Species introductions



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CHRISTIAN LÉVÊQUE Since antiquity, fish have been introduced and translocated between and within continents. This practice was greatly developed during the 20th century with the primary aim of improving fishing production and fish farming development. Fish have been introduced on every continent, but this chapter focuses only on Africa.

While species introductions have been encouraged more or less throughout the world in order to improve aquaculture production, they have become controversial in recent decades among scientists and aquatic ecosystem managers. The introduction of new species sometimes has enormous consequences on native fish populations. Some believe that humans should not play with fire and that any introduction is causing irreversible damage to native fauna. On the contrary, others think that nature has not necessarily gone in the right direction, and that the introduction of species to improve fisheries production is justified in a number of cases. This debate is far from resolved and should prompt us to adopt a precautionary approach.

Goals of introductions

There have been several introductions of alien fish species to African waters, and many translocations of African fish species within Africa to areas outside their natural ranges (tables 23.1 and 23.11) (see also box "Some semantic explanations"). The goals of these introductions are varied, and have been detailed by Welcomme (1988), Moreau *et al.* (1988), Ogutu-Ohwayo & Hecky (1991) and Lévêque (1997b). Nearly 50 species from other continents have been introduced more or less everywhere in Africa.

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SOME SEMANTIC EXPLANATIONS (REPRODUCED FROM LAZARD & LÉVÊQUE, 2009)

There is some confusion regarding the use of certain terms. We propose the use of **introduction** to designate species that have been intentionally or accidentally transported and introduced by humans into a system found outside the natural area of distribution for that species. Meanwhile, **translocations** (or transfers) correspond to the deliberate or accidental transport of individuals of a species to other

sites within the natural area of distribution of the species. The genomes of these translocated individuals may differ from that of the native population, leading to a modification in gene flows. Species are referred to as indigenous, native, or autochthonous when they originate from the area under consideration. They are introduced, exotic, or allochthonous when they originate from another area of distribution. A cryptogenic species is one for which there is no clear evidence whether or not it is introduced.

Acclimatization is the adaptation of a specimen to new conditions. This does not automatically result in the establishment of a population, as reproduction is not necessarily guaranteed. When a population of an introduced species develops in the natural system, that is, it lives and reproduces there, this is called **naturalisation**.

Introduced for sport fishing, the European brown trout (*Salmo trutta*) has now acclimatized in different upland aquatic systems. This is the case as well for the black bass (*Micropterus salmoides*) originally from the United States, now acclimatized in Kenya and Madagascar. Among the Cyprinidae, the European carp (*Cyprinus carpio*), as well as the goldfish (*Carassius auratus*) were also introduced in the 19th century in Madagascar. Asian species such as the gourami (*Osphronemus goramy*), introduced in the mid-19th century, and the snakehead *Channa* sp., (according to Lowe-McConnell, 1987) of more recent introduction, now populate Malagasy waters.

Sport fishing

Among the many reasons to perform introductions, nostalgia of displaced peoples for familiar fauna to surround them would seem to rank fairly high (Welcomme, 1988) and, in the past, fishery officers introduced alien species to improve sport fisheries, such as in Morocco, South Africa, Kenya and Madagascar where bass (*Micropterus salmoides* from North America) (Moreau *et al.*, 1988) and trout (*Salmo trutta* from Europe) (Baglinière & Maisse, 1991) were introduced.

The controversial introduction of *Lates niloticus* (figure 23.1) in Lake Victoria (see box "The case of *Lates niloticus* in Lake Victoria") could have also been partly motivated by the wish to develop sport fishing.

Fish culture

More than a hundred fish species have been introduced for aquaculture purposes around the world, but few of such introductions involve tropical Africa. The carp (*Cyprinus carpio*) is one of the rare non-indigenous species for which farming



TABLE 23.I.

Alien (from other continents) species introduced in Africa. Total: number of countries where the species has been introduced. Species established in the wild (E); species not established in the wild (NE), data unknown (U) (data synthetized from Froese & Pauly, 2010 and Lever, 1996).

Species	Families	Algeria	Angola	Botswana	Burundi	Cameroon	CAR	Congo	Côte d'Ivoire	Egypt	Eritrea	Ethiopia	Ghana	Kenya	Lesotho
Anguilla anguilla	Anguillidae				-						Е			NE	
Astronotus ocellatrus	Cichlidae								NE						
Astyanax orthodus	Characidae														
Barbus barbus	Cyprinidae														
Carassius auratus auratus	Cyprinidae											Е			
Carassius carassius	Cyprinidae											U		NE	
Catla catla	Cyprinidae														
Channa maculata	Channidae														
Channa striata	Channidae	<u> </u>													
Cichla ocellaris	Cichlidae													NE	——–
Ctenopharyngodon idella	Cyprinidae	NE	U		NE				Е	Е		Е			NE
		INE	U	- E		Б	Б		E	E					
Cyprinus carpio carpio	Cyprinidae		0	Е	U	Е	Е		Е	Е		E		NE	U
Esox lucius	Esocidae	E					-		* 1	-		E	* *		
Gambusia affinis	Poeciliidae						E		U	E			U	E	
Gambusia hilbrooki	Poeciliidae											Е		Е	
Gobio gobio	Cyprinidae														/
Hucho hucho	Salmonidae														
Hypophthalmichthys molitrix	Cyprinidae	NE								NE		Е			NE
Hypophthalmichthys nobilis	Cyprinidae	NE								NE					NE
Ictalurus punctatus	Ictaluridae								U	NE					
Labeo rohita	Cyprinidae														
Lepomis cyanellus	Centrarchidae							NE						U	
Lepomis gibbosus	Centrarchidae							Е							
Lepomis macrochirus	Centrarchidae							NE						U	
Lepomis microlophus	Centrarchidae														
Macropodus opercularis	Osphronemidae														
	Centrarchidae	<u> </u>													
Micropterus dolomieu		──	NIT												
Micropterus punctulatus	Centrarchidae		NE			NT		NIC		NTC				- F	r
Micropterus salmoides	Centrarchidae	E		Е		NE		NE		NE				E	E
Mylopharyngodon piceus	Cyprinidae									U					
Oncorhynchus mykiss	Salmonidae					U		NE			E	E		Е	E
Osphronemus goramy	Osphronemidae	U							NE						
Perca fluviatilis	Percidae														
Phalloceros caudimaculatus	Poeciliidae														
Poecilia latipinna	Poeciliidae													Е	
Poecilia reticulata	Poeciliidae													Е	
Pseudorasbora parva	Cyprinidae	Е													
Rutilus rutilus	Cyprinidae														
Salmo trutta fario	Salmonidae													Е	
Salmo trutta trutta	Salmonidae											Е		E	Е
Salvelinus fontinalis	Salmonidae	<u> </u>													-
Sander lucioperca		NE													
Scardinius erythrophthalmus															
Scarainius eryinrophinaimus Silurus glanis	Cyprinidae	NE													
0	Siluridae	INE													
Tanichthys albonubes	Cyprinidae	<u> </u>													
Tinca tinca	Cyprinidae														
Trichogaster trichopterus	Osphronemidae														
Xiphophorus helleri	Poeciliidae														
Xiphophorus maculatus	Poeciliidae														
Total		9	3	2	2	3	2	5	6	8	2	9	1	15	7

