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# Lake Victoria Region: A natural experiment in 'adaptive ecology' and 'speciation mechanisms'

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## Lake Victoria Region

The Lake Victoria Region (LVR) has long been considered a unique zoogeographical area. Among the characteristics which set it apart from other localities is the concentration of different freshwater lakes within the region that each contain a repeated set of similar fish faunal groups. Evolution appears to have repeated itself numerous times in the LVR- some of these repetitive patterns are attributable to evolutionary parallelism, while others are probably the result of seemingly improbable but nonetheless real dispersal events among lake basins. It is thought that historically the LVR was once occupied by a more expansive lake, with adjoining east-west running rivers. This historical system broke up following the tectonic earth movements and volcanic activity that characterized the early history of the LVR to form the present lakes. The LVR is now comprised of five large lakes, Victoria, Kyoga, Edward, George and Kivu, each containing similar species groups that likely share a common origin. The lakes, though zoogeographically similar, are geologically, hydrologically and limnologically different from each other. Further, each of the large lakes in the region is associated with surrounding minor water bodies, from a few to several small lakes. We commonly refer to these small lakes around large lakes as "satellite lakes" of the larger systems. There are a variety of satellite lakes, from crater lakes of western Uganda around Lakes Edward and George, swamp lakes of the Kyoga basin, rift valley lakes of Kenya and Tanzania, and small lake systems, such as those of Nabugabo, the Koki lakes and the lakes of the Yala system in Lake Victoria Basin.

## LVR as a natural experiment

The differences in geology, hydrology and limnology of different lakes of the LVR present contrasting conditions that offer different challenges and opportunities for scientific exploration and inquiries into fish faunal evolution and trends in the historical limnology of the region. Most of the lakes in the LVR are of recent origin and are characterized by a history of dramatic changes, brought about most importantly by volcanism and/or long spells of complete drying up. The largest of the lakes in the region, Lake Victoria, is known to have been formed about 750,000 years ago and geological evidence indicates that it has gone through at least one, and probably several long cycles of completely drying up and then refilling. The last time of drying for Lake Victoria is thought to have occurred as recently as 14,000 years ago, and lasted for an estimated 2000 years. Lake Edward is believed to have been a more expansive lake than it is presently, one that possibly stretched as far east as the shores of the current Lake Victoria. This history makes it a possible source of progenitor fish species which reinvaded Lake Victoria after the last dry spell. With volcanism, the ancient Lake Edward is believed to have receded and finally broken up into Lakes George, Kivu, the current Edward, and several satellite lakes. The history of Lake Kyoga is quite different. Lake Kyoga has a mean depth of only three meters and is a massive swampy area thought to have been turned into a lake when the outflow connecting Lake Victoria to the nilotic water system filled a shallow trough on the course of River Nile to the north.

This variety of lake geologies and lake histories presents a scientific challenge in understanding the relationships among the water bodies and among their associated floral and faunal content. The challenge is increased by the apparent similarity in fish species composition among lakes of the LVR. One of the most intriguing facts about the diversity of the fish fauna, though shared with other African Great Lakes regions, is the enormous adaptive radiation of cichlid fish species in all the LVR lakes and the high level of localized endemism associated with each of the lakes, again especially among the cichlid species. It is astonishing that estimates suggest that, for Lake Victoria alone, nearly 600 species have evolved in only the 12,000 years which have elapsed since its last dry spell.

The short evolutionary history of the fishes in the LVR presents an opportunity rarely found in other natural faunal systems anywhere else in the world. In the case of the LVR cichlids the opportunity exists to examine phylogenetic linkages with ancestral taxa that are actually still extant. In most cases evolutionary relationships must be reconstructed from extant species and through fossil remains of ancestral forms in what is often a very patchy or absent fossil record. The enormous and repetitive adaptive radiation of the haplochromine cichlids into the numerous ecological habitats presented by various water bodies in the LVR, while maintaining their basic body plan, allows investigators to study morphogenesis along phyletic lineages, and investigate how organisms adjust morphologically to changing habitat over very short evolutionary time scales. The conditions in the LVR also present scientists with possibilities to correlate the limnological and geological history of the region with the history inferred from relationships derived from the phylogeny among species of the different groups and or water bodies.

## Human influence on the Lake Victoria Region – a few 'pleasantries' out of an ecological disaster

The introduction of Nile perch and non indigenous tilapiine fishes into the LVR left little refuge for the native fish species, especially in the big lakes. This happened at a time of heightened fishing pressure, contributing to the collapse of the native commercial species. The native commercial fishes included primarily the only two native tilapiine species and large native predatory fish species in Lakes Kyoga and Victoria. The collapse of the native fishery also overlapped a time of limnological changes in the lake, from a predominantly diatomous ecosystem to one which is now blue-green algal (cyanobacterial) dominated. It could be argued that supplanting a native tilapia fishery by a fishery based on Nile perch and Nile tilapia has been good for the economics of the fishery, but the introduction of these exotic species has been implicated as one of the primary causes of the worst vertebrate extinction event of the 20$^{th}$ century, with an estimated 200 species of endemic cichlids feared completely lost. While the main lakes have been severely impacted by the introduction of exotic species, only a few of the minor lakes (such as Lake Nabugabo in the Victoria Basin and Lake Nyasala in Lake Kyoga Basin) have experienced the domination of the Nile perch and the INFLUENCE of its 'extinction machinery' on the endemics. In some of the minor lakes, such as Lake Bisina in Lake Kyoga Basin, the Nile perch flourished early following introduction, but has since been knocked back by selective fishing mortality. High fishing pressure and explosion of the water hyacinth has also brought down the numbers of Nile perch in some areas of the large lakes, making the waters where the Nile perch has collapsed a haven for the resurgence of many original native cichlid species. Such situations now provide us with natural experiments on the mechanisms of cichlid speciation and/or other factors that have been thought to have led to the resurgence of fish species in LVR as a whole. Together with new data on the evolutionary history of the species of the LVR, on information about the changing limnology, and on new knowledge concerning the hydrological history of the region we may well begin to clarify some of the contentious issues pertaining to evolutionary theories and how new species are derived from existing forms. The numerous satellite lakes surrounding the large lakes, the vast number of species, human influence, and the recent history of the LVR provide us with great opportunity and challenge to scientifically unravel the confusing picture presented to us by nature.

