Journal of Fisheries & Livestock Production
ISSN: 2332-2608

DOI: 10.4172/2332-2608.1000235

Research Article Open Access

Interspecific Hybridization of Tilapiines in Lake Victoria, Kenya

Wasonga AG[1]*, Daniel WA[2] and Brian O[3]

[1]Department of Fisheries and Aquatic Sciences, University of Eldoret Eldoret, Kenya
[2]Department of Fish Disease Beyazıt Kampüsü, Istanbul University, Taş Odalar, Beyazıt, Istanbul, Turkey
[3]Institute of Hydrobiology, University of Chinese Academy of Sciences Wuhan, China

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,

***Corresponding author:** Wasonga AG, Department of Fisheries and Aquatic Sciences, University of Eldoret, Box 1125-30100, Eldoret, Kenya, Tel :+254 705 148611; E-mail: dwandera1@ogr.iu.edu.tr

Received May 07, 2017; **Accepted** June 07, 2017; **Published** June 13, 2017

Citation: Wasonga AG, Daniel WA, Brian O (2017) Interspecific Hybridization of Tilapiines in Lake Victoria, Kenya. J Fisheries Livest Prod 5: 235 doi: 10.4172/2332-2608.1000235

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

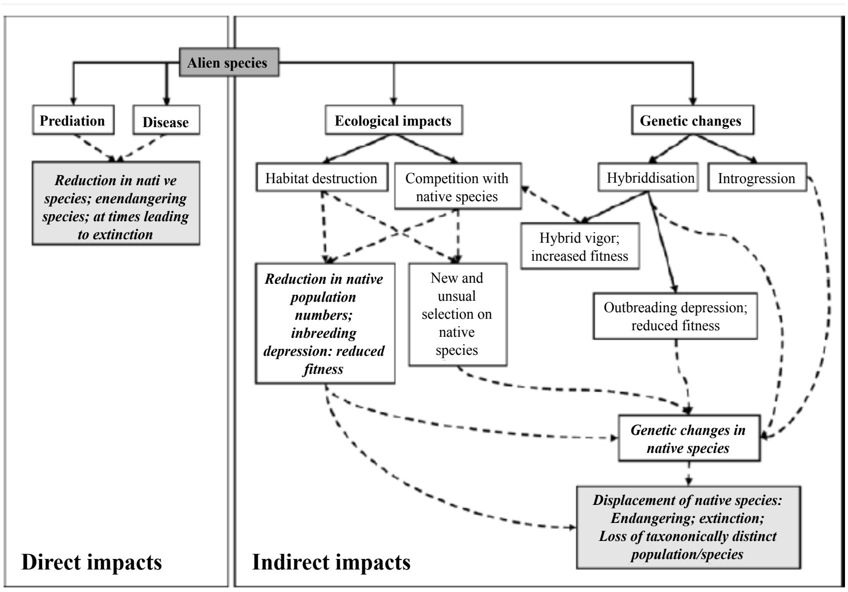

Figure 1: Schematic diagram of the potential direct and indirect effects on biodiversity impacts from alien species.

