

Plenary lecture

Biodiversity conservation in African inland waters: Lessons of the Lake Victoria region

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The biodiversity crisis in inland waters

Fresh waters are among the most seriously threatened ecosystems on the planet, having suffered intense human impacts over the past century (SALA et al. 2000, COWX & COLLARES-PEREIRA 2002, DUDGEON et al. 2005). In their direct comparison of rates of species loss in freshwater vs. terrestrial ecosystems, RICCIARDI & RASMUSSEN (1999) projected a future extinction rate of 4% per decade for North American freshwater faunas. This is 5 times greater than that for terrestrial faunas and matches estimates for tropical rainforest communities. Although rates of species loss from tropical freshwaters are less known (DUDGEON et al. 2005), the limited data on North America is a serious alarm call for tropical faunas. These distressing trends reflect salient characteristics of both freshwater ecosystems and humans. People have settled disproportionately near waterways for millennia, and their impacts on inland waters have followed development and population growth throughout history. Fresh water is a resource that may be extracted, diverted, contained, eutrophied, or contaminated by humans; the effects are intensified by the landscape position of many inland waters as “receivers” of effluents (SALA et al. 2000). The result of these multiple stressors on inland waters has been a massive reshaping of aquatic communities, with the pace of change quickening in the tropics.

With respect to vertebrate faunas, there is little doubt that freshwater fishes represent the most threatened set of vertebrates in the world due to both extensive and intensive human impacts, but also because of the disproportionate richness of inland waters (DUDGEON et al. 2005). Over 10 000 fish species live in freshwater, representing approximately 41% of global fish diversity (LUNDBERG et al. 2000). Despite this extraordinary richness of species, surface freshwater habitats contain a relatively small proportion of the earth's water supply. The combination of species-rich faunas, high endemism, and the disproportionate richness of the inland waters as habitat has led to a global biodiversity crisis for fresh waters. Of the native

freshwater species of North America, 21.3% (217 species) are imperiled (WILLIAMS et al. 1989).

A significant challenge to conservation of freshwater fishes results from their patchy nature, imposed by catchment divides and saltwater barriers (LUNDBERG et al. 2000, STIASSNY 2002a, DUDGEON et al. 2005). This same heterogeneity that has fostered wild allopatric speciation – hundreds of species are known only from one drainage or lake system – severely limits possibilities for faunal rescue. Fish like to be in water, and most cannot easily move from one aquatic system to another without it; they therefore have to adapt to changes *in situ* or disappear. An additional challenge to freshwater conservation is our limited knowledge of fish diversity (STIASSNY 2002a, 2002b). This problem is particularly serious in tropical waters where less intensive exploration and accelerating environmental change in these species-dense systems rob us of potential future discoveries. Some of the most poignant cases are found in equatorial Africa where several fish species have suffered anonymous extinction, the most notable example being Lake Victoria, the largest tropical lake in the world.

Key words: African fish, East Africa, eutrophication, invasive species, physiological ecology

African fresh waters: Threats

Africa is a continent with many unique and remarkable inland waters. From Victoria Falls to the floodplain of the Niger delta, from the equatorial swamp forest of the Congo to wetlands of the Okavango, from the rift lakes (some of the largest in the world), to the small crater lakes of western Uganda and Ethiopia – the inland waters of Africa, particularly tropical Africa are incredibly diverse (LÉVÊQUE 1997). Matching this richness of systems is a spectacular diversity of aquatic life and strategies for

survival in some of the most extreme environments in the world, from the dense interior of papyrus swamps where low-oxygen stress is the norm of daily life, to the alkaline lakes of the Great Rift Valley and piping hot springs in Uganda and Kenya. In fact, even when water is not there, some fishes persist, like the infamous lungfishes *Protopterus* spp. and the less well-known (except to aquarium hobbyists) *Nothobranchius*, a killifish that survives the dry season as desiccation-resistant cysts, awaiting rehydration at a later time (GENADE et al. 2005).

The extraordinary diversity of terrestrial taxa in African rainforests and savannas is mirrored by the richness of its fish fauna. Africa has over 2,850 known species (a conservative estimate) of indigenous freshwater fishes within 40–50 families (LUNDBERG et al. 2000). However, Africa's evolutionary phenomena – its “living fossils” and species flocks – add a particular distinctiveness to the fauna. Africa has an unparalleled assemblage of more archaic fish families, mostly endemic (LÉVÊQUE 1997, LUNDBERG et al. 2000). Examples include the bichers (polypterids) and African lungfishes (some of the oldest fishes on earth), and a stunning array of osteoglossomorphs, including the African arowana and the extraordinary mormyrids or elephant-nose fishes, the weakly electric fishes of Africa. The larger species among these phylogenetic treasures are important food fishes and have been locally depleted by overexploitation in many regions (GOUDSWAARD et al. 2002a, KAUFMAN 2003). Outstanding species radiations are the hallmark of the Great Lakes of East Africa, but radiations also have taken place in some of the smallest (crater lakes) and shallowest (soda lakes) water bodies as well (KAUFMAN 2003). More than 15% of the world's freshwater fish species live in the Great Lakes of East Africa (THIEME et al. 2005). The Congo River basin is also host to an extremely diverse fish fauna, with the highest richness of any river on the African continent, and second only to the Amazon on a global scale (CHAPMAN 2001, CHAPMAN & CHAPMAN 2003).

For hundreds of millions of African people, the health of their inland waters is inextricably linked to their own well being. These systems provide drinking water, hydroelectric power, water for irrigation, foods with critically needed protein, and much more. However, increasing demands for services of inland waters is placing great strain on these environments. Africa is facing not only a continent-wide shortage of potable water, but overall water quality has declined markedly due to multiple perturbations, including progressive deforestation, exponentially increasing human populations, industrialization, and urbanization. And while Africa makes a relatively small contribution to global climate change, African lakes seem very sensitive to such change (LIVINGSTONE

2003). The current emphasis on sustainable management of natural resources contained in the Convention for Biological Diversity (CBD 1994) and of fisheries as formulated in the Food and Agricultural Organization of the United Nations (FAO) Code of Conduct for Responsible Fisheries, imposes a need to explore, understand, and predict the influence of human pressures on African inland waters, from the challenges of freshwater supply to wetland degradation to the introduction of non-indigenous species.

We review the major threats to African inland waters and discuss key lessons learned from the Lake Victoria region that highlight both the vulnerability and lability of fishes in the face of environmental change. We focus on mechanisms that have fostered persistence of native species, in particular the use of structural and physiological refugia to sidestep invader impacts. We explore cascading effects of Nile perch on the trophic structure of invaded systems. Finally, we consider the consequences of faunal collapse and recovery on resurging species.

Supply of fresh water

Among the challenges currently facing Africa, none is more trenchant than threats to the ability of the continent's supply of fresh water to sustain human life in the future. Several basins in Africa, including Lake Chad, the Nile, the Niger, and the Volta, are projected to support >10 million people by 2025 and will suffer water stress (WRI 1994, REVENGA & CASSAR 2002). In the more arid regions of southern Africa where population pressures are as high as the land is dry, provision for storage of more than an annual supply of water must be engineered to withstand droughts that can persist for years. In principal, West Africa currently has adequate water resources. However, many of the region's rivers have been impounded to form reservoirs ranging from small farm dams to large multi-million-dollar dams such as the Akosombo on the Volta. The vast shifts in hydrology and ecology brought about by water containment and diversion can massively influence natural systems and services (WELCOMME 2003). Water deficits in Africa are exacerbated by water quality issues including industrial and mine effluents, sewage, runoff of nutrients and pesticides, siltation, and salinization. Pollution of surface and groundwater is becoming a serious threat from countries with burgeoning human and livestock populations and the rapid development of a continent-wide industrial base, but also from deforestation, mining, and agriculture (REVENGA & CASSAR 2002, THIEME et al. 2005). An estimated 86% of Africa's total water withdrawals are directed toward agricul-

ture (FAO 2005a). Given that the population of Africa is projected to more than double between 2005 and 2050 (UNITED NATIONS POPULATION DIVISION 2006), and given that most of the next generation is predicted to continue to live subsistence lifestyles, Africa is expected to undergo tremendous agricultural expansion (THIEME et al. 2005), which will place brutal demands on water supply.

