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The bounty of minor lakes: the role of small satellite water bodies in evolution and conservation of fishes in the Lake Victoria Region, East Africa

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Abstract

The Lake Victoria Region (LVR) encompasses the large lakes Victoria, Kyoga, Edward, George and Kivu, as well as scores of small satellite lakes within the parent catchments. Taken as a whole, the LVR originally harbored a unique fish fauna that included in excess of 600 endemic species of cichlid fishes. As a result of human influence, including a commercial fishery and the introduction of several exotic species, nearly 200 cichlid species and several endemic genera have become extinct from lakes Victoria and Kyoga. Recently, we have discovered that some of the apparently extinct taxa survive as extant representatives in the satellite lakes. Here, we summarize the findings of our ecological survey of the fish species of the satellite lakes. We also discuss the results of some preliminary genetic analyses, and highlight major genetic and ecological changes in the fish fauna that have taken place in the regional fishery. Minor lakes now play a crucial role in conserving the endangered species of the entire region, and also as living museums of East African ecological history. Our findings allude to the historical importance of minor satellite lakes as natural refugia for the fishes of the Lake Victoria Region, a region characterized by a history of geological and climatic instability.

Introduction

More species of vertebrates are thought to have become extinct from the Lake Victoria Region (LVR) in the 20th century than from anywhere else in the world (Kaufman, 1992). Nearly 200 species of haplochromine cichlids have disappeared, most especially in lakes Victoria and Kyoga (Trewavas et al., 1985; Barel et al., 1985; Ogutu-Ohwayo, 1990; Witte et al., 1992a, b). Disappearances have followed the introduction and establishment of the Nile perch and other non-indigenous fishes and dramatic limnological changes in the waters of the Lake Victoria Region (Hecky & Bugenyi, 1992).

Following losses from the cichlid fauna, there has been a concerted effort both locally and internationally, to establish and conserve remnant populations of cichlids species (Kaufman, 1993). Given the continued presence of exotic species, and with threatening alterations in limnology remaining largely unimproved, efforts to conserve remnant cichlid species have been broadened to include small water bodies in the region which contain no Nile perch and are limnologically unaltered. Embedded within the extensive swamps of the region, many small lakes are more or less shielded from exotic species and nutrient enrichment, although artisanal fishing occurs throughout. The species richness of these small satellite lakes has not been studied or surveyed. The goal of our study is to describe the communities of the satellite lakes and assess their potential for illuminating the evolution, and ensuring the conservation of indigenous fishes in comparison the region.

The LVR, like Lake Malawi and Lake Tanganyika, is known for the rapid radiation and enormous species richness of its cichlid fishes. The Lake Victoria Region is interesting in that it is geologically much younger than the other two Great lakes. Lake Victoria appeared no more than 750 000 years ago, and is thought to have last dried up completely only 12 000 years ago (Johnson et al., 1996). Despite its young age, Lake Victoria is estimated to have contained over 600 cichlid species prior to human induced changes during the last century (Kaufman, 1997). Overfishing, introduction of exotic species and change in aquatic environment in the LVR resulted in nearly 200 fish species becoming extinct, with many more believed to be at a great risk of extinction. Unfortunately, large portions of the extant cichlid fauna remain undescribed, as was the larger portion of extinct taxa. This puts increased urgency on the need for studies to assess populations that remain.

Study sites

The Lake Victoria Region has a variety of minor satellite lakes that vary in the mode of formation, hydrological regime, limnological conditions and associated biological communities. Examples include swamp valley lakes, lakes formed as cut-off embayments of larger lakes, saline or soda lakes, crater lakes, the Rift Valley lakes and many others whose origins are less obvious: e.g. Lake Wamala, Lake Eyasi and Lake Bunyonyi. Recently, the investigation of biodiversity has been broadened to include these satellite lakes (Kaufman & Ochumba, 1993; Kaufman et al., 1997). Satellite lakes contain many more species than reported by earlier scientists (Worthington, 1937; Fryer & Iles, 1972; Greenwood, 1981), mostly because previous visits to these sites were brief (Worthington, pers. com.). For example, Greenwood's classic work on the Lake Nabugabo fauna (Greenwood, 1965, 1974) did not include three small satellite lakes within the larger Juma-Katonga system to which Nabugabo is biogeographically related (Kaufman & Ochumba, 1993; Chapman et al., 1995). Although few dispute Greenwood's theory that satellite lakes can generate endemic taxa, there has been contention over the likelihood that lakes such as Nabugabo could have acted as source seed for the recolonization of the main lakes following the drying that the region is thought to have undergone (Johnson et al., 1996). The principle objection is that any major drying period affecting the main lakes would certainly have dried up the small satellite lakes, even before the main lakes had dried completely.

Clarification of the limnological history of the minor lakes and the history of their associated biological communities will help us understand to what extent the LVR satellite lakes function in species multiplication and/or adaptive diversification, and whether or not minor lakes are microcosms of the greater systems. We have begun paleolimnological studies of representative types among these minor lakes for a better understanding of the historical and evolutionary perspective of changes in the regional fishery (Crissman et al., in prep., Beuning et al., in prep.). Such studies, combined with ecological and evolutionary studies, can illuminate the exact role of minor lakes in the evolution and enormous radiation of cichlid fishes in this extensive but relatively young system.

