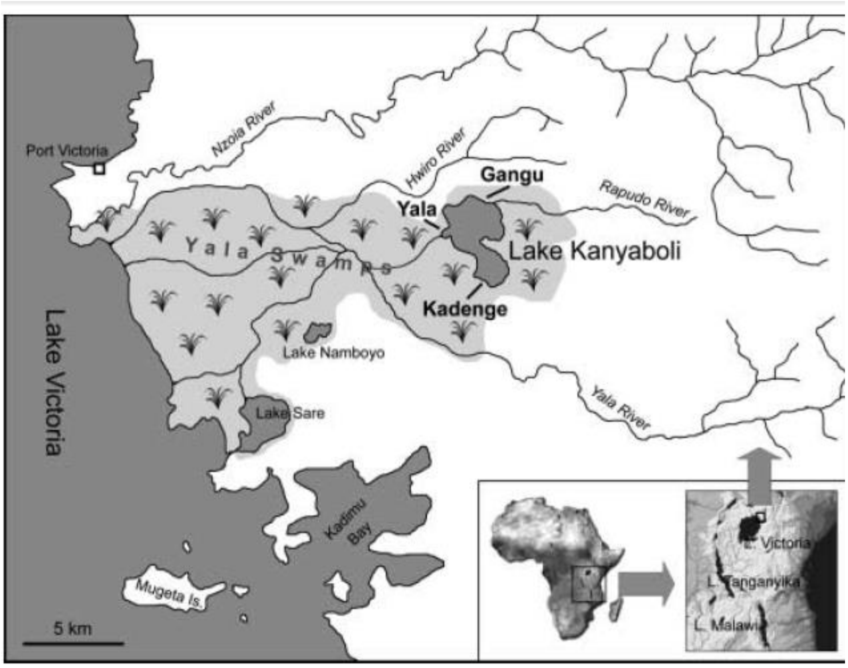

Figure 3: Map showing Lake Victoria and the satellite lakes kanyaboli, Sare and Namboyo, Kenya.

changes were observed for *O. niloticus* in Lake Victoria that grew faster, was more fecund and attained maturity at lower sizes than previously reported [52,53]. *Oreochromis leucostictus* may have been introduced into Lake Baringo to improve fish production and to slow the decline of *O. niloticus* populations. Although there are no gazetted transfers of *O. leucostictus* from Lake Naivasha or other systems into Lake Baringo, an introduction in the past few decades remains the best explanation for the appearance of *O. leucostictus* (non-native) mitochondrial DNA (mtDNA) haplotypes in L. Baringo, which has the indigenous *O. niloticus baringoensis*. This introduction was probably carried out on the assumption the species being stocked in the lake was *O. niloticus*, when in fact it was *O. leucosticus*. Misidentification of tilapias species is quite possible, especially among fishery managers who lack taxonomic skills. However, this introduction carries serious implications for tilapia species biodiversity and productivity of the lake's fishery. A possible hybridization between the two species, and/or competition for resources could lower tilapia catches in the lake. A species transfer was carried out in the Lake Victoria when *O. niloticus* was introduced after a decline in the production of the native tilapias, *Oreochromis variabilis* and *O. esculentus*. This introduction, in combination with other ecological factors, led to the extinction of these native species from the lake. It is, therefore, important to determine the effects of introductions and their possible consequences in Lake Baringo [31].

The decline of indigenous tilapias in L. Victoria due to effects of alien species underscores the fact that it is never certain how an alien species will affect a fishery, especially among the highly prolific tilapias which easily hybridize. Therefore, fish species introductions should be carried out only after adequate research has been carried out for scientific data to support the introduction (Table 5).

Conclusions and Recommendations

The environmental, biological, fishery and socio-economic effects of introduced/invasive species can be very severe, as has been witnessed in L. Victoria. The problems in the L. Victoria ecosystem result directly from human activity. *L. niloticus* and *O. niloticus* introduced in L. Victoria severely affected *O. esculentus* and *O. variabilis*, leading to their dramatic decline. Therefore, any further introductions to the lake, or to any other ecosystem, should be avoided. Where an introduction is deemed necessary, intensive studies should be done in advance on the biological and ecological behavior of the species to determine the potential impacts. Monitoring programmes should then determine the effects of introductions on local biodiversity to provide information that may help people recognize threats at an early stage. The three satellite lakes are reservoirs for some endemic fish species that disappeared from Lake Victoria, especially the tilapiines and the haplochromines. Therefore, the biodiversity of these lakes should be conserved by avoiding reclamation of the Yala swamp that houses the satellite lakes. The Yala Swamp and the lakes should be declared as national parks or reserves, to enhance their conservation [54-65].

Species	Date first introduction	Location	Origin
O. leucostictus	1951	L. Victoria	L. Edward, Uganda
T. zillii	1953	L. Victoria	L. Edward, Uganda
T. rendalli	1953	L. Victoria, Kianmu	Unknown
O. mossambicus	1961	L. Victoria catchment	Unknown

Table 5: List of the tilapia species introduced into Lake Victoria and its catchment waters (Odero, 1979).

Hybridization, with or without introgression, frequently threatens populations in a wide variety of plant and animal taxa because of various human activities. Probably cases reported in the literature do not adequately convey the magnitude of the problem. Increased use of molecular techniques, which are more informative than morphological techniques, should be applied to monitor the genetic purity of tilapias and other fish species, especially those used in aquaculture production, to help detect hybridization. Further, the increasing pace of three interacting human activities—habitat modification, fragmentation, and the introduction of exotic species-that contribute to this problem suggests it will worsen and therefore these activities should be avoided, to safeguard fish species fauna [66-75].

More specific recommendations include: Close pathways for the unintentional introduction of non-native species. Conduct risk assessments of proposed introductions of non-native species that include biogeographical factors and potential climate scenarios; and Develop early detection and rapid response systems targeting likely pathways and points of introduction, taking into account climate change dynamics. Eradicate invasive species already present in a system where feasible; Control known invasive species and as necessary damaging native species if eradication is not feasible; and Monitor known invasive species as well as suspect non-native and native species with the potential for biological invasion. Monitoring, early detection and rapid response systems can be used in the management of both existing and potential introductions of invasive species. Monitor existing species, including known invasive, suspect non-native species and potentially damaging native species, for possible *range shift* and in *post-disturbance surveys* looking for new or expanded infestations; and develop early detection and rapid response capacity to prevent the establishment and spread of new biological invasions focused on key pathways for introduction (including movement by storms, strong *El Niño* events as well as man-made vectors like ships, airplanes and construction equipment) and on areas that might be particularly vulnerable to new invasions (e.g., areas experiencing glacial retreat, warming coastal areas, disturbed areas) [75-118].

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