Species introductions

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Species	Families	Madagascar	Malawi	Morocco	Mozambique	Namibia	Nigeria	RDC	Rwanda	South Africa	Sudan	Swaziland	Tanzania	Togo	Tunisia	Uganda	Zambia	Zimbabwe	Total
Anguilla anguilla	Anguillidae																		2
 Astronotus ocellatrus	Cichlidae																		1
 Astvanax orthodus	Characidae					Е													1
 Barbus barbus	Cyprinidae			Е		2													1
 Carassius auratus auratus	Cyprinidae	Е		2		Е				Е								Е	5
Carassius carassius	Cyprinidae					Ľ				Ľ								Ľ	2
Catla catla	Cyprinidae																NE		1
 Channa maculata	Channidae	Е															IL		1
 Channa striata	Channidae	E																	1
 Cichla ocellaris	Cichlidae	Ľ																	1
 Ctenopharyngodon idella	Cyprinidae		NE	Е	NE		U		NE	NE	Е		U		Е	NE	NE	NE	20
 Cyprinus carpio carpio	Cyprinidae	Е	NE	E	U	Е		NE	E	E	NE	U	U	U	E	E	NE	E	20
 Esox lucius	Esocidae	NE	INE	E	0	Е	Е	INE	Е	Е	INE	0	0	0	NE	U	INE	Е	6
	Poeciliidae	E		E						Е	Е				INE	U	NE	Е	11
 Gambusia affinis		E		Е						Е	E						INE	Е	
 Gambusia hilbrooki	Poeciliidae	Е		F															3
 Gobio gobio	Cyprinidae			E															1
 Hucho hucho	Salmonidae			NE											-		* *	* *	1
 Hypophthalmichthys molitrix	Cyprinidae	NE	NE	E	NE		NE		NE	NE			NE		E		U	U	15
 Hypophthalmichthys nobilis	Cyprinidae	NE		U	NE														6
 Ictalurus punctatus	Ictaluridae						U												3
 Labeo rohita	Cyprinidae	U					NE											U	3
 Lepomis cyanellus	Centrarchidae	NE		Е						U		Е					Е	NE	8
Lepomis gibbosus	Centrarchidae			Е															2
Lepomis macrochirus	Centrarchidae	E	Е	Е						Е		Е					NE	Е	9
Lepomis microlophus	Centrarchidae			Е															1
Macropodus opercularis	Osphronemidae	Е																	1
Micropterus dolomieu	Centrarchidae									Е		NE	Е				NE	NE	5
Micropterus punctulatus	Centrarchidae									Е		U						Е	4
Micropterus salmoides	Centrarchidae	Е	Е	Е	U	Е	U			Е		Е	U		Е	U		Е	19
Mylopharyngodon piceus	Cyprinidae			U															2
Oncorhynchus mykiss	Salmonidae	Е	Е	Е	U					Е	Е	Е	Е		NE	U	NE	Е	18
Osphronemus goramy	Osphronemidae	Е														NE			4
Perca fluviatilis	Percidae			Е						Е									2
Phalloceros caudimaculatus	Poeciliidae		Е																1
Poecilia latipinna	Poeciliidae																		1
Poecilia reticulata	Poeciliidae	Е	NE			Е	NE			Е						Е	Е		8
Pseudorasbora parva	Cyprinidae																		1
 Rutilus rutilus	Cyprinidae	NE		Е															2
Salmo trutta fario	Salmonidae	Е																	2
Salmo trutta trutta	Salmonidae	Е	NE	NE						Е		Е	U					Е	10
 Salvelinus fontinalis	Salmonidae			NE														Е	2
 Sander lucioperca	Percidae			Е											Е				3
Scardinius erythrophthalmus	Cyprinidae	NE		Е											Е				3
 Silurus glanis	Siluridae			-											NE				2
Tanichthys albonubes	Cyprinidae	Е																	1
Tinca tinca	Cyprinidae	NE		Е						Е					NE		NE	E	6
 Trichogaster trichopterus	Osphronemidae			-		Е				-					111		1,12	Ы	1
 Xiphophorus helleri	Poeciliidae	Е				E				Е							U		4
 Xiphophorus maculatus	Poeciliidae	E				ы	Е			<u>ь</u>							0		2
	1 occinitae											6	-						<u> </u>
Total		25	9	23	6	7	8	1	3	16	4	8	7	1	10	7	11	16	236

TABLE 23.II.