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

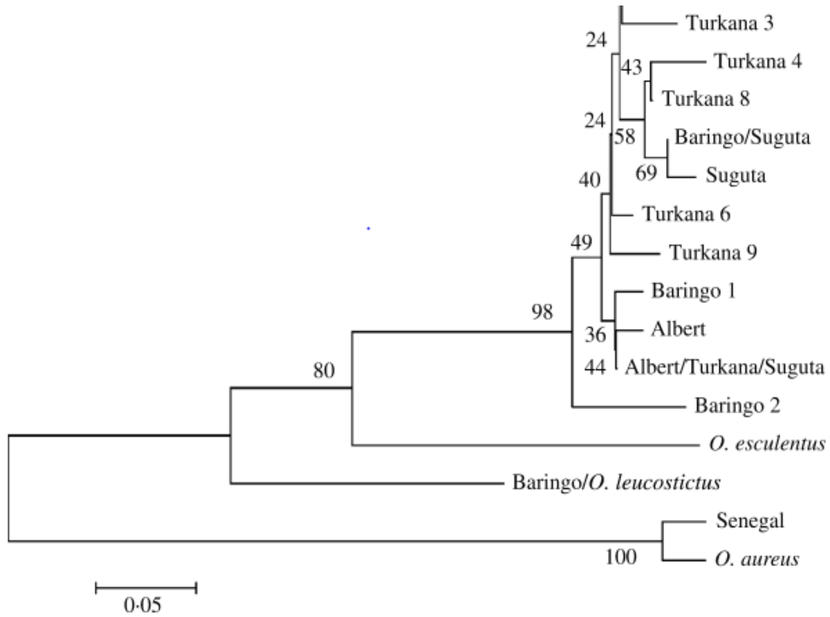

Figure 2: Neighbor joining consensus tree of mitochondrial DNA haplotypes based on kimura's two parameter sequence divergence between DNA sequences of *Oreochromis*.

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).

<table>
<tr><th>Lake</th><th>Surface area (km²)</th><th>Average Depth (m)</th><th>D.O content (mg/L)</th><th>Indigenous Fish species</th><th>Exotic Fish Species</th></tr>
<tr><td rowspan="5">Kanyaboli</td><td rowspan="5">10.5</td><td rowspan="5">3</td><td rowspan="5">7.3</td><td>O. esculentus</td><td rowspan="5">O.leucostictus O. niloticus.</td></tr>
<tr><td>O. variabilis</td></tr>
<tr><td>Six species of Haplochromines</td></tr>
<tr><td>P. aethiopicus</td></tr>
<tr><td>C. gariepinus</td></tr>
<tr><td rowspan="6">Namboyo</td><td rowspan="6">0.01</td><td rowspan="6">20</td><td rowspan="6">4.8</td><td>Haplochromis spp. (9–10)</td><td rowspan="6">O. niloticus</td></tr>
<tr><td>P. aethiopicus,</td></tr>
<tr><td>S. victoriae,</td></tr>
<tr><td>S. afrofischeri,</td></tr>
<tr><td>Barbus spp.</td></tr>
<tr><td>C. gariepinus</td></tr>
<tr><td rowspan="3">Sare</td><td rowspan="3">5</td><td rowspan="3">5</td><td rowspan="3">8.1</td><td>Oreochromis esculentus</td><td rowspan="3">O. leucostictus</td></tr>
<tr><td>Haplochromis spp.</td></tr>
<tr><td>Clarias gariepinus</td></tr>
</table>

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

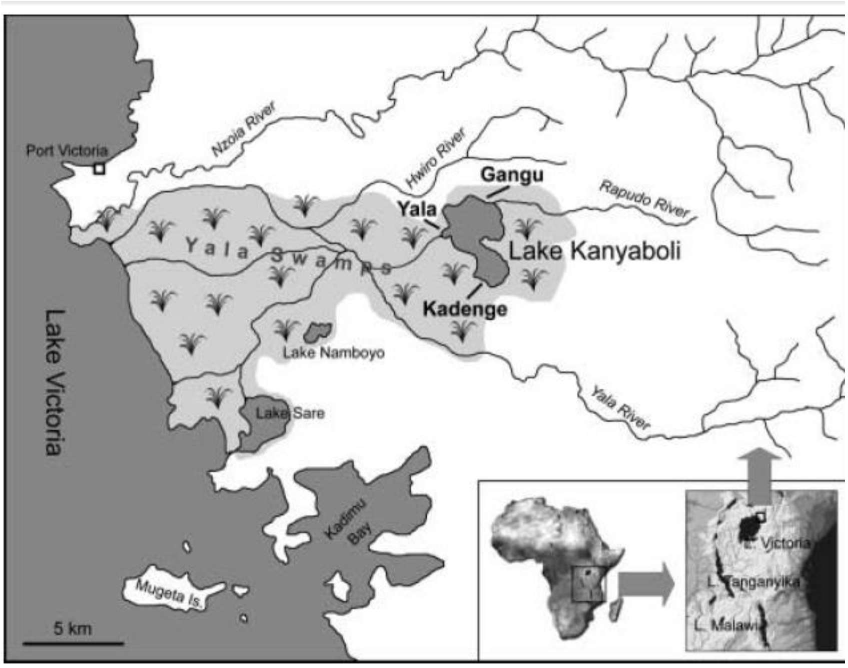

Figure 3: Map showing Lake Victoria and the satellite lakes kanyaboli, Sare and Namboyo, Kenya.