Deforestation

In sub-Saharan Africa, tropical forests are increasingly threatened by forest conversion and degradation, with recent estimates suggesting a conversion rate of 0.4–0.5% per year (LANLY et al. 1991, FAO 1993, MAYAUX et al. 2005). Rain forests once covered an estimated 3 620 000 km² of the African continent before anthropogenically-induced habitat alterations (MARTIN 1991); now Africa ranks second only to South America in net rate of forest loss (FAO 2005b). Deforestation has reduced rain forest in Central Africa to 55% of its original area, but it has been much more severe in West Africa (72% loss). An estimated 28% of the rain forests that once covered East Africa remain (MARTIN 1991), with the majority of land clearing associated with subsistence farming and fuelwood harvest.

Deforestation threatens aquatic faunas on several dimensions: indirectly through the effects of forest removal on water quality and flow regimes, and directly through loss of allochthonous input generated by the forest. There is critical need to understand the functional links between large-scale land use and aquatic ecosystem change, and the implications of protected areas on watershed integrity. A growing number of studies in Africa indicate significant effects of deforestation on a diverse suite of aquatic communities, including inshore habitats in Lake Tanganyika (COHEN et al. 1993); high-altitude rainforest rivers (KASANGAKI et al. 2006); crater lakes of western Uganda (EFITRE 2007); and small Malagasy streams (BENSTEAD et al. 2003). Interest within Africa in the use of aquatic invertebrates as indicators of water quality and ecosystem change (DALLAS 1997, THORNE et al. 2000, NDARUGA et al. 2004, KASANGAKI et al. 2006) is growing along with the recognition that these indicators are not easily translated from temperate to tropical systems and must be developed *in situ*.

Wetland degradation

Africa has some of the largest wetland systems in the world, including approximately 85 000 km² of permanent

swamp and 400 000 km² of seasonally inundated swamps (THOMPSON & HAMILTON 1983, DENNY 1985). The emergent sedge papyrus (*Cyperus papyrus*) dominates much of the permanent swamp on the African continent. Papyrus is the fastest growing sedge in the world, normally attaining heights of 3–4 m, and typically comprising >95% of the plant biomass of the swamp (THOMPSON 1976, THOMPSON et al. 1979, ELLERY et al. 1995). The dense canopy and root mats of papyrus limit both mixing of the water column and light (THOMPSON et al. 1979, JONES & MUTHURI 1985). In combination with high rates of organic decomposition, these conditions result in extremely low oxygen levels in the water beneath the swamp canopy and create a very unique habitat for aquatic organisms (CARTER 1955, BEADLE & LIND 1960, CHAPMAN & LIEM 1995, CHAPMAN et al. 1998), including a highly specialized fish fauna adapted for life in deoxygenated waters (ROBERTS 1975, CHAPMAN et al. 2002).

Many African wetlands are not permanent swamps but seasonal floodplains associated with major rivers, and they often host rich fish faunas that depend on these habitats for breeding, nurseries, feeding, and refuge (CHAPMAN et al. 2001, WELCOMME 2005). Fish populations in these wetlands tend to reach high density and undergo predictable seasonal migrations, factors that favour the development of fisheries (WELCOMME 2005). Wetlands also attract humans because of their rich soils, their water supply, and opportunities for grazing of domestic stock, which is particularly important in the dry season. Africans have lived with and within wetlands throughout history, and many human exploitation activities in wetlands can be sustainable; however, an expanding and accelerating trend is large-scale drainage and conversion to large tracts of agricultural land (CHAPMAN et al. 2001). Wetlands are also threatened by irrigation schemes, development of waterways to improve transport, industrial pollution, and mining extracts (CHAPMAN et al. 2001). Estimates of wetland loss range from 40% in Cameroon to 70% in Liberia (WRI 1994), a scale comparable to forest degradation on the continent.

Over-exploitation of fisheries

In Africa, many fisheries have been exploited to levels that have produced substantial degradation (WELCOMME 2005), dramatically restricting one of the most important protein sources for Africa's expanding human population. Often this degradation involves a "fishing-down" process, the successive loss of the largest individuals and species in favor of smaller, faster, and shorter-lived fishes (REGIER & HENDERSON 1973, WELCOMME 1995). These

shifts have been carefully documented for the Oueme River fishery in West Africa (Benin; WELCOMME 1999) and the Central Delta of the Niger in Mali (LAE 1994). Reductions in size are accompanied by changes to many of the fundamental parameters of the fish community. The number of species in the fishery tends to increase; large species are eliminated from the fishery, and survival of many species occurs through use of connected refugia (WELCOMME 2003, 2005). Clearly this situation is undesirable for conservation and probably unsustainable for fisheries, and reports on many African fisheries suggest they are or have been fished at levels that incur damage to the assemblage (THIEME et al. 2005, WELCOMME 2005). On a positive note, WELCOMME (2005) argues that African waters, particularly floodplain systems where ups and downs are part of life, may be quite resilient if the stress is removed; an excellent example is the reestablishment of normal fish catch in rivers of the Niger Basin after the Sahelian drought (WELCOMME & HALLS 2004).

Non-indigenous species

The transfer or introduction of non-native fish species has been widespread in Africa and continues (FAO/CIFA 1985). The primary purpose of such transfers has been to maintain or increase fish yield, although some introductions have been undertaken to expand sport fisheries or for biological control (OGUTU-OHWAYO & HECKY 1991, PRINGLE 2005). About 50 fish species have been introduced into or translocated within the inland waters of Africa, 23 of which are from outside Africa (WELCOMME 1988). In the Congo basin, for example, WELCOMME (1981) reported 7 international transfers of fishes including: *Astatoreochromis alluaudi* (cichlid, for the control of snail vectors of bilharzia); *Clarias gariepinis* (catfish, for experimental fish culture and predation on stunted tilapia); *Heterotis niloticus* (African arowana (an osteoglossomorph), escaped from aquaculture installations); *Lepomis gibbosus* (North American sunfish, for forage for *M. salmoides*); *Micropterus salmoides* (North American bass, control of stunted tilapia); *Sarotherodon macrochir* (South African tilapia, aquaculture); and *Tilapia rendalli*. Perhaps the most widespread continental travelers have been the tilapias, introduced into many African waters to stock natural lakes where tilapias did not occur to fill apparently vacant trophic niches, to compensate for depleting commercial fisheries of native tilapias, to develop new fisheries in man-made waterbodies, and for biological control of aquatic vegetation (LÉVÊQUE 1997, BALIRWA et al. 2003). Even though Africa has seen an increase in non-native fish production through such introductions

and aquaculture, local communities that had depended on the native fish did not necessarily benefit, but further transfers are inevitable given the accelerating interest and donor support for aquaculture activities in regions of Africa.

Dynamics of the Lake Victoria Region – biodiversity lost & (partly) found

Major threats to the aquatic systems of Africa, which are numerous and complex, are also (not surprisingly) inter-related. Rarely do threats occur singly, and most imperilled species are subjected to multiple interacting stressors (REVENGA et al. 2005). For example, high human population density leads to accelerating deforestation, conversion to agricultural land, high nutrient input, and eutrophication of water bodies. The increase in primary production may increase fish yield, at least for awhile. At the same time, high population density can spark increased fishing pressure and create a decline in stocks that can lead to an increase in alternative livelihoods such as charcoal production. Species introductions are also often used to compensate for depleting commercial fisheries, but they can have devastating effects on native fish communities (Fig. 1). These complex interactions are particularly well exemplified in the Lake Victoria basin of East Africa, a region that has experienced massive, fundamental changes in its ecology over the past century. The dynamic eco-history of the basin highlights both the vulnerability and lability of native and introduced species in the face of environmental change and supports a reconciliation of biodiversity maintenance and fisheries sustainability in the region. To explore the response of the fish fauna to multiple environmental stressors we (a) summarize the history of biodiversity loss in the Lake Victoria Region, and (b) examine characteristics of the fishes that persisted, those that prospered, and those that are recovering coincident with heavy fishing on Nile perch.

