of problem organisms is reflected in the effort of community groups working on private and public lands to remove pests and weeds and to restore and replant native species. However, this more aggressive stand toward invasive species, especially mammals, can lead to polarized attitudes within local communities. For example, the control of possums and associated by-kill of deer spawned a coordinated campaign against compound 1080 and the agencies that use it; this has even included threats to sabotage conservation sites through the deliberate release of pests. Furthermore, within Auckland, attitudes to the spread of Btk against introduced moths differed between suburbs, with orchestrated campaigns of resistance to its use in western Auckland and claims of serious health effects and allergic reactions not encountered when the same product was used in eastern suburbs. The government has been willing to react massively with campaigns and funds against potential economic threats to agriculture, but less so with the same threats to biodiversity. For example, in 2006, the Animal Health Board had sufficient funds to treat 5.3 million ha against possums to contain BTb and protect beef and deer herds. However, the Department of Conservation could commit sufficient funds to treat only 302,000 ha against the effects of possums (and other vertebrate pests) on biodiversity. Once there is sufficient control of BTb, large-scale control of possums will cease, with subsequent increases in possum numbers. Unless other methods of large-scale control of possums are found, any gains to biodiversity as a spinoff of BTb control will then be lost.

Nonetheless, island eradications continue on an increasing scale, with proposals to rid Auckland Island (51,000 ha) of all pigs and the Rangitoto-Motutapu Islands (3,800 ha) of seven species of introduced mammals including mice. The technology developed in New Zealand to enable these eradications is now exported globally. Much can also be learned about the effects and effectiveness of fenced sites and intensive pest control on the mainland. Well-researched accounts of these enterprises are also needed if they are to maintain public support. However, this understanding will also require patience because the outcomes of the island eradications and mainland pest control may take decades to be fully understood.

### SEE ALSO THE FOLLOWING ARTICLES

Acclimatization Societies / Databases / Eradication / Game Animals / Invasibility, of Communities and Ecosystems / Predators / Restoration

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# NILE PERCH

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The Nile perch (*Lates niloticus*) is a large (over 2 m in length—and over 200 kg in weight) piscivorous fish native to East, Central, and West Africa, including the Congo, Niger, and Nile river systems. In the 1950s and 1960s, this species was introduced into multiple lakes and dams in the Lake Victoria region—where it did not occur naturally. Over the subsequent 40 years, the Nile perch has become one of the most famous invasive species in history, inspiring hundreds of technical publications, a popular book (*Darwin's Dreampond*), and an Oscar-nominated documentary film (*Darwin's Nightmare*). The fish did two things to deserve such celebrity. First, it played a major role in the extinction of 200 or more of the approximately 500-species radiation of endemic cichlid fishes (*Haplochromis* spp.) in the Lake Victoria region. Second, it transformed a local artisanal fishery into a half-billion-dollar global industry, transfiguring millions of human lives in the process.



From Daniel Simberloff and Marcel Rejmánek, editors, *Encyclopedia of Biological Invasions*, Berkeley and Los Angeles: University of California Press, 2011.