## Species extinction – exactly how much have we lost?

Despite its young age, Lake Victoria is estimated to have contained over 500 species of cichlids prior to changes in the lake caused by human activity that have taken place during this century. It is estimated that these changes resulted in the extinction of nearly two hundred species, and with more species found to be at a great risk of extinction with every expedition made to the lakes. Unfortunately, large portions of the extant cichlid fauna in the LVR remain undescribed, as was the largest portion of the extinct taxa. Continued changes in the lake ecosystem have put increased urgency on the need for studies to assess what is left in the wild. This urgency exists even if there is no reprieve for many of the most endangered species. We must at least try to tap the invaluable evolutionary information contained in species that may be going extinct at a rate greater than we can currently study them. Some solace can be taken that knowledge about some of the rarer forms may not yet be lost. Our exploratory surveys so far have revealed that significant portions of the cichlid fauna previously considered extinct in the large lakes may be still surviving in several of the satellite lakes. Some of the satellite lakes, such as the Nabugabo lakes on the northwestern side of Lake Victoria still have small number of species found nowhere else. Other satellite lakes, such as the Kyoga lakes in central Uganda, have a wide variety of species which include both known species and several undescribed species that seem to be sister species to some now extinct from the larger lakes. For example, we have discovered the scale-eating haplochromines of the genus *Allochromis*, thought endemic to Lake Victoria, alive and well, though extremely uncommon, in the Kyoga lakes.

Although studies during the 1980's and early 1990's revealed no marked genetic differences between various Lake Victoria haplochromine species, newly developed types of molecular markers (microsatellite DNA markers), produced specifically for LVR haplochromine cichlid species in our laboratory, can differentiate populations and species even at a very fine scale. We are currently using these methods to investigate several phylogenetic and macroevolutionary questions in the haplochromine species. It is especially important to our understanding of the evolutionary and hydrological processes that have shaped the LVR system for us to determine whether the fish species of these small water bodies are of recent origin or reflect longer historical changes in LVR. Efforts to conserve the aquatic biodiversity of the region hinge largely on our knowledge about the species and the relationships among extant evolutionary and ecological groups. Molecular tools have a clear advantage in such studies because information about historical relationships and evolutionary linkages among species, extant and extinct, is directly embedded in the molecules (DNA and enzymes) targeted by such tools. Molecular information will be of direct use in making decisions about fisheries management and conservation practices. Therefore, interested parties in the LVR fishes, such as FISA and LVFO, will want to foster such studies to allow the generation of the knowledge base urgently needed to conserve and manage fisheries biodiversity of the LVR. We must all foster a greater understanding of the importance of this genetic information for the future development and conservation of the LVR fisheries, through education of fisheries scientists and by encouraging the development of locally based genetic research.

## Satellite lakes versus large lakes

On the macroevolutionary level a question of major interest has been the historical nature of satellite lakes. Are the satellite lakes residual ponds left behind with large portions of the diversity as the originally expansive large lakes receded during extensive desiccation periods, or are they nursery beds for cichlid species that acted as lifeboats during periods of desiccation and later fed their trapped fauna back into the large lakes? Of no doubt is the role these minor lakes are currently playing as refugia for endemic species ravaged by the dramatic human impact in LVR since the turn of this century.

The bounty of cichlid fishes in these minor lakes was first considered by Greenwood in several of his papers (Greenwood, 1981). Among the lakes on which Greenwood worked were the Nabugabo lakes west of Lake Victoria. He found these minor lakes to be not as speciose as Lake Victoria but containing sister taxa to those in the larger lakes. Greenwood concluded that minor lakes can act as nursery beds that multiply species which later move into the larger systems. Our recent discovery in satellite lakes in the LVR of cichlid fauna equivalent to portions of the extinct species of the large Lakes Kyoga and Victoria, has led us into speculation of a broader, and rather different role for satellite lakes than Greenwood had envisioned. Minor satellite lakes can act as refugia of the equivalent species in the big lakes. Satellite lakes generate species through allopatric isolation and local selection regimes, but on a smaller scale as the large lakes, while their sheltered habitats offer protection (to species equivalent to those in the greater systems) from the drastic changes that the big lakes have been experiencing. We think small lakes have often been part of the ontogenetic speciation cycles of big lakes. Remembering that this is so may help explain some of the faunal peculiarities of these systems. We are currently doing evolutionary analysis of these recent discoveries using both morphological and molecular tools to elucidate the evolutionary history of the two interconnected systems (satellite lakes versus large lakes).

## Further readings

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