Biodiversity loss

Lake Victoria is the largest tropical lake in the world, with its waters shared by 3 countries: Tanzania, 51%; Kenya, 6%; Uganda, 43%. The lake harbors Africa's largest inland fishery, yielding 500 000 MT since the 1990s (BALIRWA 2007), but it is best known to scientists for its 500+ endemic species of haplochromine cichlids, representing one of the most rapid, extensive, and recent radiations of vertebrates known (GREENWOOD 1974, SEE-

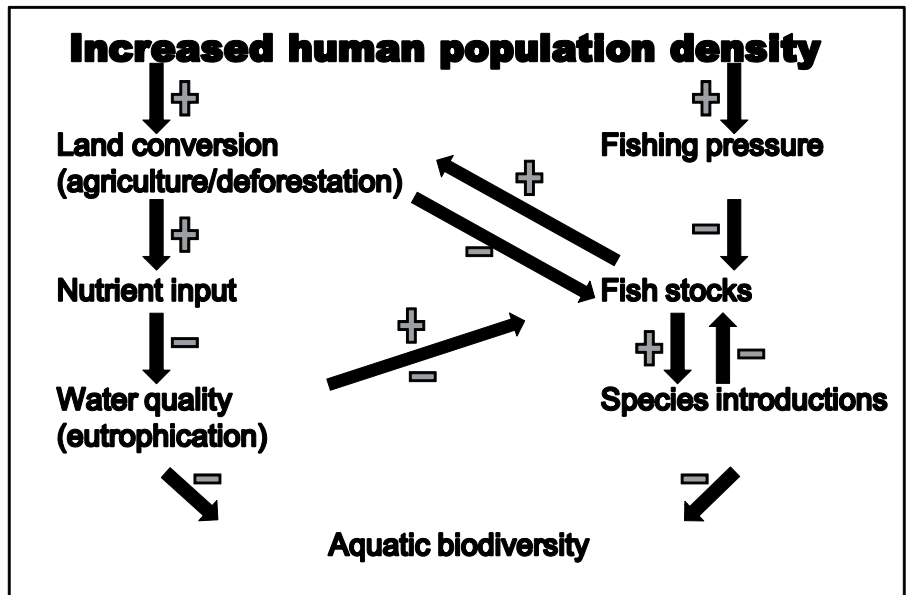


Fig. 1. Figurative representation of the interaction of multiple stressors on fisheries sustainability and biodiversity in inland waters.

HAUSEN 1996, KAUFMAN et al. 1997, SEEHAUSEN et al. 2003b, VERHEYEN et al. 2003). In addition, a diverse assemblage of non-cichlids inhabits the basin (CORBET 1961, GREENWOOD 1966, 1974, van OIJEN 1995).

Throughout the 20th Century, Lake Victoria underwent massive and fundamental changes in its ecology, and the fish stock of the lake was subjected to 3 major series of interacting events: overfishing, species introductions, and habitat degradation. Fishing intensified over the century with the introduction of new technologies, and by the 1950s and 1960s, there was alarming evidence that

many important food fishes were overexploited (OGUTU-OHWAYO 1990, BALIRWA et al. 2003). Changes in the Lake Victoria fish stocks conform in a general way to the “fishing-down” model as indicated in the catch per unit effort of some economically important fishes in Tanzania between 1958 and 1970 (Fig. 2). By the late 1950s, the catch of key migratory species in the fishery had fallen (CADWALLADR 1965), and the fishery focused on tilapia and bagrid catfish. By the late 1960s, these and other species, including the lungfish, had fallen dramatically. The fishery was characterized by a drift to the smallest spe-

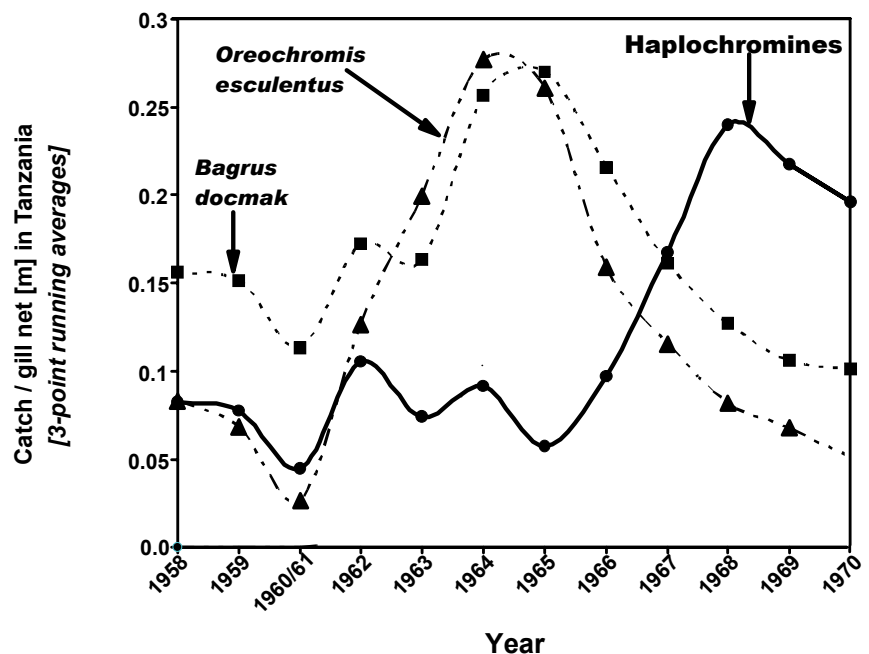


Fig. 2. Fish catch per gill net (metric tonnes) in the Tanzanian waters of Lake Victoria (1958–1970). Data are expressed as 3-point running averages and were derived from KUDHONGANIA & CORDONE (1974). Figure adapted from (BALIRWA et al. 2003).

cies, the haplochromine cichlids (BALIRWA et al. 2003), and even here intensive trawl fishing rapidly eliminated local stocks (WITTE et al. 1992b).

New fish species were introduced to compensate for depleted commercial fisheries. The large Nile perch (*Lates niloticus*) was first introduced into lakes of the Lake Victoria basin in the mid-1950s to convert low value haplochromines into higher value and more easily captured fish and to foster a sport-fishing industry (JACKSON 2000, PRINGLE 2005). Nile perch, which reaches >2 m in length and >200 kg in weight (OGUTU-OHWAYO 2004), feeds on invertebrates at a small size and then switches to piscivorous feeding (OGUTU-OHWAYO 1994, SCHOFIELD & CHAPMAN 1999). Nile perch numbers were low in the lake until the 1980s when trawl surveys (GOUDESWAARD et al. 2006) and catch landings in the 3 riparian countries (BALIRWA et al. 2003, MATSUISHI et al. 2006) showed a dramatic population increase. The upsurge of Nile perch did not exhibit lake-wide synchrony, but was first observed in the Nyanza Gulf of Kenya in 1979, in Ugandan waters 2–3 years later, and in the Mwanza Gulf of Tanzania 4–5 years later (GOUDESWAARD et al. 2006). Mechanisms underlying the Nile perch boom are not fully understood; however, GOUDESWAARD et al. (2006) hypothesize that the decline of haplochromines associated with exploitation decreased predatory and competitive effects on juvenile Nile perch, facilitating juvenile survival. The upsurge of Nile perch created a new industry and a huge export market for Uganda, Kenya, and Tanzania, causing a rapid expansion of the fish-freezing industry to more than 30 factories in the 1990s (BALIRWA 2007). In 2003, fish exports were valued at \$243 million US (LVFO 2005, BALIRWA 2007), but a catastrophic change occurred in this species-rich system. Although many fish stocks in Lake Victoria had declined before the upsurge of the Nile perch, including the haplochromines in some areas, the increase in the Nile perch coincided with the further decline or disappearance of many native species. For example, the final disappearance of haplochromine cichlids in Mwanza Gulf was reported after the upsurge of Nile perch, (GOUDESWAARD et al. 2006), most notably the disappearance of >40% of the endemic haplochromine cichlids (KAUFMAN 1992, WITTE et al. 1992a, 1992b, KAUFMAN & OCHUMBA 1993, SEEHAUSEN & BOUTON 1997). Certainly other changes in the Lake Victoria system, including increasing eutrophication (see below), contributed to the faunal collapse, but the Nile perch seems to have been an important player (BALIRWA et al. 2003, GOUDESWAARD et al. 2006). The situation in Lake Victoria has been followed closely by the international community because of its economic importance and catastrophic biodiversity loss. But similar changes have occurred with the introduction

of Nile perch into other lakes in the basin, including lakes Kyoga and Nabugabo, providing replication of this ecologically devastating, but economically lucrative situation.