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

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).

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].

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].

Acknowledgement

The Author wish to thank Mr. Wasonga who commissioned this review in preparation to his Master Thesis on Tilapiine hybridization in Lake Victoria.

References

1. Trewavas E (1983) Tilapiine Fishes of the Genera Sarotherodon, Oreochromis and Danakilia. London: British Museum (Natural History): 583.
2. Vareschi E (1979) The ecology of Lake Nakuru (Kenya) II. Biomass and spatial distribution of fish (Tilapia grahami Boulenger Sarotherodon alcalicum grahami Boulenger). Oecologia (Berlin) 37: 321-335.
3. Cnaani A, Hulata G (2011) Improving salinity tolerance in tilapias: Past experience and future prospects. Israeli. Journal of Aquac.-Bamidge IIC: 1-21.
4. Cnaani A, Hallerman EM, Ron M, Weller JI, Indelman M, et al (2003) Detection of a chromosomal region with two quantitative trait loci, affecting cold tolerance and fish size, in an F2 tilapia hybrid. Aquaculture, 223: 117-128.
5. Abucay JJS, Mair GC, Skibinski DOF, Beardmore JA (1999) Environmental sex determination: the effect of temperature and salinity on sex ratio in Oreochromis niloticus L. Aquaculture 173: 219-234.
6. Seegers L, Okeyo DO, De Vos L (2003) Annotated checklist of the freshwater fishes of Kenya (excluding the lacustrine haplochromines from Lake Victoria). Journal of East African Natural History 92: 11-47.
7. Fitzsimmons K (2011) Potential to increase global tilapia production. Global outlook for aquaculture leadership, Kuala-Lumpur.
8. Macaranas JM, Augustine LQ, Ablan MCA, Pante MJR, Eknath AE, et al. (1995) Genetic improvement of farmed tilapias: biochemical characterization of strain differences in Nile tilapia. Aquaculture International 3: 43-54.
9. Eknath AE, Tayamen MM, Palada-de Vera MS, Danting JC, Reyes RA, et al (1993) Genetic improvement of farmed tilapias: the growth performance of 8 strains of Oreoochromis niloticus tested in different farm environments. Aquaculture 111: 171-188.
10. Balirwa JS (1992) The evolution of fishery of Oreochromis niloticus (Pisces: Cichlidae) in Lake Victoria. Hydrobiologia 232: 85-89.
11. Ogutu-Ohwayo R (1990) The decline of native fish species of Lake Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus and Nile tilapia Oreochromis niloticus. Env Biol Fishes 27: 81-96.
12. Twongo T (1995) Impacts of fish species introductions on the tilapias of Lake Victoria and Kyoga. In: Pitcher TJ, Hart PJB editors. The Impacts of Changes in African Lakes. Chapman Hall, London.
13. Welcome RL (1966) Recent changes in the stocks of tilapia in Lake Victoria. Nature. 212: 52-54.
14. Welcomme RL (1967) Observation on the biology of the introduced species of tilapia in Lake Victoria. Revue de Zoologie et de Botanique Africaine 526: 249-279.
15. Loiselle PV (1997) The natural history and aquarium husbandry of the Mbiru (*Oreochromis variabilis*). Aquarium Frontiers and Fancy Publications Inc. Animal Network.
16. Searle JB (1993) Chromosomal hybrid zones in eutherian mammals. In: Harrison RG, editor. Hybrid Zones and the Evolutionary Process. Oxford: Oxford University Press: 309-353.
17. Mair GC, Abucay JS, Beardmore JA, Skibinski DOF (1995) Growth performance trials of genetically male tilapia (GMT) derived from YY-males in Oreochromis niloticus on-station comparisons with mixed sex and sex reversed males. Aquaculture 137: 313-322.