African translocated species. Number: number of countries where the species has been translocated. Species established in the wild (E); species not established in the wild (NE), data unknown (U) (data synthetized from Froese & Pauly, 2010 and Lever, 1996).

Species	Families	Algeria	Angola	Benin	Botswana	Burkina Faso	Burundi	Cameroon	CAR	Chad	Congo	Côte d'Ivoire	Egypt	Eritrea	Ethiopia	Gabon	Ghana
Aphanius fasciatus	Cyprinodontidae																
Astatoreochromis alluaudi	Cichlidae							Е	Е		NE	,					
Bagrus meridionalis	Bagridae																
Barbus anoplus	Cyprinidae																
Boulengerochromis microlepis	Cichlidae																
Butis koilomatodon	Eleotridae																
Clarias gariepinus	Clariidae						Е	Е			Е	NE				Е	
Distichodus nefasch	Distichodontidae										Е						
Heterotis niloticus	Arapaimidae							U	Е		Е	U				Е	
Labeobarbus aeneus	Cyprinidae																
Labeobarbus kimberleyensis	Cyprinidae																
Labeobarbus natalensis	Cyprinidae																
Lates niloticus	Latidae										Е						
Limnothrissa miodon	Clupeidae																
Microctenopoma ansorgii	Anabantidae																
Oreochromis andersonii	Cichlidae																
Oreochromis aureus	Cichlidae											NE					
Oreochromis esculentus	Cichlidae																
Oreochromis karongae	Cichlidae																
Oreochromis leucostictus	Cichlidae						U										
Oreochromis macrochir	Cichlidae	NE	U	NE	,	Е	U	NE	E		NE	Е	Е			Е	Е
Oreochromis mortimeri	Cichlidae																
Oreochromis mossambicus	Cichlidae	E	U	Е			U				Е	NE	Е				
Oreochromis niloticus eduardianus	Cichlidae																
Oreochromis niloticus niloticus	Cichlidae				Е		Е	Е	U		Е	Е		Е		U	
Oreochromis shiranus shiranus	Cichlidae																
Oreochromis spilurus niger	Cichlidae																
Oreochromis spilurus spilurus	Cichlidae			U				U			U	U	U				
Oreochromis tanganicae	Cichlidae						U										
Oreochromis urolepis hornorum	Cichlidae											Е					
Pachypanchax playfairii	Aplocheilidae																
Protopterus aethiopicus aethiopicus	Protopteridae																
Sarotherodon galilaeus boulengeri	Cichlidae															Е	
Sarotherodon galilaeus galilaeus	Cichlidae										Е						
Schilbe mystus	Schilbeidae										E						
Serranochromis robustus jallae	Cichlidae																
Serranochromis robustus robustus	Cichlidae																
Stolothrissa tanganicae	Clupeidae																
Tilapia guinasana	Cichlidae				U												
Coptodon rendalli	Cichlidae		U				Е	NE	NE	E	Е	NE			Е	Е	
Tilapia sparrmanii	Cichlidae																
Coptodon zillii	Cichlidae	NE										NE		Е	Е		
Total		3		3	2	1	7	7	5	1	12	10		2		6	1
10(2)	i	1 5	3	3	-	1	'	'	3	1	14	10	3	-	-	U	1

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Species	Families	Guinea	Kenya	Lesotho	Liberia	Madagascar	Malawi	Morocco	Mozambique	Namibia	Nigeria	RDC	Rwanda	Sierra Leone	South Africa	Sudan	Swaziland	Tanzania	Togo	Tunisia	Uganda	Zambia	Zimbabwe	Total
Aphanius fasciatus	Cyprinodontidae							Е																1
Astatoreochromis alluaudi	Cichlidae											Е										NE		5
Bagrus meridionalis	Bagridae																		Ν	ΕN	Е			2
Barbus anoplus	Cyprinidae									Е														1
Boulengerochromis microlepis	Cichlidae																		N	ΙE				1
Butis koilomatodon	Eleotridae										Е													1
Clarias gariepinus	Clariidae			E								NE												7
Distichodus nefasch	Distichodontidae																							1
Heterotis niloticus	Arapaimidae					Е						Е							Е					8
Labeobarbus aeneus	Cyprinidae																			E				1
Labeobarbus kimberleyensis	Cyprinidae																			NE				1
Labeobarbus natalensis	Cyprinidae																			E				1
Lates niloticus	Latidae		Е					NE										Е			Е			5
Limnothrissa miodon	Clupeidae								Е			Е	Е									Е	Е	5
Microctenopoma ansorgii	Anabantidae					Е																		1
Oreochromis andersonii	Cichlidae		U									Е			Е			Е					NE	5
Oreochromis aureus	Cichlidae		U			Е									Е						NE	Е	U	7
Oreochromis esculentus	Cichlidae												Е					Е						2
Oreochromis karongae	Cichlidae						Е																	1
Oreochromis leucostictus	Cichlidae		U									Е	Е					Е			Е			6
Oreochromis macrochir	Cichlidae		Е		U	Е						Е	Е		U	Е		U	U			Е	Е	23
Oreochromis mortimeri	Cichlidae											Е										U		2
Oreochromis mossambicus	Cichlidae		U			Е				Е		Е			Е			Е		Е	Е			15
Oreochromis niloticus eduardianus	Cichlidae		Е															Е			Е			3
Oreochromis niloticus niloticus	Cichlidae	NE	Е		U	Е			U			U	Е	U	Е			Е		Е		Е	Е	21
Oreochromis shiranus shiranus	Cichlidae					NE																		1
Oreochromis spilurus niger	Cichlidae		NE			Е			U													U		4
Oreochromis spilurus spilurus	Cichlidae					NE			U			Е									Е			9
Oreochromis tanganicae	Cichlidae																							1
Oreochromis urolepis hornorum	Cichlidae																							1
Pachypanchax playfairii	Aplocheilidae																	Е						1
Protopterus aethiopicus aethiopicus	Protopteridae												Е											1
Sarotherodon galilaeus boulengeri	Cichlidae																							1
Sarotherodon galilaeus galilaeus	Cichlidae														NE									2
Schilbe mystus	Schilbeidae																							1
Serranochromis robustus jallae	Cichlidae														Е		Е							2
Serranochromis robustus robustus	Cichlidae																Е					U		2
Stolothrissa tanganicae	Clupeidae											NE												1
Tilapia guinasana	Cichlidae																							1
Coptodon rendalli	Cichlidae		Е			Е	U						Е			NE		Е			Е	Е		17
Tilapia sparrmanii	Cichlidae					Е									Е			NE						3
Coptodon zillii	Cichlidae		Е			Е									NE			Е			Е			9
Total		1	11	1	2	12	2	2	4	2	1	12	7	1	9	2	2	12	2	2	8	11	9	183