Coincident with severe anthropogenic changes in the watershed (e.g., increased population density, industrialization, deforestation), Lake Victoria changed from a mesotrophic system in the 1930s to a eutrophic system (HECKY 1993, HECKY et al. 1994). Primary productivity doubled, and algal biomass increased 8–10-fold (MUGIDDE 1993), accompanied by a shift in algal species composition from large chain-forming diatoms to blue-green algae (HECKY 1993). High-resolution palaeolimnological data show that the increase in phytoplankton production evident from the 1930s parallels human-population growth and associated agricultural expansion in the basin (MUGIDDE 1993, VERSCHUREN et al. 2002). The switch in phytoplankton communities may have facilitated a decline in the native tilapiine *Oreochromis esculentus*, an apparent specialist on the large chain diatom *Aulacoseira* (formerly *Melosira*) spp. both in plankton and detrital deposits. The switch perhaps also triggered an upsurge in the introduced *Oreochromis niloticus*, which can eat almost anything from minute cyanobacteria up through large animal prey (BATJAKAS et al. 1997). The change in trophic status of the lake was also accompanied by a decrease in water transparency. Loss of water clarity caused loss of genetic and ecological differentiation among haplochromine species, and is likely to be partially responsible for loss of species diversity among littoral cichlids (SEEHAUSEN et al. 1997a).

Another dramatic change to the Lake Victoria system has been the development of hypolimnetic anoxia induced by eutrophication in the lake basin. The deeper part of the lake became stratified throughout much of the year (HECKY 1993, HECKY et al. 1994), and the duration and severity of hypoxia has also increased in shallower areas (WANINK et al. 2001). The eutrophication-induced loss of hypolimnetic oxygen seems to have started in the early 1960s after at least 140 years of adequate year-round dissolved oxygen in the bottom waters (VERSCHUREN et al. 2002). TALLING (1966) reported anoxia only in the deepest parts of the lake in 1960–1961, while HECKY (1993) reported widespread, long-lasting (Oct–Mar) anoxia in deeper waters in 1990–1991. Fish kills associated with upwellings of anoxic water, in addition to the possible effects of phytotoxins, provide evidence of high risk for some species (OCHUMBA 1990, KAUFMAN & OCHUMBA 1993).

Ecological changes in the lake, including declining oxygen availability, also reflect invasion of the nonindigenous water hyacinth, *Eichhornia crassipes*. Water hya-

cinth (native to South America) appeared in Lake Kyoga in Uganda in 1988 and in Lake Victoria in 1989 (TWONGO et al. 1995) and spread rapidly. In the Ugandan waters, stationary fringes were estimated to cover 2 200 ha along 80% of the shoreline by 1995 (NARO 2002). The invasion had significant socio-economic and environmental impacts, including disruption of transport, fishing activities, reduction of water supply, negative impacts on water quality for humans and livestock, and spread of water-borne diseases (TWONGO 1996, NARO 2002, NJIRU et al. 2002). Surprisingly, water hyacinth rapidly disappeared almost completely over most of its previous range in the late 1990s. A number of interactive factors apparently account for its remission, including mechanical and manual removal and the introduction of weevils *Neochetina eichhorniae* and *N. bruchi* for biological control. However, recently WILLIAMS et al. (2007) argued that while weevils almost certainly played a part, the synchronous lake-wide reduction of water hyacinth during the second quarter of 1998 was the result of the 1997/1998 El Niño that caused stable shoreline water hyacinth stands to become dislodged and then destroyed by wave action. Despite the rapid remission of the invasive plant, scientists remain concerned. A recent outbreak of water hyacinth observed in Mwanza Gulf (Mary Kishe-Machumu, pers. comm. Feb 2007) confirms the expectation of periodic outbreaks of water hyacinth that will demand continuous vigilance and control efforts (NARO 2002).

These various events influenced the structure of the fish stock in Lake Victoria and resulted in the fishery being converted from a multi-species system exploiting native fishes to one in which 3 species comprise almost the whole of the catch, 2 of which are introduced. Entire functional groups disappeared in the 1980s, as did the wealth of ecological services that they provided. The Lake Kyoga system that lies downstream of Lake Victoria and forms from a dendritic expansion of the Nile has been extremely useful in understanding effects of Nile perch on functional and specific fish diversity. The Kyoga satellite system is comprised of species-rich lakes where Nile perch are absent or rare and low diversity lakes where Nile perch are abundant (MBABAZI et al. 2004, SCHWARTZ et al. 2006). Food web studies in 6 of these lakes revealed shorter food chains in perch lakes, suggesting a reduction in the number of pathways from primary production to apex consumers in the presence of the predator and modified food web (SCHWARTZ et al. 2006).

It has been recently argued that eutrophication poses the most serious threat to the Lake Victoria fish fauna; however, the relative importance of different environmental stressors is still not fully understood. The lake was initially heavily influenced by overfishing, and this

soon led to fish introductions that further complicated the web of species interactions and system dynamics. Anthropogenic changes in the watershed (increased population density, industrialization, change in fish composition, deforestation) and the introduction of water hyacinth contributed to the formation of an enduring anoxic hypolimnion and changes in water quality. Greatly increased primary productivity, one outcome of the interplay of stressors, can initially foster a rise in fish productivity. However, coincident decreases in water transparency threaten any such gains while also threatening a diverse, haplochromine-rich food base that can enhance Nile perch production (Fig. 1). Note that the faunal composition of lakes Nabugabo and Kyoga changed dramatically even though they experienced less intense watershed transformation than Lake Victoria.

The residual fauna and physiological exclusion

Despite a radically altered food web structure, some indigenous species have both persisted with Nile perch and been resilient to increasing eutrophication and other human-induced stressors. Understanding conditions that allow some species to endure these multiple stressors while others succumb is critical to conservation of freshwater faunas and the management of human impacts. Over the years, interest in conservation of the residual fauna has sparked several studies directed toward identification of faunal refugia; habitats where native fishes are protected from Nile perch predation and that could form the basis of biodiversity restoration. Currently, we recognize 4 major types of biodiversity banks: satellite lakes, rivers, rocky habitats, and wetlands.

A small portion of the fauna considered extirpated from lakes Kyoga, Victoria, and Nabugabo can still be found in satellite water bodies around the main lakes (OGUTU-OHWAYO 1993, KAUFMAN et al. 1997, MWANJA 2004). For example, the Lake Kyoga complex (the main lake and satellite lakes) harbours a rich assemblage of an estimated 40 haplochromine cichlids, with the satellite lakes contributing 37 species comprising 11 trophic groups and the main lake harbouring 15 species comprising only 2 trophic groups (MBABAZI et al. 2004). In many cases, dense hypoxic swamps separate these satellite lakes from the main Lake Kyoga and seem to act as a biological filter preventing Nile perch colonization, which are unable to survive in hypoxic waters (SCHOFIELD & CHAPMAN 2000), and probably also nutrient influx (BALIRWA et al. 2003, SCHWARTZ et al. 2006).

Rivers are also an important refugium for indigenous species in the Lake Victoria region. The Victoria Nile

harbors an interesting and partially endemic haplochromine assemblage. Upstream, before and after the Owens Falls Dam are species typical of Lake Victoria. Where the Victoria Nile joins Lake Kyoga are taxa such as *Pyxichromis orthostoma* and undescribed taxa characteristic of the Kyoga satellite lake refugia (L. Kaufman, pers. observ.). The Victoria Nile is also home to remnants of the Nile's once formidable population of migratory fishes, including *Barbus altianalis* and *Labeo victorianus*, as well as several regionally endemic mormyrids.