18. United States Fish and Wildlife Service (1988) Endangered Species Act of 1973. As Amended Through the 100th Congress. Washington.
19. Barton NH, Hewitt GM (1989) Adaptation, speciation and hybrid zones. Nature 341: 497-503.
20. Anderson E, Hubricht L (1938) Hybridization in Tradescantia III, The evidence for introgressive hybridization. Am J Bot 25: 396-402.
21. Arnold ML (1997) Natural Hybridization and Evolution. Oxford University Press, New York.
22. DeMarais BD, Dowling TE, Douglas ME, Minckley WL, Marsh PC (1992) Origin of Gila seminuda (Teleostei: Cyprinidae) through introgressive hybridization: implications for evolution and conservation. Proc Natl Acad Sci USA 89: 2747-2751.
23. Smith GR (1992) Introgression in fishes: significance for paleontology cladistics and evolutionary rates. Systematic Biology 41: 41-57.
24. Martinsen GD, Whitham TG, Turek RJ, Keim P (2001) Hybrid populations selectively filter gene introgression between species. Evolution 55: 1325-1335.
25. Campton DE (1987) Natural hybridization and introgression in fishes: methods of detection and genetic interpretation. In: Ryman N, Utter FM editors. Population Genetics and Fishery Management: 161-192.
26. Billington N, Hebert PDN (1991) Mitochondrial DNA diversity in fishes and its implications for introductions. Canadian Journal of Fisheries and Aquatic Sciences 48: 80-94.
27. Verspoor E, Hammar J (1991) Introgressive hybridization in fishes: the biochemical evidence. Journal of Fish Biology 39: 309-333.
28. Mwanja W, Kaufman L (1995) A note on recent advances in the genetic characterization of tilapia stocks in Lake Victoria region. African Journal of Tropical Hydrobiology & Fisheries 6: 51-53.
29. Agnese JF, Adepo-Gouene B, Abban EK, Fermon Y (1997) Genetic differentiation among natural populations of the Nile tilapia, *Oreochromis niloticus*. Heredity 79: 88-96.
30. Angienda PO, Hyuk JL, Elmer KR, Abila R, Waindi EN, et al (2011) Genetic structure and gene flow in an endangered native tilapia fish (Oreochromis esculentus) compared to invasive Nile tilapia (O. niloticus) in Yala swamp, East Africa. Conservation Genetics 12: 243-255.
31. Aloo PO (2003) Biological diversity of the Yala swamp lakes, with special emphasis to fish species composition in relation to changes in the lake Victoria basin (Kenya): threats and conservation measures. Biodiversity and Conservation 12: 905-920.
32. Rognon X, Guyomard R (2003) Large extent of mitochondrial DNA transfer from Oreochromis aureus to O. niloticus in West Africa. Molecular Ecology 12: 435-445.
33. Fryer G (1961) Observations on the biology of the cichlid Tilapia variabilis Boulenger in the northern waters of Lake Victoria (East Africa). Rev Zool Bot Afr 64: 1-33.
34. Welcomme RL (1964) The habitats and habitat preferences of the young of the Lake Victoria Tilapia (Pisces: Cichlidae). Revue Zool Bot Afr 70: 1-28.

35. Balirwa JS, Chapman CA, Chapman LJ, Cowx IG, Heheb K, et al (2003) Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? Bioscience 53: 703-715.

36. Kaufman LS, Ochumba P (1993) Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in Northern Lake Victoria. Conservation Biology 7: 719-730.

37. Mbabazi D, Ogutu-Ohwayo R, Wandera SB, Kizito Y (2004) Fish species and trophic diversity of haplochromine cichlids in the Kyoga satellite lakes (Uganda). African Journal of Ecology 42: 59-68.