was attempted several times in various African countries. Many tilapia species have also been translocated to different sites on the African continent (Moreau *et al.*, 1988; Lazard, 1990a) or introduced more or less everywhere in the world (see chapter *Fish culture*). In the intertropical zone, *Oreochromis niloticus* (figure 23.1) and to a lesser extent *Oreochromis mossambicus* currently account for most of aquaculture production.

Improvement of wild stocks

Fisheries managers have often attempted to introduce species in order to improve the fish production of an aquatic ecosystem, particularly when they believe that certain ecological niches are vacant and that the resources of a given system are not optimally exploited by indigenous fishes.

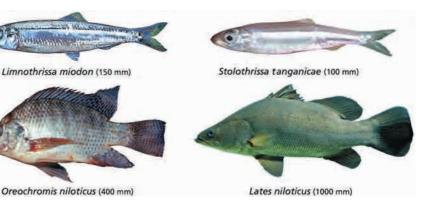
Hence, *Limnothrissa miodon* and *Stolothrissa tanganicae* (figure 23.1), two small Clupeidae endemic to Lake Tanganyika, were introduced into Lake Kivu in 1958-1960 where they occupied a vacant niche by exploiting pelagic zoo-plankton. This introduction is considered a success from the economic viewpoint (Spliethoff *et al.*, 1983) and allowed the establishment of a fishery in the early 1980s (see also box "Genetic evolution of introduced species").

Species introduction has also been justified at times by the creation of new habitats. For instance, fluvial species that prefer running water are not always suited to reservoirs. We can thus seek out species that are likely to colonize these new systems and use their resources more efficiently. This is why *Limnothrissa miodon* was also introduced into Lake Kariba (an artificial reservoir) in order to use the pelagic zone's zooplankton more optimally. It became wellestablished there and now occupies the entire lake, where it serves as food for *Hydrocynus vittatus* and allowed the development of a fishery (Marshall, 1984b). Fishery production which stood at 1,000 tonnes in 1974 increased to 24,000 tonnes by 1985 (Marshall, 1988).

FIGURE 23.1.

Four main African fish species introduced in other environments to improve fisheries: two pelagic zooplanktivorous clupeids Limnothrissa miodon and Stolothrissa tanganicae, one omnivorous cichlid Oreochromis niloticus and one ichtyophagous Lates niloticus In brackets: common size of the species.

The introduction of *Heterotis niloticus* and *Oreochromis niloticus* in Lake Kossou, Côte d'Ivoire, was also intended to encourage colonization of this reservoir by fishes that were more suited to lacustrine conditions (Lazard, 1990b) and the two species have become well-established there with no apparent consequences to date on the native fauna.



To justify introductions, fisheries managers highlight other examples deemed positive for fisheries development. The introduction of different tilapia species of African origin (particularly *Oreochromis mossambicus*) in natural lakes and artificial reservoirs has made it possible to improve subsistence fishing in many African countries (Fernando, 1991; Fernando & Furtado, 1975; Holcik, 1984). Tilapias (*Oreochromis* sp. and *Sarotherodon* sp.) are very good colonizing species for their biological characteristics (species practicing parental care), their great physiological tolerance, and their ability to feed on seaweed and detritus which are often poorly-used resources in many tropical systems (Philippart & Ruwet, 1982). They have been introduced in Africa in many small agro-pastoral reservoirs that have been constructed over the last two decades.

Another example is that of Lake Kyoga where *Lates niloticus* and *Oreochromis niloticus* were introduced in the 1950s and rapidly thrived (Gee, 1969). In 1977 each species accounted for about 40% of artisanal fishing, estimated at 167,000 tonnes, a far cry from the 4,500 tonnes recorded in 1956. In 1985 the situation had changed with *O. niloticus* accounting for 78% of catches compared with only 17% for *L. niloticus* (Ogutu-Ohwayo, 1990).

Finally, in Lake Victoria improved fishing technology (nylon gillnets and outboard motors) combined with increased fishing effort resulted in a severe drop in catches of the endemic tilapia species by the beginning of the 1970s, well before the Nile perch (*Lates niloticus*) was established (Fryer & Iles, 1972). In this case, as the native species declined, new fisheries were established targeting other newly introduced species (particularly *Lates niloticus* and *Oreochomis niloticus*). The total catch reached 0.9 million tonnes at the end of the 2000s (figure 23.2). The question now is how stable the new fishery, based on non-native species, will be over the longer term as the catch composition appears to be undergoing a period of quite dramatic change (Witte *et al.*, 2007b).