Rocky shores and offshore rocky islands are major refugia within Lake Victoria, harboring a large number of rock-dwelling specialists (SEEHAUSEN 1996, SEEHAUSEN & BOUTON 1997, SEEHAUSEN et al. 1999, WITTE et al. 2007). They also serve as refugia for a number of species that were not specialized rock-dwellers in the pre-Nile perch era, but either shifted to these habitats or had a broader pre-Nile perch distribution that included these habitats (WITTE et al. 1992a, SEEHAUSEN 1996, 1997). In their long-term survey of haplochromine communities in the littoral, sub-littoral and rocky shores of Mwanza Gulf, Tanzania, WITTE et al. (2007) found that haplochromines from rocky shores were the least affected of these habitat-associated assemblages.

Wetlands in the Lake Victoria basin serve as both structural and low-oxygen refugia for fishes that can tolerate wetland conditions and function as barriers to dispersal of Nile perch (CHAPMAN et al. 1996a, 1996b, BALIRWA 1998, SCHOFIELD & CHAPMAN 1999, CHAPMAN et al. 2002, MNAYA et al. 2006). Unlike Nile perch, some haplochromine cichlids and some native noncichlids are relatively tolerant of hypoxia (CHAPMAN et al. 1995, ROSENBERGER & CHAPMAN 2000, SCHOFIELD & CHAPMAN 2000, CHAPMAN et al. 2002, RUTJES 2006), thus permitting some fishes to persist in wetlands under reduced predator pressure from both Nile perch and other large piscivores (CHAPMAN et al. 2002). The ecotone of the wetland/open water is a particularly important refugium because interaction with the main lake waters elevates dissolved oxygen. Nile perch are rare in these ecotonal wetlands, and species richness is higher than in the interior swamp (CHAPMAN et al. 1996a, 1996b, BALIRWA 1998, SCHOFIELD & CHAPMAN 1999, CHAPMAN et al. 2002). However, even areas deep within the fringing swamp are important in the maintenance of a subset of the basin fauna (CHAPMAN et al. 1996b, CHAPMAN et al. 2002).

The physiological exclusion of Nile perch from the dense interior of hypoxic wetlands has been critical in minimizing predator-prey overlap and in limiting Nile perch invasion of the Kyoga satellites. This highlights the importance of environmental stressors in modulating predator-prey interactions. A growing body of empirical

support (beyond the Victoria basin) demonstrates size-sensitive tolerance to hypoxia in fishes: in particular, field studies supporting physiological exclusion of large piscivore predators from hypoxic habitats. ROBB & ABRAHAMS (2003) evaluated hypoxic tolerance of small yellow perch (*Perca flavescens*) and fathead minnows (*Pimephales promelas*), both potential prey of large yellow perch. They found that both within and between the 2 species, smaller individuals were the most tolerant of hypoxic environments, and suggest that low-oxygen habitats have the potential to act as a refuge for these smaller fish. MCNEIL & CLOSS (2007) found a generally high level of tolerance to periodic hypoxia in the fishes of the Owens River floodplain in south-east Australia with the exception of 3 species, one of which was the predacious introduced redfin perch (*Perca fluviatilis*), again supporting the role of hypoxic habitats as refuge for tolerant prey. Small Amazonian oscars seek out hypoxic habitats as refuge; evidence suggests that they are not more tolerant than larger conspecifics, but rather accept a greater physiological compromise to access hypoxic shelter (SLOMAN et al. 2006). All these examples point toward the importance of hypoxic stress as a predator-prey modulator.

Two success stories: fishes that flourished with Nile perch

Many fish species vanished coincident with the upsurge of Nile perch; others persisted through use of structural, physiological, and behavioural refugia; and others have prospered. In addition to the Nile perch, 4 nonindigenous tilapiines (*Tilapia zillii*, *O. niloticus*, *O. leucostictus*, and *Tilapia rendalli*) were also introduced at various points around Lake Victoria from 1953 onward in response to reduced catch per unit effort (CPUE) of the 2 regionally endemic tilapiines (*Oreochromis esculentus* and *Oreochromis variabilis*) that had been the main target of the local fisheries. By 1960, these 4 exotic tilapiines had also been introduced in lakes Kyoga, Nabugabo, and later into other lakes within the region (BEAUCHAMP 1958, WELCOMME 1967, WELCOMME 1988). However, of all the native and introduced tilapiines in the Lake Victoria region, only *O. niloticus*, the Nile tilapia, has become abundant and commercially important in the presence of Nile perch (GOUDSWAARD et al. 2002b).

This successful establishment of *O. niloticus* has been attributed to several factors, including their dietary plasticity, their flexibility in life history traits, and their ability to withstand a broad range of environmental variation (LOWE-McCONNELL 1958, BALIRWA 1998, LÉVÊQUE 2002, GOUDSWAARD et al. 2002b). *Oreochromis niloticus* juve-

niles are very tolerant of hypoxic stress and penetrate deep swamp refugia with the lake basin (CHAPMAN et al. 1996a, 1996b, CHAPMAN et al. 2002). In Lake Nabugabo, juvenile Nile tilapia are the most abundant tilapiine in hypoxic wetlands, where Nile perch tend to be rare (BWANIKA et al. 2006, Chapman and colleagues, unpubl. data). When they reach about 8 cm they tend to move into more open water, where they exceed the gape size of at least smaller Nile perch. In the Mwanza Gulf of Lake Victoria, GOUDSWAARD et al. (2002b) reported the largest (>20 cm) Nile tilapia from the most offshore sites, whereas the smallest size classes were caught between the fringing vegetation where the density of piscivorous Nile perch was much lower. Nile tilapia also shows a high degree of dietary flexibility both within and among lakes. Studies on the diet of *O. niloticus* in both its indigenous and new habitats in East Africa date back to the early 1950s. Earlier studies described the diet of *O. niloticus* as predominantly herbivorous, comprised mainly of algae, epiphytic diatoms, and bottom debris (FISH 1955, LOWE-McCONNELL 1958, MORIARITY & MORIARITY 1973). Studies undertaken shortly after the establishment of *O. niloticus* in the Victoria region still recorded a predominantly herbivorous diet (WELCOMME 1967). Indeed, *O. niloticus* is remarkable in its ability to efficiently collect and assimilate even the smallest (and sometimes toxic) cyanobacterial cells using a specialized feeding mechanism that Lake Victoria's native tilapiines lack (SANDERSON et al. 1996, BATJAKAS et al. 1997). Recent studies, however, indicate a shift in the dietary composition of *O. niloticus* to include a broad spectrum of items with high proportions of macroinvertebrates and detritus (GOPHEN et al. 1993, BALIRWA 1998). The haplochromines of Lake Victoria consisted of a wide range of trophic groups including detritivore/phytoplanktivores, zooplanktivores, durophages, snail winklers, epiphytic and epilithic algal grazers, macrophyte browsers, cleaners, piscivores including paedophages, and both generalized and morphologically specialized insectivores (GOLDSCHMIDT et al. 1993, WITTE et al. 2007). Their disappearance from various water bodies where Nile perch have been introduced may have produced feeding opportunities for other taxa. BWANIKA et al. (2006) explored the hypothesis that Nile tilapia exhibit increased omnivory coincident with the Nile perch invasion and the radical reorganization of the food web. They recorded an omnivorous diet dominated by detritus and invertebrates for *O. niloticus* in lakes Nabugabo and Victoria (2 lakes with Nile perch), while a predominantly herbivorous diet was characteristic of *O. niloticus* in 4 lakes without Nile perch (BWANIKA et al. 2006). They also demonstrated that Nile tilapia from a lake without Nile perch (Wamala) grew slower and ex-

hibited a lower energy density than Nile tilapia from Lake Nabugabo (BWANIKA 2005, BWANIKA et al. in press). In Lake Victoria, comparisons of recent growth rates for Nile tilapia (MUHOOZI 2003) indicate that growth is higher than that reported in earlier studies (GETABU 1992, MOREAU et al. 1995). Possibly the higher growth rate of Nile tilapia was driven by the predatory effects of Nile perch on haplochromine cichlids through release of a new and highly preferable prey base to the tilapia (BWANIKA et al. 2006). Another possibility could be, at least to some degree, intensive fishing of tilapia (MUHOOZI 2003) or indirect effects that do not require the invocation of direct trophic competition between haplochromines and tilapiines.