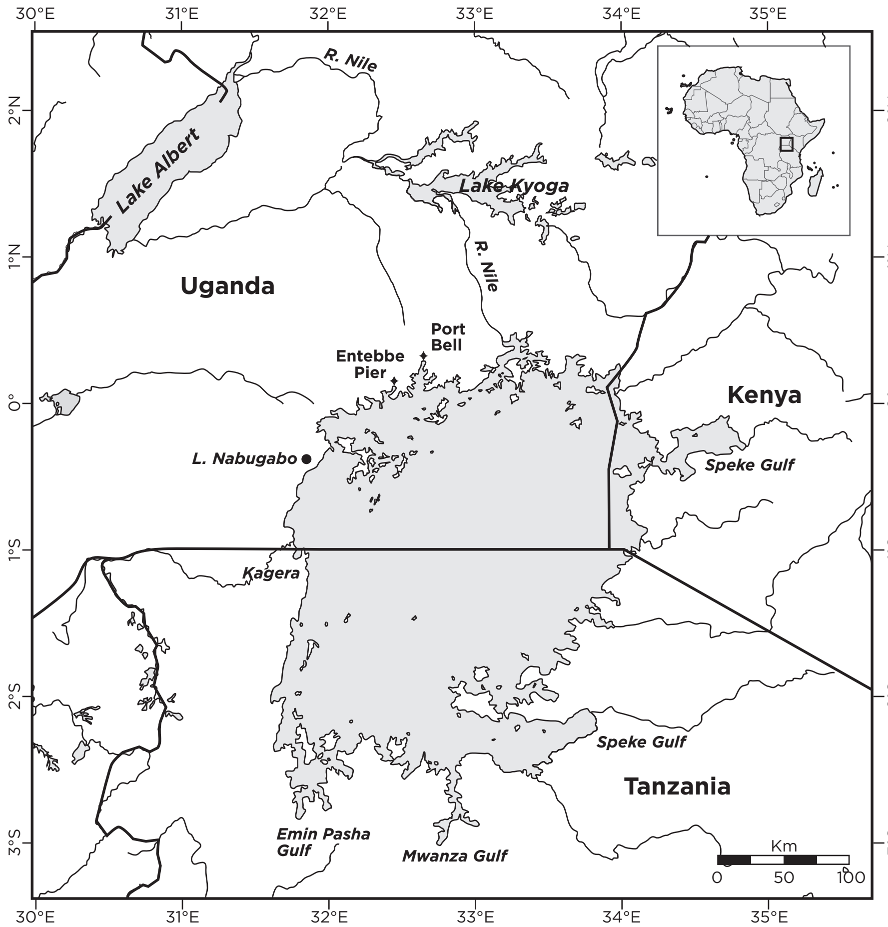


FIGURE 1 The Lake Victoria region. Stars mark the probable original sites of Nile perch introduction in the mid-1950s at Entebbe Pier and Port Bell; labels mark the locations of catch statistics presented in Fig. 3.

## ORIGINS

The transfer of Nile perch into Lake Victoria was discussed for decades within the British colonial administration of East Africa. Researchers opposed the proposition on precautionary grounds, while some management officials—most vocally members of the Uganda Game and Fisheries Department—supported it as a means of enhancing production and creating a sport fishing industry. No formal decision was ever reached, as Nile perch started appearing in Lake Victoria in 1960. Written records and interviews with former colonial officials suggest that Nile perch from Lake Albert were introduced deliberately (but secretly) at Port Bell and Entebbe Pier in 1954 (Figs. 1, 2). Throughout the early 1960s, officials performed additional sanctioned introductions into Lake Victoria, as well as into Lakes Kyoga, Nabugabo, and others.

## A NEW ECOLOGY

At first, little happened. In the mid-1970s, several ecologists deemed the introduction a success: the catch of native fishes appeared stable, while Nile perch were supplementing yields and drawing tourism revenue from anglers.

Ten years later, a commentary in *Nature* magazine declared that Lake Victoria's fisheries had been "not merely damaged but destroyed" by Nile perch. For reasons that remain incompletely understood, Nile perch densities had increased roughly 100-fold between the mid-1970s and mid-1980s, with a corresponding crash in the density and diversity of haplochromine cichlids (Fig. 3). One hypothesis proposed to explain this "Nile perch boom" is that intensifying human exploitation of haplochromine stocks released juvenile Nile perch from predation by and competition with cichlids; the recruitment of these juveniles to sizes at which they could consume cichlids


FIGURE 2 Freshly caught Nile perch (A) and the native minnow *R. argentea* (B). (Photographs courtesy of the author.)

further depleted cichlid populations and enhanced Nile perch recruitment in a positive-feedback loop. Migratory subadult Nile perch then colonized new parts of the lake, where the process repeated. This hypothesis is consistent with both the asynchronous upsurge of Nile perch in different parts of the lake and the astonishing rapidity of the faunal shift.

Nile perch was not the only factor contributing to haplochromine extinctions. A century of human population growth and agricultural expansion in the basin increased nutrient inputs to the lake, causing a doubling of primary production, a nearly order-of-magnitude increase in algal biomass, and the development of anoxic conditions in deeper waters. The corresponding decrease in water clarity reduced the ability of cichlids to mate assortatively based on color morph, slackening reproductive isolation and likely leading to widespread hybridization.

It is currently impossible to determine the relative importance of top-down (Nile perch predation) and bottom-up (eutrophication) forces—and their interactions—in driving the cichlid extinctions in Lake Victoria. Haplochromine populations also plummeted in invaded lakes, such as Uganda's Nabugabo, where eutrophication was not so dramatic, confirming the importance of Nile perch predation. In any case, these two forces were linked: the Nile perch boom spurred migration toward the lakeshore, prompted expansion and development of lakeshore villages and cities, and hastened landscape conversion and tree clearing (for wood to smoke fish, among other things), all of which accelerated nutrient loading of the lake.