38. Abila R (2011) Preliminary gut content and dentition analysis reveal subtle resource partitioning and feeding adaptations within a haplochromine cichlid community of Lake Victoria satellite lake. African Journal of Environmental Science and Technology 5: 457-563.

39. Crafter SA, Njuguna SG, Howard GW (1992) Wetlands of Kenya. In: Proceedings of KWWG seminar on wetlands of Kenya. National Museums of Kenya, Nairobi, Kenya.

40. Opiyo SV (1991) Feeding ecology of Oreochromis esculentus (Graham) (Pisces: Cichlidae) in Lake Kanyaboli, Kenya, M.Sc. Thesis, University of Nairobi: 147.

41. Abila R, Barluenga M, Engelken J, Meyer A, Salzburger W (2004) Population-structure and genetic diversity in a haplochromine fish cichlid of a satellite lake of Lake Victoria. Mol Ecol 13: 2589-2602.

42. Lung'ayia HBO, M'Harzi A, Tackx M (2000) Phytoplankton community structure and environment in the Kenyan waters of Lake Victoria. Freshwat Biol 43: 529-543.

43. Njiru M, Waithaka E, Muchiri M, van der Knaap M, Cowx IG (2005) Exotic introductions to the fishery of Lake Victoria: what are the management options? Lakes and Reserv Res Manage 10: 147-55.

44. Goldschmidt T, Witte F, Wanink J, van Oijen M, Goudsward K (1992) The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34**:** 1-28.

45. Odongkara K, Abila RO, Onyango PO (2005) Distribution of economic benefits from the fisheries. In: The State of the Fisheries Resources of Lake Victoria and Their Management. Proceedings of the Regional Stakeholders' Conference: 124-131.

46. Abila R, Salzburger W, Ndonga MF, Owiti DO, Barluenga M, et al. (2008) The role of the Yala swamp lakes in the conservation of Lake Victoria region haplochromine cichlids: evidence from genetic and trophic ecology studies. Lakes Reservoirs: Res Manage 13: 95-104.

47. Witte F, Goldshmidt T, Ligtvoet W (1992) Species extinction and concomitant ecological changes in Lake Victoria. Neth J Zool 42: 214-232.

48. Maithya J, Njiru M, Okeyo-Owuor JB, Gichuki J (2012) Some aspects of the biology and life history strategies of Oreochromis variabilis (Boulenger 1906) in the Lake Victoria basin. Lakes and Rivers: Research and Management 17: 65-72.`

49. Chapman LJ, Chapman CA, Nordlie FG, Rosenberger AE (2002) Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region. Comp Biochem Physiol A 133: 421-437.

50. Mwanja WW (2004) The role of satellite water bodies in the evolution and conservation of Lake Victoria Region fishes. Afr J Ecol 42: 14-20.

51. Walther GR, Roques A, Hulme PE, Sykes MT, Pysek P, et al (2009) Alien species in a warmer world: Risksand opportunities. Trends in Ecology and Evolution 24: 686-693.

52. Balirwa JS (1998) Lake Victoria wetlands and tile ecology of the Nile tilapia, Oreochromis niloticus (L.). PhD Thesis. University of Rotterdam: 247.

53. Njiru M, Ojuok JE, Okeyo-Owuor JB, Muchiri M, Ntiba MJ, et al (2006) Some biological aspects and life history strategies of Nile tilapia Oreochromis niloticus (L.) in Lake Victoria, Kenya. Afri J Eco 44: 1-8.

54. Agne JF, Ade´po-Goure`ne B, Abban EK, Fermon Y (1997) Genetic differentiation among natural populations of Nile tilapia Oreochromis niloticus. Heredity 79: 88-96.

55. Agne`se JF, Ade´po-Goure`ne B, Pouyaud, L (1998) Natural hybridization in tilapias. In Genetics and Aquaculture in Africa, Agne`se JF editors. 125-133.

56. American Ornithologists' Union (1979) The proceedings of ninety-seventh meeting of the AOU College station. Texas Resolutions Auk 97: 10.