A second striking example of a fish that has flourished in the presence of perch is the small pelagic minnow *Rastrineobola argentea*. By the late 1980s, *R. argentea* was the only indigenous zooplanktivore still abundant and had shown a surprising 6-fold increase in biomass (WANINK 1999) coupled with an explosion in landings (BALIRWA et al. 2003). This native cyprinid has flourished in the open waters of lakes Victoria, Kyoga, and Nabugabo, despite the fact that it is comprised a major part of the prey of the introduced Nile perch (OGUTU-OHWAYO 1994, SCHOFIELD & CHAPMAN 1999). The dramatic increase in *R. argentea* has been attributed to the relaxation of competitive pressure by haplochromines subsequent to the Nile perch boom, and a shift from juvenile to adult mortality has probably increased the number of fish recruiting (WANINK & WITTE 2000a).

A biased recovery

By the 1990s the fisheries of lakes Victoria, Kyoga, and Nabugabo were dominated by the Nile perch, the co-invading Nile tilapia, and native cyprinid *R. argentea*. But remnant populations of species remained within refugia, and these have provided seeds of resurgence over the past decade. In some lakes of the Victoria basin (Nabugabo, Kyoga, Basina) and some sections of Lake Victoria, intense fishing pressure has coincided with a resurgence of some fishes, most notably, an increase in the biomass of haplochromine cichlids (WITTE et al. 2000, CHAPMAN et al. 2003, MATSUSHI et al. 2006, SCHWARTZ et al. 2006, WITTE et al. 2007).

Levels of fishing effort in Lake Victoria grew exponentially between the early 1980s and 2000, from around 12 000 boats in 1983, to 22 700 in 1990, and more than 42 500 in 2000; the number of gillnets has grown more than 8-fold over the same time, with 20% of the nets below the legal mesh size of 5 inches (UNECIA 2001, MUHOOZI

2003, MATSUISHI et al. 2006). Recent frame surveys carried out since 2000 revealed a 36% increase in the fishers on Lake Victoria between 2000 and 2002, and 24% increase in the number of fishing crafts (LVFO 2005). Acoustic surveys indicated that the Nile perch biomass index decreased from 1.59 to 0.89 million tones over the 2 years prior to September 2001 (UNECIA 2001). Over the same period the biomass of small pelagic fishes (*Rastrineobola argentea* and pelagic haplochromine cichlids, mostly *Yssichromis* spp.) increased (UNECIA 2001, GETABU et al. 2003). Trawl surveys conducted at this time indicated that Nile perch comprised the largest component of the catch; however, approximately 70% of their catch by mass was immature (UNECIA 2001), and fishery independent surveys (reviewed in MATSUISHI et al. 2006) indicate that large numbers of juvenile Nile perch are still present in Lake Victoria, suggesting no recruitment bottleneck. A similar pattern is evident in Lake Nabugabo (Chapman and colleagues, unpubl. data). MATSUISHI et al. (2006) suggest that because Nile perch is a highly fecund pelagic spawner, a lesser number of larger individuals might find refuge from the fishery in the deeper offshore waters and facilitate recruitment.

The size at maturity (L_{m50}) for Nile perch has undergone dramatic changes over the course of its invasion. Soon after its introduction, Nile perch in lakes Victoria and Kyoga matured at a much smaller size than in their native habitat (30–34 cm total length (TL) in males and 50–54 cm in females (OGUTU-OHWAYO 2004)). It increased dramatically over the next few decades, reaching 60–70 cm TL in males and 95–100 cm TL in females in 1988, but then declined to 54–64 cm and 73–78 cm TL in males and females, respectively, in 1999/2000 (UNECIA 2001). In Uganda, the size at maturity seems to have stabilized at 56–60 cm TL for males and 66–70 cm for females (FIRRI 2005).

The community- and ecosystem-level effects of intense pressure on the Nile perch fishery are still not well understood, and there is current debate on lakewide and regional patterns of Nile perch population dynamics. Some native fish species are clearly resurging; however, these comprise a biologically filtered fauna, representing species that persisted in the face of eutrophication, deoxygenation of deepwater, and Nile perch. The resurgence of haplochromine cichlids in the sublittoral zone of the Mwanza Gulf (which has been well documented) and elsewhere (less well documented) involves only a few species that occur in large quantities and only a few trophic groups, mainly zooplanktivores and detritivores (SEEHAUSEN et al. 1997b, WITTE et al. 2000, 2007). In Mwanza Gulf, the detritivores and phytoplanktivores originally formed the most important guild of haplochromine

cichlids, with more than 13 species making up 31% of the cichlid biomass, followed by the zooplanktivores with 12 species comprising 27% of the biomass (WITTE et al. 2000). In their recent 2005 survey WITTE et al. (2007) found that 5 detritivorous species were regularly caught again, but at low abundance. Eight zooplanktivores were caught with overall densities higher in 2005 as before the upsurge of Nile perch, whereas densities of detritivores are about 10 times lower (WITTE et al. 2007).

Resurgence is also evident in other lakes in the region. Intense fishing of Nile perch in Lake Nabugabo has coincided with a reappearance of some indigenous species in the open waters, particularly haplochromines, and a shift in the distribution of Nile perch (CHAPMAN et al. 2003). In a 1995 survey of nearshore areas of Lake Nabugabo, SCHOFIELD & CHAPMAN (1999) compared the catch per unit effort (CPUE) of Nile perch in habitats 5 m and 20 m from the shore in 2 ecotones: wetlands and forest (exposed) edge. At that time Nile perch were most abundant in the 20-m offshore transects at forest edge sites. By 2005, there was no detectable difference in the catch per unit effort of Nile perch between inshore and 20-m offshore waters of exposed and wetland ecotones (Fig. 3). Over the same time frame, the average size of Nile perch in experimental gill nets declined, and Nile perch are now significantly larger in wetland areas than exposed areas (Chapman and Paterson, unpubl. data). These patterns may reflect, at least in part, intense harvest of Nile perch in their preferred habitat. Haplochromine cichlids were extremely rare in Lake Nabugabo the early-mid 1990s, mostly found in inshore areas, and the small juveniles were found almost exclusively in wetlands (OGUTU-OHWAYO 1993, SCHOFIELD & CHAPMAN 1999). By 2000, they had increased substantially in abundance and started to move offshore. By 2005, they were more abundant 20 m offshore than near the shore (Fig. 3), although small juveniles were still most abundant in wetland ecotones. Their overall abundance on the nearshore transects had declined from 2000, but was still higher than in 1995. Part of this trend reflects continued movement offshore; in 2005, haplochromines were captured in nets set 600 m offshore, a habitat virtually unoccupied by haplochromines in 1995. This increases the potential for interaction of Nile perch and haplochromines in offshore waters. However, the decrease in Nile perch density and size in this habitat may sufficiently reduce risk on haplochromines to foster both resurgence and movement away from inshore refugia.