The winners of the Nile perch boom included Nile tilapia (*Oreochromis niloticus*, itself introduced), the native minnow *Rastrineobola argentea* (Fig. 1), and the freshwater shrimp *Caridina nilotica*, all of which expanded dramatically in the absence of competition and predation from haplochromines. These species also provided a prey base for Nile perch after haplochromines became scarce. By 2000, Nile perch, Nile tilapia, and *R. argentea* constituted more than 99 percent of the fishery. One scientist compared this shift to clear-cutting a rainforest and replacing it with a monoculture of fast-growing plantation trees. This contraction of the fish community essentially created a brand new ecology, one with lower functional diversity, shorter food chains, less oxygen, and greater numbers of the true apex predator in the system, *Homo sapiens*.

## A NEW ECONOMY

The changes for the roughly 30 million people living in the lake basin were no less dramatic. As the estimated annual catch from Lake Victoria mushroomed from about 30,000 tons in the late 1970s to about 500,000 tons at the turn of the century, export earnings increased from approximately $1 million to around $260 million—90 percent of it from Nile perch. The estimated number of fishermen and fishing vessels operating on Lake Victoria also rose sharply; available statistics suggest that both have increased more than 300 percent from the early 1980s and continue to rise. With such tremendous profit potential came development aid, private investment, and class stratification. Fish-processing factories appeared around the lake, and the number of roads and refrigeration facilities at landing beaches increased. A new class of middlemen arose, who purchased fish at beaches and delivered them to factories for processing. Wealthier fishermen invested in multiple boats and nets, employing crews who did the actual fishing. Others borrowed money to purchase new boats and gears, creating enduring debts to entrepreneurs and processing facilities.

One can draw different conclusions about the local responses to Nile perch depending on where in the literature one looks. Many have argued that the Nile perch has been a disaster for small-scale fishermen, who dislike the fish. Others have highlighted positive effects of economic growth and favorable reactions by fishermen. In reality, local perceptions of the Nile perch and its effects on life are nuanced, variable, and temporally dynamic. Many early reactions were negative, because the fish was too big to be fished or preserved in traditional ways. But as the Nile perch boom created a new, globally integrated, cash-based economy, people adapted. Walking into a lakeside fishing community today and asking people how they feel about Nile perch is roughly analogous to walking into a General Motors plant and asking workers and job applicants how they feel about cars. Many respondents will tell you about their own financial troubles and the vagaries of the industry as a whole, and about the difficulties and indignities of life on the lower rungs of a multinational, multimillion dollar industry. They may or may not personally use the product that they produce, but their livelihoods depend on the global demand for it, and most are too young to remember the horse-and-buggy days. Many fishermen desire the restoration of a more diverse fish community, but few would opt to return to the quieter economy of the pre–Nile perch era. Indeed, many are attracted to the increasingly urban culture that has developed at the more successful landings, where a profusion of microbusinesses offer food, drink, clothing, entertainment, and sex to fishermen with cash in hand.

Ironically, given the increases in fish yields and value, childhood malnutrition rates remain comparable to national averages in Kenya, Uganda, and Tanzania. Household gender dynamics may explain this apparent paradox. Men control the fishing, and hence the cash, and they tend to spend money profligately outside the household, often on alcohol and affairs; women, who are active in onshore trading, consistently identified children as their first- or second-greatest expense. To bring income back into the household, many women market alcohol and sex to fishermen. Transactional sex and migrancy have both facilitated the spread of HIV/AIDS, which has had major (albeit poorly characterized) impacts on the demographic and social structures of the region.

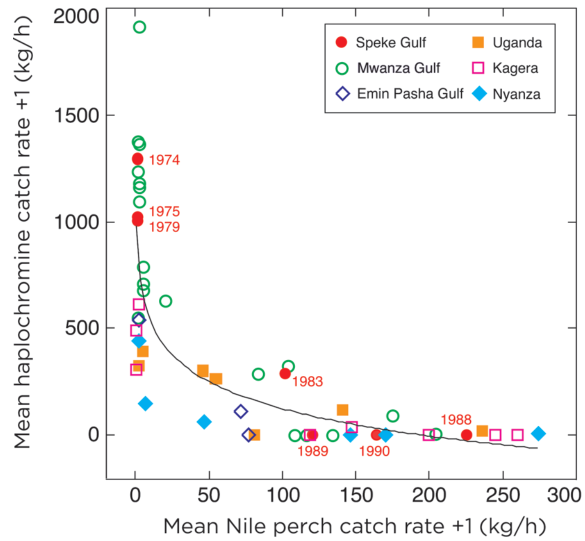


**FIGURE 3** The Nile perch boom. Catch rates of haplochromine cichlids decreased precipitously as catch rates of Nile perch increased at six sites across Lake Victoria. The temporal dynamics (exemplified by the years of data points from Speke Gulf, shown) suggest that intensifying local exploitation of haplochromines may have facilitated the Nile perch boom (1980–1990), reinforcing haplochromine declines, followed by intensive exploitation and declines of Nile perch. Together, location and Nile perch catch rate explain 77 percent of the variance in haplochromine catch rate. (Data from Goudswaard, et al., 2007.)