57. Arnold SJ, Avise JC, Ballou J, Eldridge J, Flemming D, et al. (1991) Genetic management considerations for threatened species with a detailed analysis of the Florida panther (Felis concolor coryi). Washington, DC: USFWS.

58. Atkinson I (1989) Introduced animals and extinctions. Conservation for the Twenty-First Century, Western D, Pearl MC editors. Oxford University Press, New York: 54-75.

59. Avise JC (1994) Molecular Markers, Natural History and Evolution. New York: Chapman & Hall: 2381-2389

60. Bagenal TB (1978) Aspects of fish fecundity. In: Ecology of Freshwater Fish Production, Gerking SD editor. Blackwell Scientific Publications Ltd, Oxford: 75-101.

61. Bardakci F, Skibinski DOF (1994) Application of the RAPD technique in tilapia fish: species and subspecies identification. Heredity 73**:** 117-123.

62. Barel CDN, Dorit R, Greenwood PH, Fryer G, Hughes N, et al (1985) Destruction of fisheries in Africa's Lakes. Nature 315: 19-20.

63. Barton NH (2001) The role of hybridization in evolution. Molecular Ecology 10: 568.

64. Bernatchez L, Met GLH, Wilson CC, Danzmann RG (1995) Introgression and fixation of Arctic char (Salvelinus alpinus) mitochondrial genome in an allopatric population of brook trout (Salvelinus fontinalis). Canadian Journal of Fisheries and Aquatic Sciences 52: 179-185.

65. Butler D (1994) Bid to protect wolves from genetic pollution. Nature 370: 497.

66. Cade TJ (1983) Hybridization and gene exchange among birds in relation to conservation 126: 288-309.

67. Callejas C, Ochando MD (1998) Identification of Spanish barbel species using the RAPD technique. Journal of Fish Biology 53**:** 208-215.

68. Compton DE (1990) Application of biochemical and molecular markers to analysis of hybridization. In Electrophoretic and Isoelectric Focusing Techniques in Fisheries Management, Whitmore DH editor. 241-264.

69. Cowx IG, Knaap VM, Muhoozi LI, Othina A (2003) Improving fishery catch statistics for Lake Victoria. J Ecosys Health Manage 6: 299-310.

70. De Silva SS, Nguyen TT, Turchini MG, Amarasinghe US, Abery NW (2009) Alien Species in Aquaculture and Biodiversity: A Paradox in Food Production. Royal Swedish Academy of Sciences. Ambio 38: 24-25.

71. Diamond J (1989) Overview of recent extinctions. In: Western D, Pearl MC editors. Conservation for the Twenty First Century, Oxford University Press, New York: 37-41.

72. Dowling TE, DeMarais BD (1993) Evolutionary significance of introgressive hybridization in ciprinid fishes. Nature 362: 444-446.

73. Dowling TE, Hoech WR (1991) The extent of introgression outside the contact zone between Notropis cornutus and N. chrysocephalus (Teleostei: Cyprinidae). Evolution 45: 944-956.

74. Dukes JS (2000) Will the increasing atmospheric CO2 concentration affect the success of invasive species? In Mooney HA, Hobbs RJ (Eds.) Invasive Species in a Changing World. Island Press, Washington, DC, US.

75. DuRietz GE (1930) The fundamental units of biological taxonomy. Svensk Bot Tidskr 24: 333-428.

76. Ellstrand NC (1992) Gene flow by pollen: implication for plant conservation genetics. Oikos 63: 77-86.

77. Elmer KR, Reggio C, Wirth T, Verheyen E, Salzburger W (2009) Pleistocene desiccation in East Africa bottlenecked but did not extirpate the adaptive radiation of Lake Victoria haplochromine cichlid fishes. Proc Natl Acad Sci USA 106: 13404-13409.