GENETIC EVOLUTION OF INTRODUCED SPECIES

Do species introduced into new systems keep their genetic characteristics, or can an evolution be observed in a relatively short time span? The answer depends in part on the techniques used. *Limnothrissa miodon* was introduced in 1959 into Lake Kivu from populations caught in Lake Tanganyika. Hauser *et al.* (1995) have shown that 34 years later, the translocated population differs from the original population both morphologically and genetically. While no allozyme diversity was observed, the Kivu population shows nonetheless poorer diversity of mitochondrial DNA (mtDNA haplotype diversity). This loss of variation which suggests a founder effect may have been caused by high individual mortality (several tens of thousands) after the introduction, such that the current population may come from only a few dozen surviving individuals. This loss of variability in mitochondrial DNA controlling enzymes needed for cell physiology may in theory have consequences on the physiological adaptability of the species.

THE CASE OF LATES NILOTICUS IN LAKE VICTORIA

Lake Victoria is the second-largest lake in the world, covering an area of 68,000 km². In the mid-1980s, the lake's fish community and fishery changed drastically from being dominated by a few hundred endemic haplochromine species to a catch of basically three species: the introduced Nile perch (Lates niloticus) and dagaalomena (Rastrineobola argentea) in the open waters; and the introduced Nile tilapia (Oreochromis niloticus) along the shores. The endemic cichlids (haplochromines) that vanished almost completely as the fish community changed, have been reappearing in catches since 2000 and are probably recovering slowly. The inshore demersal species, originally mainly endemic tilapias (Oreochromis esculentus and O. variabilis), Nile catfish (Bagrus docmak), lungfish (Protopterus aethiopicus), the elephant-snout fish (Mormvrus kannume). and the ningu (Labeo victorianus), are all depleted. except the lungfish. Today, the Nile tilapia dominates, its abundance is increasing in surveys and it is considered moderately exploited. Dagaa stocks and catches have been increasing steadily. Since 2005, it has been the most important fishery in the lake by weight, but there are no signs of overexploitation (figure 23.2).

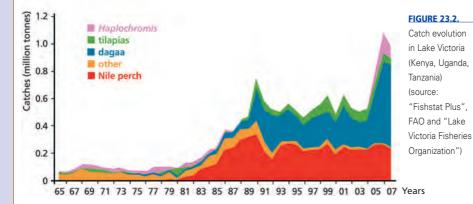
The explosion of *Lates* populations associated with the vanishing of small cichlid populations led many scientists to claim that *Lates* exterminated endemic haplochromines. They denounced the ecological disaster following the introduction of the exotic top predator and its impact on the naïve endemic ichthyofauna. In most textbooks *Lates* became the archetype of mismanagement of aquatic systems by man leading to environmental disaster.

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The situation is actually much more complex. Detailed analysis has shown that the dynamics of fish production in Lake Victoria are, to a large extent, environmentally driven. Changes in land-use practices and a huge increase of human settlements in the lake basin have led to an increased input of nutrients, resulting in an eutrophication process which poses a serious threat to the entire ecosystem.

Eutrophication began as early as the 1940s to 1950s as revealed by diatom analysis. The timing of the eutrophication means that Nile perch population growth could not be the primary cause. Long-term human population growth, agricultural and urban development, and the associated increases in nutrient pollution and soil erosion are the most likely underlying causes of the recent changes in water quality, with climatic conditions sometimes amplifying those effects.

The main consequences of eutrophication are the deoxygenation of bottom waters and loss of habitat (endemic cichlids built nests on the bottom), and increased turbidity (the benthic cichlids use visual signals for sexual recognition). Meanwhile, eutrophication led to an increased primary production that benefits shrimp (*Caridina*), and pelagic fish (Rastrineobola), whose biomass exploded, providing food to Lates. As a result, Lates may have contributed to the depletion of small cichlid populations, but the eutrophication was a serious threat to these populations that may have been endangered even in the absence of Lates. This is a different story from the one singling out Lates as a "devil" fish. It is possible to control eutrophication through water purification plans, but it will be costly. Who is ready to pay?



Biological control

Fish species introduction was also practiced to control disease vectors. Certain species such as *Gambusia affinis* or *Poecilia reticulata* were used in different regions of Africa in an attempt to control malaria-bearing mosquitoes. There was also a proposal to use the mollusciverous cichlid *Astatoreochromis alluaudi* from East Africa to fight schistosomiasis vectors (Slootweg, 1989). This species was introduced into different locations in Africa without any visible ecological effects, but without proving its effectiveness as a means of disease control either. Finally, African fishes are sometimes used to control aquatic vegetation, with the example of *Coptodon rendalli* which was introduced into irrigation canals in Sudan.

Accidental introductions

Introductions that are accidental (or thought to be) are relatively frequent. Many, if not all, species introduced for aquaculture purposes escaped from fish farms during uncontrolled events such as exceptional floods, whereas their presence was not desired in the natural environment. This is thought to be the case in Madagascar of the snakehead, *Channa striata*, a fish of Asian origin that spread in many aquatic systems after a flood destroyed the fish farming station where the species was stocked.

The transport of fishes via the ballast of vessels is also considered a major source of transfers. This is the hypothesis advanced by Miller *et al.* (1989) to explain the introduction of an Eleotridae (*Butis koilomatodon*) originating in the Indo-Pacific into the mangroves of Lower Guinea.

As transfers of aquarium fishes are not controlled, there are more and more so-called accidental introductions of these species in aquatic systems around the world. These are often individuals released by amateur aquarists into the natural environment.

Consequences of introductions for the aquatic environment

The introduction of new species into an ecosystem is sometimes behind competition phenomena that can lead to the elimination of indigenous or introduced species. But there may also be indirect changes, generally more difficult to observe, via trophic chains. To interpret the impact of introductions accurately, it is necessary to distinguish between several levels of intervention:

• the transplantation of species from one point to another within the same watershed;

• the introduction of species missing from the watershed but present in the same biogeographic area;

• the introduction of species from biogeographically different areas, or even different continents.