## RECENT DEVELOPMENTS AND FUTURE OF THE FISHERY

In the early 1990s, Nile perch catches peaked and began to decline, as did the average size of individuals and the catch per unit effort. Because fishing effort continues to increase, the total annual catch hovers around 500,000 tons, but biologists question the sustainability of the industry. In 2004, Ugandan fish-processing facilities operated at less than 50 percent of capacity.

Nile perch declines enabled a partial recovery of native fishes, including some *Haplochromis* species feared extinct. By 2005, densities of zooplanktivorous haplochromines in Mwanza Gulf actually exceeded pre–Nile perch levels, but diversity had declined from 12 species to 8. Five (of an original 13) detritivorous species appeared regularly in 2005, but at a tenth of their previous density. Piscivorous and insectivorous species were hardest hit: only one of an original 30 species was found in Mwanza Gulf from 2001–2005. Physical and physiological refugia—habitats too structurally complex or low in oxygen to support Nile perch—enabled some native species to withstand the onslaught and to repatriate subsequently.

And the haplochromines, models of explosive radiation, continue to evolve rapidly: many remaining species now display adaptations (such as increased gill surface area for enhanced oxygen uptake) that facilitate their coexistence with Nile perch.

The immediate future of the fisheries and remaining biodiversity of Lake Victoria hinges largely on fishing pressure. Recent models suggest that a 20 percent increase in fishing effort could drive Nile perch biomass down further—to extinction in some areas, stabilizing at low levels in others—enhancing the resurgence of the remnant native fauna. But eradicating the Nile perch would have complex and unpredictable consequences on biodiversity and human welfare, many of them undesirable. The seemingly optimal strategy is maintenance of fishing effort at levels high enough to allow the persistence of native fishes yet not high enough to extinguish Nile perch, while attempting to reverse eutrophication—a delicate balancing act. At present, management organizations and the lake's three governments are incapable of regulating fishing effort so precisely; Lake Victoria remains, for all practical purposes, an open-access resource.

### SEE ALSO THE FOLLOWING ARTICLES

Eutrophication, Aquatic / Fishes / Invasion Economics / Lakes

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# NITROGEN ENRICHMENT


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Nitrogen (N) is abundant on Earth in the form of atmospheric dinitrogen ($N_2$), but its availability to organisms is strongly limited by processes that convert $N_2$ to biologically available (reactive) forms. Historically, fixation by N-fixing microbes and (to a lesser extent) lightning provided all reactive nitrogen. Through the production of synthetic nitrogen fertilizers, land management changes, and fossil fuel combustion, humans now add approximately 150 Tg/year more reactive nitrogen (N) to the surface of the Earth, more than doubling the nitrogen available to biotic organisms over the last 200 years. Nitrogen enrichment is particularly acute in most of the world's biodiversity hotspots, and it is expected to double again in the next 50 to 100 years. Nitrogen enrichment favors nitrophilic organisms (often exotic invaders) over many native species, resulting in biodiversity changes and losses.

## NITROGEN ENRICHMENT IN TERRESTRIAL SYSTEMS

### Nitrogen Enrichment Effects on Plant Communities

Most terrestrial ecosystems are N-limited, and 70 percent of global N enrichment occurs on land. The majority of this enrichment is a result of the production of synthetic nitrogen fertilizers, land management changes, and fossil fuel combustion. Fertilization of N-limited environments typically results in increased productivity, reduction in plant density and diversity, and increases in the size and abundance of nitrophilic species, particularly grasses. In addition to anthropogenic N enrichment, increases in abundance or extent of plants with N-fixing symbionts, high N litter, or susceptibility to periodic mass insect herbivory can also substantially enrich localized areas, advantaging nitrophilic invaders. These phenomena have increased the abundance of invasive grasses in coastal California grasslands after N enrichment from leguminous shrubs and have led to the dominance of grasses across many northern European heathlands.

Communities most at risk from N enrichment include those in historically nutrient-poor environments, those