78. Fryer G, Iles TD (1972) The Cichlid Fishes of the Great Lakes of Africa. Oliver and Boyd, Edinburgh.

79. Glmet H, Blier P, Bernatchez L (1998) Geographical extent of Artic char (Salvelinus alpinus) mtDNA introgression In brook char populations (S. fontinalis) from eastern Qu.bec, Canada. Molecular Ecology**7**: 1655-1662.

80. Hammar J (1989) Freshwater ecosystems of polar regions: vulnerable resources. Ambio 18: 6-22.

81. Harlan JR (1983) Some merging of plant populations, Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations. Biol Conserv Ser, pp: 267-276

82. Harrison RG (1993a) Hybrids and hybrid zones: Historical perspective. Fourth International Congress of Systematic and Evolutionary Biology, Harrison RG editor. In Hybrid zones and the evolutionary process, Oxford Univ Press, New York, pp: 3-12.

83. Hauser L, Adcock GJ, Smith PJ, Ramirez JHB, Carvalho GR (2002) Loss of microsatellite diversity and low effective population size in an overexploited population. Proceedings of the National Academy of Science, USA 18: 11742-11747.

84. Heusmann HW (1974) Mallard-Black Duck relationships in the Northeast. Wildl Soc Bull 2: 171-77.

85. Hubbs CL (1955) Hybridization between fish species in nature. Systematic Zoology 4: 1-20.

86. Johnsgard PA (1961) Evolutionary relationships among North American Mallards. Auk 78: 3-43

87. Kaufman LS (1989) Challenges of fish faunal conservation programmes as illustrated by captive biology of Lake Victoria cichlids. Fifth World Congress on Breeding Endangered Species in Captivity: 10-20.

88. Khater AA, Smitherman A (1988) Cold tolerance and growth of three strains of Oreochromis niloticus. Pullin RSV, Bhukaswan T, Tonguthayi K, Maclean JL (editors), the Second International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings, Manila, Philippines 15: 215-218.

89. Kudhogania AW, Cordone AJ (1974) Batho-spatial distribution pattern and biomass estimate of the major demersal fishes in Lake Victoria. Afr J Hydrobiol Fish 3: 15-31.

90. Kudhongania AW, Chitamweba DBR (1995) Impact of environmental change, species introductions and ecological interactions on the fish stocks of Lake Victoria. Pitcher TJ, Hart PJB editors. The Impacts of Species Changes in African Lakes, Chapman Hall, London, pp: 19-32.

91. Lever C (1996) Naturalized Fishes of the World. Academic Press.

92. Lu G, Basley DJ, Bernatchez L (2001) Contrasting patterns of mitochondrial DNA and microsatellite introgressive hybridization between lineages of Lake Whitefish (Coregonus clupeaformis); relevance for speciation. Molecular Ecology 10: 965-985.

93. Maithya J (1998) A survey of the Itchthyofauna of Lake Kanyaboli and other small water bodies in Kenya: alternative refugia for endangered fish species. NAGA, ICLARM 3: 54-56.

94. Maithya J (2008) Ecology, Biology and Aquaculture Potential of Oreochromis variabilis (Boulenger 1906) in Lake Victoria Basin. PhD thesis, Moi University, Kenya.

95. Maithya J, Njiru M, Okeyo-Owuor JB, Gichuki J (2012) Some aspects of the biology and life history strategies of Oreochromis variabilis (Boulenger 1906) in the Lake Victoria basin. Lakes and Rivers: Research and Management 17: 65-72.`

96. Mann MJ (1966) A preliminary report on a survey of fisheries of the Tana River, Kenya. East African Fresh water Fisheries Organization, Annual Report 1965: 36-43.

97. Mann MJ (1968) A note on a second survey of the fisheries of the Tana River, Kenya. East African Freshwater Fisheries Organization, Annual Report 1967: 38-41.

98. Mavuti KM (1989) Account of some important freshwater wetlands of Kenya. Crafter SA, Njuguna SG, Howard GW (eds), IUCN Conference Proceedings on Wetlands of Kenya pp: 23-35.