Several observations appear to indicate that most species introductions do not have noticeable ecological effect, and that the socio-economic impact has often been beneficial (table 23.III). Nonetheless, despite its highly interesting findings, this widely-disseminated table is not accompanied by the methodology that allowed these conclusions to be drawn, and we cannot verify their pertinence. The discussion remains partially unresolved (Lazard & Lévêque, 2009).

Impact	Fisheries	Aquaculture	Aquarium trade	Biological control	Unknown	Others
Negative	36 (2)	78 (8)	17 (5)	23 (9)	13 (0)	40 (12)
Beneficial	16 (87)	52 (283)	11 (42)	11 (19)	3 (10)	6 (15)
Unknown	28 (16)	76 (49)	9 (9)	8 (2)	21 (3)	
Nil	196 (299)	949 (815)	169 (150)	106 (122)	459	283 (328)

TABLE 23.III.

Effects of introduced fish on ecological (and socio-economic) environments (from Lazard & Lévêque, 2009).

Interaction with native species

Introduced species can compete with indigenous species and eventually eliminate them. This is particularly true when predator species are introduced. One of the most spectacular cases is the introduction into Lake Victoria of *Lates niloticus*, a piscivorous fish that can reach a weight of more than 100 kg. For some scientists, this predator could be the reason for the decline and probable disappearance of several species belonging to a rich endemic fauna of small Cichlidae that it preyed upon (see box "The case of *Lates niloticus* in Lake Victoria"). It is also believed that the introduction of black bass in Lake Naivasha in 1929 for sport fishing could have been responsible for the disappearance of some indigenous species, as well as that of species such as *Gambusia* and *Poecilia* sp. that were introduced to control mosquito larvae.

Non-predator species can also have an impact on indigenous fauna, as was shown in Lake Luhondo (Rwanda) (De Vos *et al.*, 1990). Until 1934, three Cyprinidae species were known in the lake: a small barb, *Barbus neumayeri*, and two large species, *Barbus microbarbis* and *Varicorhinus ruandae*. *Oreochromis niloticus* had been voluntarily introduced in 1935, along with a few *Haplochromis* species that were apparently accidentally introduced. In the 1950s, *O. niloticus* became the dominant species but the *Haplochromis* started flourishing, to the point of being the most abundant fish at present. Meanwhile *B. microbrabis* has disappeared, and the two other Cyprinidae are now restricted to the small tributaries of the lake.

The spread of alien invasive plants and animals is recognized to be a major threat for freshwater biodiversity (Dudgeon *et al.* 2005; Leprieur *et al.* 2009). Until now, only a few true exotic species have been deliberately introduced into African freshwaters, with the exception of Madagascar (Benstead *et al.*, 2003). More often, there have been species translocations from one African water system to another. For example, Nile tilapia, *Oreochromis niloticus*, has been

introduced both for aquaculture and fisheries throughout most of inter-tropical Africa where it is reported to have negative impacts on the indigenous fish fauna (Canico *et al.*, 2005). On the other side fish farmers promote the introduction of tilapia species as an important species group for improving fish production in many African water bodies.

In South Africa, alien fishes introduced for angling are a particularly serious threat (Darwall *et al.*, 2009). Smallmouth bass (*Micropterus dolomieu*), together with largemouth and spotted bass (*M. salmoides* and *M. punctulatus*) and bluegill sunfish (*Lepomis macrochirus*), all from North America, and banded tilapia (*Tilapia sparmanii*) from further north in Africa now dominate the fish fauna in more than 80% of the Olifants River system, with indigenous fish often surviving in less than 1 km of river in headwater streams. Rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) have had major impacts in cooler headwater streams.

Impact on the aquatic ecosystem

The introduction of a predator into an aquatic ecosystem may have an impact on the system's biological function through its effects on trophic chains. A spectacular example of the trophic cascade (see chapter *Role of fish in ecosystem functioning*) is the one that followed the introduction of Nile perch, *Lates niloticus*, into Lake Victoria, which may be responsible for the near-disappearance in the 1980s of the detritivorous/phytoplanktivorous group of haplochromines (endemic Cichlidae), as well as the zooplanktivorous group that respectively accounted for 40 and 16% of the biomass of demersal fishes (figure 23.3). The detritivorous were replaced by the indigenous shrimp *Caridina nilotica*, and the zooplanktivorous by the pelagic cyprinid *Rastrineobola argentea* (Witte *et al.*, 1992a), with the latter two species becoming the main food source for perch after the haplochromines vanished.

The introduction of planktonic species appears to have consequences on zooplanktonic communities. Green (1985) has noted that *Limnothrissa* introduced into Lake Kariba has reduced zooplankton abundance by 2.4 to 44 times, depending on the taxa under consideration. In Lake Kivu, several species of large planktonic crustaceans are believed to have disappeared because of predation, as indicated by the analysis of zooplankton samples taken prior to introduction and some 20 years after it (de longh *et al.*, 1983, 1995). In 1981, *Daphnia* water fleas had completely disappeared and the average size of cyclopoids was found to be much smaller. Meanwhile, ciliates, rotifers, and small water fleas, that is, small species, were abundant. Samples taken in 1986 contained no planktonic organisms that were larger than 0.2 mm (Dumont, 1986).

Hybridizations

The introduction into the same body of water of neighbouring species that do not usually cohabit may lead to a hybridization of the introduced species. Tilapia species are particularly notorious for hybridizing (Trewavas, 1983), which can lead to genetic modifications for surviving species. For example, in Lake Naivasha, *Oreochromis spilurus* introduced in 1925 was abundant in the 1950s and 1960s, then hybridized with *Oreochromis leucostictus* introduced in 1956.

The inland water fishes of Africa

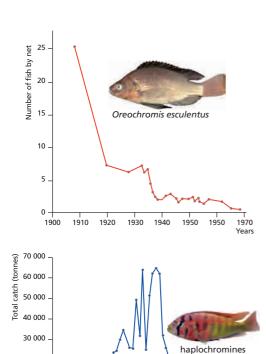
FIGURE 23.3.