The dramatic change in the faunal assemblage over the phases of the Nile perch invasion in Lake Nabugabo and Lake Victoria has been reflected in prey selection by Nile perch (OGUTU-OHWAYO 1994, CHAPMAN et al. 2003, BALIR-

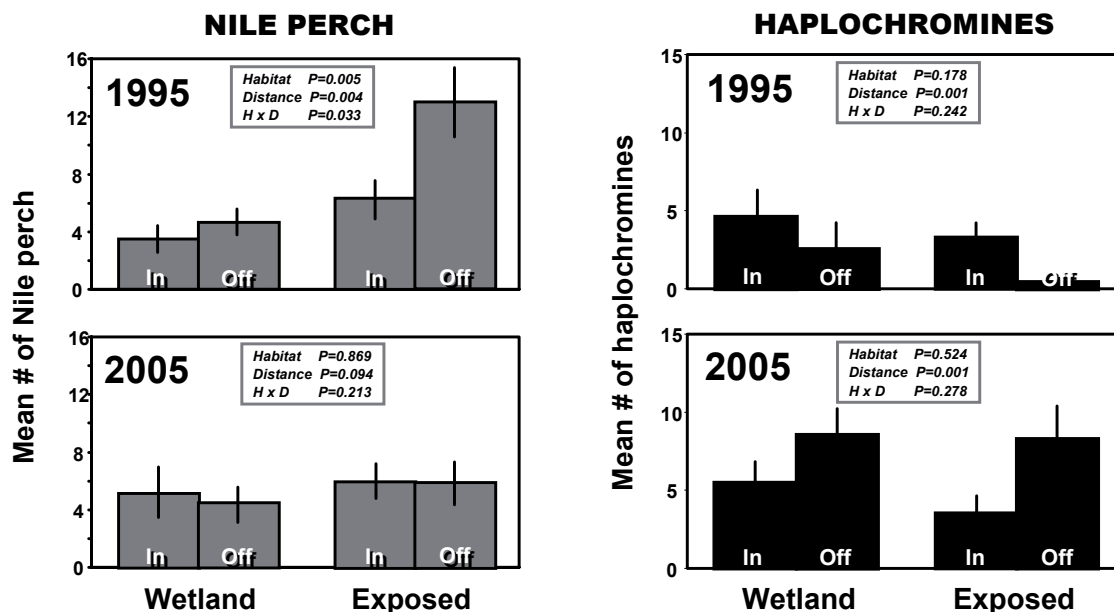


Fig. 3. Mean catch per unit effort of Nile perch (+SE) in transects with either exposed shoreline (forest edge, rocky cliff) or wetland ecotone. In each transect, experimental gill nets were placed inshore (just off the deadfall of the forest edge or just off the wetland ecotone) and away from the shoreline (~20 m offshore). Note that we do not present data here for areas of open water further offshore. CPUE represents the number of fish per experimental gill net. Source: 1995 data are adapted from SCHOFIELD & CHAPMAN (1999); 2005 data are unpublished (L. Chapman and J. Paterson).

wa 2007). In Lake Nabugabo in 1995, Nile perch fed largely on insects until reaching ~30 cm, when fish became the dominant prey by mass (SCHOFIELD & CHAPMAN 1999). By 2000, Nile perch >10 cm were feeding primarily on fish and by 15 cm were strongly piscivorous (CHAPMAN et al. 2003). The major prey taxa in 1995 were *Rastrineobola argentea* and juvenile Nile perch. By 2000, the major prey taxon was haplochromine cichlids. Between 1968 and 1977, Nile perch 20–60 cm in Lake Victoria fed heavily on the abundant haplochromine cichlids. However, by 1988, the major prey eaten by Nile perch in Lake Victoria had changed to *Caridina nilotica*, Anisoptera nymphs, juvenile Nile perch, and tilapiines, with very few haplochromines (BALIRWA 2007). This remained the main type of prey eaten by Nile perch until 2000, after which the proportion of haplochromines in the diet started to increase (KATUNZI et al. 2006, BALIRWA 2007). In Lake Victoria the shift to piscivory occurred at a larger body size after the collapse of the haplochromine cichlid fauna (OGUTU-OHWAYO 1994, SCHOFIELD & CHAPMAN 1999). Thus, the ontogenetic dietary shift in Nile perch clearly changes with the period of the invasion process. When haplochromines are rare, the size at the ontogenetic shift is substantially larger. Some current models for fisheries management assume that Nile perch begin feeding on fishes at 40 cm (e.g., MATSUISHI et al. 2006), characteristic of this species in its native range. However,

the size of the ontogenetic shift is highly labile in this species, and such information should be considered in predicting the cascading effects that fishing regimes will ultimately have on the species and the native fauna.

Phenotypic change in a filtered fauna

The situation in Lake Victoria is highly dynamic, and the Nile perch population structure is a moving target that will demand adaptive management if sustainability is elected as a priority. The future is difficult to predict, but what is clear is that fish that have endured the invasion have experienced a dynamic set of selection pressures and now find themselves inhabiting a system much changed from 40 years ago. Only a subset of the basin fauna now exists, and limnological conditions are still being strongly influenced by a basin heavily impacted by intense human land use; thus, those species that have persisted, recovered, or prospered during the invasion process may differ in phenotype from the pre-Nile perch fauna.

Some fish species have experienced generations of intense predation pressure by Nile perch. For such species, we anticipate differences between pre- and post-Nile perch populations with respect to predator-associated morphology. If fishes have survived many generations of

predation pressure by Nile perch, then they may have altered their body morphology to become faster or more difficult to swallow. Other species have survived generations of strong selection pressure for refugial characteristics, such as low oxygen, and thus we might expect phenotypic change over time that reflects these selective agents (e.g., hypoxic stress).

Scientists in the lake basin are now exploring the effects of predator pressure dynamics on haplochromines and Nile perch, and a growing body of information is demonstrating rapid phenotypic change. These studies have been done by comparing populations in lakes with and without Nile perch and by comparing archived museum specimens to contemporary conspecifics (Table 1). There is evidence for an increase in gill size in several species that have either persisted in deep swamp refugia under extreme hypoxia, or have resurged in the main lake in the 1990s under conditions of decreased oxygen concentration (Table 1). Comparisons of the haplochromine cichlid *Pseudocrenilabrus multicolor* and the mormyrids *Gnathonemus victoriae*, and *Petrocephalus catostoma* from dense hypoxic swamp refugia near Lake Nabugabo to populations from well-oxygenated waters of nearby lakes without Nile perch showed larger gills (either gill surface area or total gill filament length) in the swamp-dwelling populations for all 3 species (Table 1). This suggests that increase in gill surface area may be an adaptive response to hypoxic stress that has facilitated use of deep swamp refugia and permitted persistence with Nile perch in the Nabugabo system.

WITTE et al. (in 2008) provided more direct evidence for rapid morphological change in the Lake Victoria region by comparing archived specimens of an endemic haplochromine (*Haplochromis (Yssichromis) pyrrhocephalus*) to contemporary conspecifics (Table 1). The zooplanktivorous *H. pyrrhocephalus* nearly vanished coincident with the upsurge of Nile perch in the 1980s, but recovered in the 1990s. WITTE et al. (in press) reported a total gill surface area 64% greater in recently collected specimens (1993–2001) than in conspecifics collected prior to the Nile perch explosion (1977–1981). WANINK & WITTE (2000b) found evidence for morphological shifts in *R. argentea*. After the decline of the demersal haplochromine cichlids, *R. argentea* exhibited a habitat shift to exploit the bottom area and its macroinvertebrate prey. The habitat shift was accompanied by a significant increase in the number of gill filaments, perhaps in response to reduced oxygen concentrations in the new feeding areas, and a decrease in gill raker number related to larger prey items (WANINK & WITTE 2000a, b, WANINK et al. 2001).

Evidence for rapid morphological shifts in whole-body

morphology is also evident in the lake basin and represent a variety of selection pressures, including predation in open waters by Nile perch or selection pressures in structurally complex refugia. Using geometric morphometric tools Chapman and colleagues have found strong morphological differentiation between *P. multicolor* from swamp refugia in Lake Nabugabo and conspecifics from a nearby lake population, where they persist in well-oxygenated waters in the absence of Nile perch. Preliminary analysis suggests a strong axis of diversification characterized by a deepened midbody of the population in the Nile perch system, which may help to exceed the gape size of small Nile perch or assist with maneuverability in structurally complex refugia (Dewitt, Chapman & Langerhans unpubl. data). We also compared the whole-body morphology of *R. argentea* collected from Lake Nabugabo in 1995 when Nile perch were extremely abundant and feeding on *R. argentea* (SCHOFIELD & CHAPMAN 1999) to specimens collected in 2003 (after Nile perch had shifted back to the resurging haplochromine prey base) and to specimens from a nearby perch-less lake into which *R. argentea* was recently introduced (most probably from Lake Nabugabo). Preliminary analyses indicate that collections with higher predation intensity from Nile perch were characterized by a smaller head and larger caudal region, which match biomechanical predictions for increasing swimming speed, and show a remarkable resemblance to differences observed between predator regimes in *Gambusia* species (LANGERHANS et al. 2004); however, additional collections will be required to cover a broader size range and validate patterns (Langerhans, Chapman & Low-Decarie unpubl. data). Similar changes were observed for *H. pyrrhocephalus* (WITTE et al. in press).