99. McKaye KR (1983) Ecology and breeding behavior of a cichlid fish, Cyrtocara eucinostomus, on a large lek in Lake Malawi, Africa. Environmental Biology of Fishes, pp: 81-96.

100. Mwanja MT, Mwanja WW (2009) Escape of farmed tilapiines into the wild and entry of wild forms in fish ponds, and possible interactions between wild and farmed tilapiines from a sample of smallholder farms in Central Uganda. African Journal of Ecology 47: 469-475.

101. Nyingi DW, Agnese JF (2007) Recent introgressive hybridization revealed by mtDNA transfer from Oreochromis leucostictus to Oreochromis niloticus in Lake Baringo, Kenya. Journal of Fish Biology 70 (Supplement A): 148-154.

102. Okemwa EN (1981) A Preliminary Survey of the Fisheries and Limnology of Lake Kanyaboli and Lake Sare in Western Kenya. Proceedings of the Workshop of the Kenya Marine and Fisheries Research on ‘Aquatic Resources of Kenya: 192-211.

103. Petre T (2000) Interactions between fish and aquatic macrophytes in inland waters. A review FAO Fisheries Technical Papers 396.

104. Pullin RSV, Capili JB (1988) Genetic improvement of tilapias: problems and prospects. In: Pullin RSV, Bhukaswan T, Tonguthai K, Maclean JL editors. The Second International Symposium on Tilapia in Aquaculture, ICLARM Conference Proceedings 15, Department of Fisheries, Bangkok, Thailand, and International Center for Living Aquatic Resources Management, Philippines: 259-266.

105. Pullin RSV, Palomares ML, Casal CV, Dey MM, Pauly D (1997) Environmental impacts of tilapias. In: Fitzsimmons K (Ed.), Tilapia Aquaculture. Proceedings from the Fourth International Symposium on Tilapia in Aquaculture: 554-570.

106. Raghu S, Anderson RC, Daehler CC, Davis AS, Wiedenmann RN, et al. (2006) Adding biofuels to the invasive species fire? Science 313: 1742.

107. Rhymer JM, Williams MJ, Braun MJ (1994) Mitochondrial analysis of gene flow between New Zealand mallards (Anas platyrhynchos) and grey ducks (A. superciliosa). Auk 111: 970-978.

108. Richardson DM, Bond WJ, Dean WRJ, Higgins SI, Midgley GF, et al (2000) Invasive alien species and global change: A South African perspective. In: Mooney HA, Hobbs RJ editors. Invasive Species in a Changing World. Island Press, Washington, DC, US.

109. Rieseberg LH (1991) Hybridization in rare plants: insights from case studies in Cercocarpus and Helianthus Plants. Falk DA, Holsinger KE (eds) In Genetics and Conservation of Rare: 171-181.

110. Scott AG, Penman DJ, Beardmore JA, Skibinski DOF (1989) The ‘YY’ supermale in Oreochromis niloticus and its potential in aquaculture. Aquaculture 78: 237-251.

111. Shrader-Frechette KS, McCoy ED (1993) Method in Ecology. Strategies for Conservation, Cambridge: Cambridge Univ Press.

112. Species Survival Programme (1994) A survey of the Yala Swamp lakes and surrounding dams for endemic fish species (Unpublished report).

113. Stiassny MLJ (1991) Phylogenetic intrarelationships of the family Cichlidae: an overview. In: Keenleyside MHA editor. Chichlid Fishes: Behaviour, Ecology and Evolution Fish and Fisheries Series 2: 1-35.

114. Sutherst RW (2000) Climate change and invasive species: A conceptual framework. In: Mooney HA, Hobbs RJ editors. Invasive Species in a Changing World. Island Press, Washington, DC, US.

115. Vrijenhoek RC (1989) Population genetics and conservation. In: Western D, Pearl MC editors. Conservation for the twenty-first century: 89-98.

116. Welcomme RL (1988) International introductions of inland aquatic species. FAO Fisheries Technical Paper 294: 1-318.

117. Waddington CH (1956) Genetic assimilation of the bithorax phenotype. Evolution 10: 13.