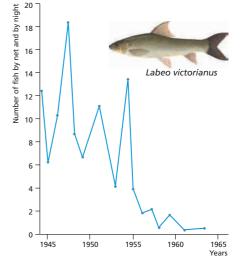
Fisheries results for main species from Lake Victoria.

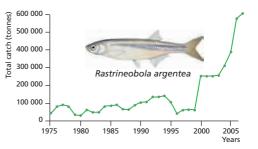
Sources: Oreochromis niloticus, Lates niloticus, haplochromines (FishStat Plus);

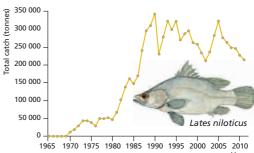
Oreochromis esculentus, Labeo victorianus (Ogutu-Ohwayo, 1990);

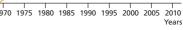
Rastrineobola argentea (Witte et al., 2009, completed by "Lake Victoria Basin Aquatic Biodiversity Meta-Database").

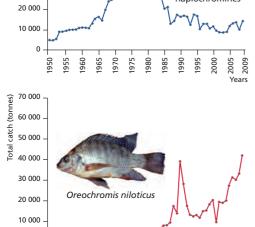












 2000 -

Years

 This resulted in the disappearance of *O. spilurus* and hybrids (Siddiqui, 1977, 1979).

The disappearance of the species *O. esculentus* and *O. variabilis*, endemic to Lakes Victoria and Kyoga, may be due to the hybridization and/or competition with introduced species (*O. niloticus*, *C. zillii*). *O. niloticus* x *O. variabilis* hybrids have been observed in Lake Victoria (Trewavas, 1983).

Cumulative impacts of introductions on wildlife and fisheries: example of Malagasy lakes

Malagasy fish fauna is relatively poor but comprises numerous endemic species belonging in particular to the Cichlidae and Bedotiidae families (Reinthal & Stiassny, 1991). The introduction of alien species began in the 20th century (Kiener, 1963; Moreau, 1979) and the current populations of many Malagasy lakes (e.g. Lake Alaotra, Lake Itasy) are made up of species from various continents (tables 23.1 and 23.11). These species cohabit very well and are behind a fairly prosperous fishery. But they also eliminated part of the indigenous fauna.

In Lake Alaotra, prior to the introduction of exotic species, the fish community was poor and dominated by *Paratilapia polleni*, *Rheocles alaotrensis*, *Ratsirakia legendrei*, and two eels (*Anguilla mossambicus* and *A. marmorata*) (Moreau, 1980). In the beginning of the 20th century, *Carassius auratus* introduced in Madagascar in 1865 was found present in the lake, and in 1925 *P. polleni* as well as *C. auratus* accounted for most of the catches of artisanal fishing (table 23.IV). In 1935, *Cyprinus carpio* introduced in 1925 was a non-negligible component of catches, and in 1954 this species was largely dominant (table 23.IV).

This was followed by a period in which three tilapia species were introduced in succession, and two of these (*Coptodon rendalli* and *Oreochromis macrochir*) proliferated during the 1960s while native species and *C. auratus* markedly regressed. The decrease of tilapias in catches during the 1970s may be due to overexploitation following the introduction of gillnets in the fishery in the

TABLE 23.IV.						
IABLE 23.IV.						

Fishing activities, introductions and changes in commercial catches (in %) in Lake Alaotra, Madagascar (from Moreau, 1980).

Years	1925	1935	1954	1957	1960	1963	1966	1969	1972	1975
Anguilla spp.	5	5	1	1	1	1	1	1	1	1
Paratilapia polleni	75	40	5	3	2	1				
Carassius auratus	20	25	14	10	4	2				
Cyprinus carpio (1925)		30	80	40	15	14	5	11	21	21
Coptodon rendalli (1954)				46	23	8	10	20	16	16
Oreochromis macrochir (1958)					55	74	85	66	56	50
Oreochromis niloticus(1961)								1	3	7
Micropterus salmoides(1961)							1	1	3	4
Total catches (tonnes)			1 800	2 200	2 700	3 000	3 200	2 500	2 100	2 100

late 1960s. The black bass *Micropterus salmoides* introduced in 1962 did not develop much, as it only accounted for 4% of catches in 1975. From 1966 to 1972, *Cyprinus carpio* juveniles were reintroduced into the lake, which could explain the slight increase in catches.

More recently, *Channa striata* spread in the natural waters of Madagascar after escaping from fish farms. This predator of Asian origin may have a significant impact on fish fauna.

A similar tale took place in Lake Itasy (Moreau, 1979) which was inhabited by several indigenous species in the beginning of the 20th century: Anguilla mossambica, Anguilla nebulosa labiata, Anguilla marmorata, Ptychochromis betsileanus, Ratsirakia legendrei, and Chonophorus macrorhynchus. Carassius auratus was introduced in 1899, and Paratilapia polleni (an endemic Malagasy species) in 1924 but they did not really prosper. In 1930, Ptychochromis betsileanus made up 40% of catches, but in 1950-1955, Cyprinus carpio which was introduced in 1925-1930, accounted for 80 to 85% of catches compared with only 10% for P. betsileanus (table 23.V). Coptodon rendalli introduced in 1955, rapidly replaced *Cyprinus carpio*, and in around 1958 represented 70% of catches. But C. rendalli itself was replaced by Oreochromis macrochir which was introduced in 1958 and accounted for the bulk of catches in 1963. In 1965, the importance of *O. macrochir* went down because of the appearance in catches of a hybrid called Tilapia 3/4, and in 1972 O. macrochir had disappeared. Tilapia 3/4 is the result of natural hybridation between O. macrochir and O. niloticus which was introduced in 1961. This spontaneous hybridization led to more fecund fertile hybrids of the same size as *O. macrochir*. But populations of O. niloticus developed slowly and in 1975 represented 55% of catches, followed by *Tilapia* 3/4 that started showing signs of degeneracy. The contribution of species to captures in 1985 was essentially similar to figures for 1975 (Matthes, 1985).