Trophic shifts have been reported in several species in response to changes coincident with the Nile perch invasion. For example, the predatory catfish *Bagrus docmak*, for which Nile perch is both a predator and competitor (GODSWAARD & WITTE 1997), exhibited a shift from a primarily piscivorous diet dominated by haplochromines prior to the Nile perch upsurge to a broader diet that included a significant proportion of invertebrates and *R. argentea* (OLOWO & CHAPMAN 1999). The endemic cichlid *H. pyrrhocephalus* reappeared in the 1990s; the former zooplanktivore exhibited a new diet that included more large prey such as fish, shrimps, and mollusks, items never encountered in this species in the past (KATUNZI et al. 2003). A post-Nile perch habitat shift in *R. argentea* was accompanied by a switch in diet from zooplankton to energetically rich macroinvertebrates (including chironomid larvae and the prawn *Caridina nilotica* (WANINK 1998).

Table 1. Summary of studies providing evidence for phenotypic change in response to changes coincident with the Nile perch introduction. Comparisons are made between (a) populations in lakes with Nile perch and populations in lakes without NP or populations within deep swamp refugia (absence of NP), and (b) specimens collected before and after the Nile perch upsurge. We have also included comparisons of Nile perch at different phases of its invasion.

Trait	Species	Comparison	Data Source
Gill size	<i>Pseudocrenilabrus multicolor</i>	Presence vs. absence of Nile perch	Rosenberger & Chapman 2000, Chapman et al. 2000
	<i>Gnathonemus victoriae</i>	Presence vs. absence of Nile perch	Chapman et al. 2002
	<i>Petrocephalus catostoma</i>	Presence vs. absence of Nile perch	Chapman et al. 2002
	<i>Rastrineobola argentea</i> <i>Haplochromis pyrrhocephalus</i>	Before vs. after Nile perch Before vs. after Nile perch	Wanink & Witte 2000a, b Witte et al. In press
Shape traits	<i>Pseudocrenilabrus multicolor</i>	Presence vs. absence of Nile perch	DeWitt, Chapman, Langerhans, unpubl.
	<i>Rastrineobola argentea</i>	Before vs. after Nile perch	Chapman, Langerhans, L-De-Carie unpubl.
Retina	<i>Haplochromis pyrrhocephalus</i>	Before vs. after Nile perch	Witte et al. In press
	<i>Haplochromis tanaos</i>	Before vs. after Nile perch	Witte et al. 2005
Size at maturity or	<i>Lates niloticus</i>	early-mid-late in the invasion	Ogutu-Ohwayo 2004, Balirwa 2007
size of ripe females	<i>Rastrineobola argentea</i>	Before vs. after Nile perch	Wanink & Witte 2000a
	Zooplanktivorous haps	Before vs. after Nile perch	Wanink & Witte 2000a
Absolute fecundity	<i>Rastrineobola argentea</i>	Before vs. after Nile perch	Wanink & Witte 2000a
	Zooplanktivorous haps	Before vs. after Nile perch	Wanink & Witte 2000a
Feeding apparatus			
Gill rakers	<i>Rastrineobola argentea</i>	Before vs. after Nile perch	Wanink & Witte 2000a, b
Muscles	<i>Haplochromis pyrrhocephalus</i>	Before vs. after Nile perch	Witte et al. In press
Diet	<i>Brycinus sadleri</i>	Presence vs. absence of Nile perch	Olowo 1998
	<i>Lates niloticus</i>	Early-mid-late in the invasion	Ogutu-Ohwayo 1994, Schofield & Chapman 1999
	<i>Rastrineobola argentea</i>	Before vs. after Nile perch	Wanink 1998
	<i>Haplochromis tanaos</i>	Before vs. after Nile perch	van Oijen & Witte 1996
	<i>Haplochromis pyrrhocephalus</i>	Before vs. after Nile perch	Katunzi et al. 2003
	<i>Bagrus docmak</i>	Before vs. after Nile perch	Olowo & Chapman 1999
	<i>Schilbe intermedius</i>	Before vs. after Nile perch	Olowo & Chapman 1999
	<i>Oreochromis niloticus</i>	Presence vs. absence of Nile perch	Bwanika et al. 2006

Recent work in Mwanza Gulf has indicated broader dietary spectra in several other haplochromine species (e.g., in the zooplanktivore *H. tanaos*, (van OIJEN & WITTE 1996); and several detritivores, M. Kishe-Machumu unpubl.). Broader diets in the haplochromines may reflect decreased competition for benthic prey following the dramatic decline in congeners and other macroinvertebrate feeders. Broader diets may also reflect the influence of reduced transparency associated with eutrophication. Fish may not be able to visually detect small prey as easily as larger prey under reduced light, and/or as their

visual encounter rate goes down, they become less choosy (SEEHAUSEN et al. 2003a).

It is unknown whether these phenotypic changes in gill size, body shape, and other traits are due to heritable response to selection, environmentally induced phenotypic plasticity, and/or hybridization; but they certainly open the door for studies of contemporary evolution. We have used common-garden rearing experiments to explore the degree to which developmental plasticity explains variation in the morpho-physiology of *Pseudocrenilabrus multicolor*, a widespread cichlid that persists in

water bodies with Nile perch (where they are confined to hypoxic refugia) and waters without Nile perch (where they persist in well-oxygenated habitats). Fish from both high- and low-predation habitats show a high degree of morphological plasticity in gill traits in response to growth under high and low-oxygen conditions, suggesting that phenotypic plasticity may contribute to persistence with Nile perch (CHAPMAN et al. 2000, CHAPMAN & GALIS, unpubl. data). RUTJES (2006) also reported high levels of plasticity in rearing experiments under low- and high-oxygen conditions in 3 haplochromine species from Lake Victoria. Studies are ongoing in the Witte and Chapman labs to explore the source of phenotypic divergence in species that have persisted or prospered with the invasion of Nile perch.

The Lake Victoria region is a hot spot for studies of phenotypic alterations in natural populations and the role of human activities in precipitating adaptive phenotypic change. In a recent review, HENDRY et al. (in press) conducted a meta-analysis based on >3000 rates of phenotypic change in 68 systems that demonstrated higher rates of phenotypic change in anthropogenic context than in natural contexts. They also point out a particularly important contribution of phenotypic plasticity, also evident in our studies of cichlids in the Lake Victoria basin.

Fisheries, faunal dynamics, and phenotypic change: a summary

Lake Victoria is a highly dynamic system, and the Nile perch population structure is a moving target that will demand adaptive management if sustainability is elected as a priority. Management strategies that facilitate a heavy, but sustainable, Nile perch fishery, may allow the coexistence of many indigenous species, but attempts to protect and restore biodiversity will only succeed if the general environmental quality permits, particularly in Lake Victoria where eutrophication seems to have played an important role in patterns of faunal collapse and recovery. A major challenge facing conservation in the lake basin is the spatial and temporal heterogeneity in patterns of faunal collapse and resurgence, and our information on this heterogeneity. Our knowledge of faunal trends and environmental change, both within and among water bodies that harbor introduced Nile perch (Kyoga, Victoria, Nabugabo, and others), should be fully exploited to detect general patterns and processes that might not occur synchronously. The future holds many challenges for the Lake Victoria region, but the basin offers a glimpse of what the future may hold for the world's fresh waters and highlights the importance of human predators

as integral forces in aquatic food web dynamics. The lake basin also contains a wealth of information on human influences on phenotypic variation and confirms a growing awareness that humans are important drivers of phenotypic change in populations.

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