TABLE 23.V.

Fishing activities, introductions and changes in commercial catches (in %) in Lake Itasy, Madagascar (from Moreau, 1979).

	1	-55															
Years	1930	1950-55	1958	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1985
Ptychochromis betsileanus	40	10	0	0													
Anguilla spp	50?			3	2	2	2	1	1	1	1	1	1	1	1	1	
Cyprinus carpio (1925)		80-85		6	6	5	4	4	4	3	3	3	3	3	3	3	1.5
Coptodon rendalli (1955)			70	5	4	4	3	3	2	1	1	1	1	1	1	*	0.4
Oreochromis macrochir (1958)				85	86	78	56	30	10	1	1	0					
Oreochromis niloticus (1961)				1	2	5	8	10	15	18	24	32	39	45	50	55	57
Tilapia 3/4				0	0	5	25	50	66	74	68	61	54	48	43	39	38
Micropterus salmoides (1961)				0	0	1	1	2	2	2	2	3	3	3	3	3	1.5
Total catches (tonnes)			1	1200	850	500	300	280	84	830	450	300	290	280	280	275	625

Certain species were also introduced, without apparent success, in Lake Itasy. This is the case for *Micropterus salmoides* introduced in 1962, *Gambusia holbrooki* introduced around 1950, and *Oreochromis mossambicus* introduced in 1961, but these species, along with *O. macrochir*, seem to have disappeared (Matthes, 1985). *Channa striata* was observed in catches in 1985 and we can imagine that this predator species will have a major impact on existing populations.

It should be noted that overfishing or at the very least changes in fishing techniques have probably also played a role in the evolution of fish populations in Lakes Alaotra and Itasy. It is however difficult to make a distinction between the consequences stemming from introductions and those resulting from a shift in the means of resource exploitation.

What can we learn from the lessons of the past?

The invasion of aquatic ecosystems by new species during geological or climatic events is not an exceptional situation on a historical scale. But the current degree and frequency of introductions caused by human activity are worrying to scientists, as we run the risk of obtaining mixtures of faunas from the most diverse origins in only a few decades, something that could not have been achieved over millions of years through geological events alone.

Many believe – not unreasonably – that these species introductions, a true gamble, can lead to ecological disasters in some cases. They thus condemn from the outset, on a more or less intuitive basis, any attempt to introduce a species without a proper evaluation of its potential merits from an economic or ecological perspective.

Can we draw a number of lessons from past experience and put forth some principles that would limit the negative consequences of introductions? First, we must remember that introductions are irreversible and that it is not possible to eradicate introduced species using the means currently available. Moreover, it seems to be well-established through numerous examples in Africa and other regions of the world that the introduction of large predators in lakes where endemic species form the bulk of the fish fauna, has often produced a catastrophic impact on this indigenous fauna. The example of Lake Victoria (see box "The case of *Lates niloticus* in Lake Victoria") is a particularly dramatic illustration of this situation.

When we examine the consequences of various introductions, we too often notice that the information is anecdotal or fragmented and that the effects of introduced species may have been obscured or amplified by environmental changes that stemmed from different causes. It is also possible that in some circumstances, some impacts may have been wrongly attributed to introductions. Conversely, we have probably not always taken into account the consequences of introductions on other aspects of the biological systems



involved. In reality, it is often difficult to distinguish the consequences of species introductions from the consequences of human activity on aquatic systems. For instance, in Lake Victoria where *Lates* is accused of causing the disappearance of numerous endemic species, it has been found that the latter had already been undermined by the introduction of new fishing techniques (trawling) and that the lake was also undergoing a process of eutrophication, which meant that an increasingly larger part of benthic habitats was being subjected to periods of anoxia, thereby limiting the space available to indigenous species.

There nonetheless remains a number of examples that tend to show that introductions can have a positive effect, at least on fisheries, in newly-created environments such as reservoirs where riverine species are not well-suited to colonizing pelagic systems (Fernando, 1991). This may also be the case in a number of regions where the fish fauna is poor for historical or biogeographical reasons.

To avoid making irreparable errors while remaining active, better communication is needed between scientists and managers. However, Balon & Bruton (1986) have clearly indicated the difficulties involved. Are managers ready to accept recommendations that run counter to their plans? Do scientists have a good enough understanding of issues to provide clear and unambiguous advice? In reality, scientists have a limited capacity to predict the impact of introductions, and a certain reluctance to tackle these questions or take responsibility. Targeted research would be needed to grasp the consequences of introductions, by drawing on field experience and using all available information. But managers and politicians must also be aware that the lack of regulations, or the absence of controls at the very least with regard the translocation of fishes, leave the door open for the occurrence of ecological changes comparable to what has been observed in Madagascar or some watercourses in South Africa.

The experience from centuries of introductions and translocations of fishes around the world reveal, in fact, a positive overall outcome, if the analysis is made from both the ecological and the socio-economic perspectives.

Today, the issue of introductions is seen in a new light: the growing preoccupation with the protection of biodiversity, which would tend to favour the development of aquaculture for indigenous species. On the other hand, scientific investigations, increasingly focused on the genome, tend to concentrate on a few model species whose farming is most developed (*Oreochromis niloticus* for example). A happy medium needs to be found in coming years between these two trends which, when not antagonistic, are at least difficult to reconcile in a given environment, by reserving introductions for situations where they are clearly justified (lack of native species of fish farming interest, vacant tropical niche, etc.). Scientific editors

Didier Paugy Christian Lévêque Olga Otero

The Inland Water Fishes of Africa

Diversity, Ecology and Human Use



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