To test postulated relationships between hydrological cycles and biological richness and/or species radiation (Kaufman, 1997), one has to understand the historical geological connection among the main lakes and their satellite lakes. This would depend upon the way in which satellite lakes were formed, which could be one of several ways:

1. fragmentation of larger lakes with a drop in water level and swamp encroachment, such as in Lake Victoria and Lake Kyoga basins;
2. desiccation where one large lake turns into one or more small lakes, for example some Rift Valley soda lakes;
3. volcanism, as occurred in the formation of crater lakes in western Uganda; and
4. damming by volcanic ashes that blocks drainage, as we believe to be the case for Lake Bunyonyi in southwestern Uganda.

Methods and materials

Cichlid fishes in the region were surveyed. The main lakes in the region (Victoria, Kyoga, George and Edward though without Kivu) were included along with several of their satellite water bodies around each of these main lakes. The survey also included the Victoria Nile between Lake Victoria and Lake Kyoga, as well

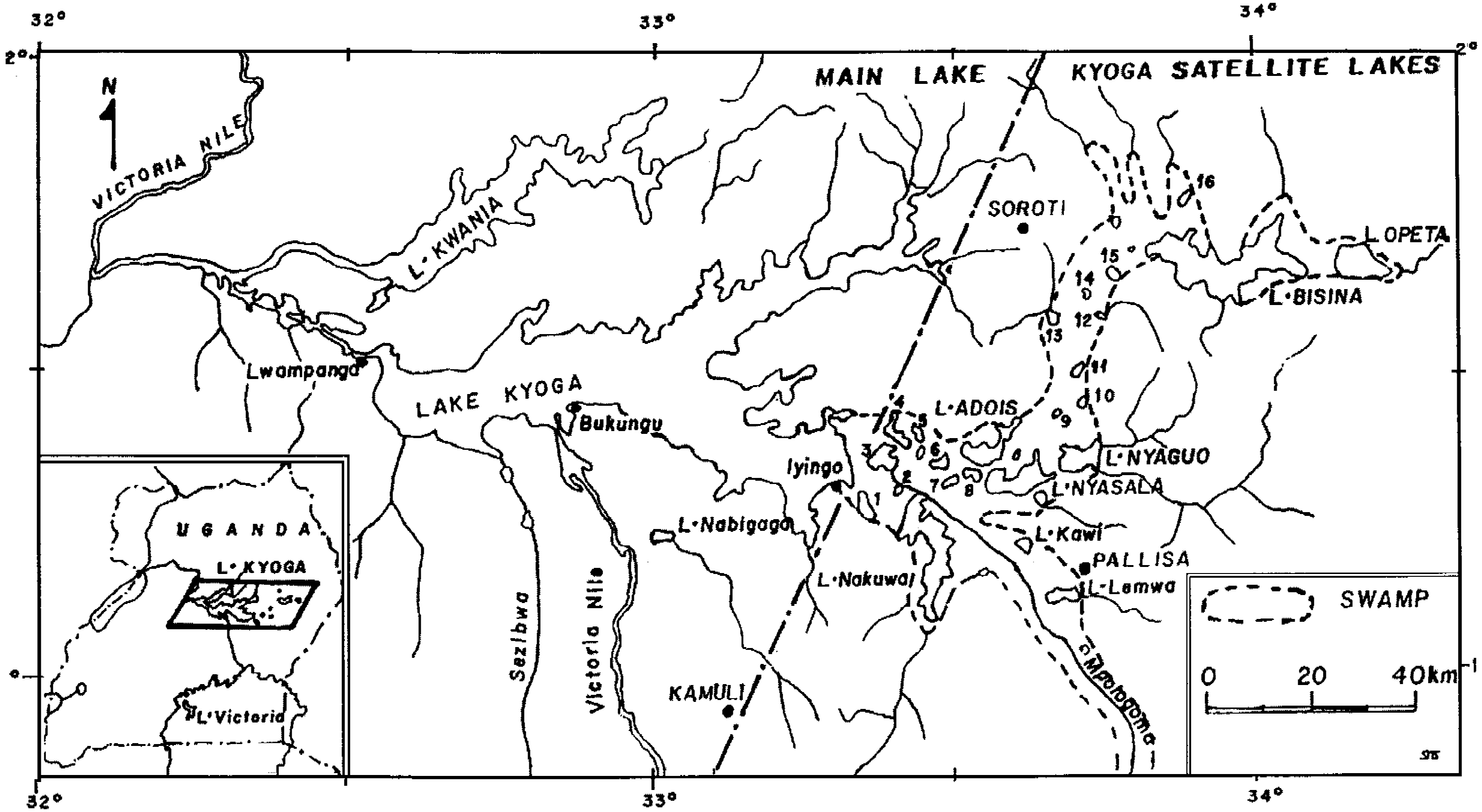

Figure 1. A Map of Lake Kyoga system showing the main Lake Kyoga and satellite lakes: 1=Nawampasa; 2=Muwuru; 3=Nabsejere; 4=Kiodndo; 5=Naragag; 6=Pachoto; 7=Kadiko; 8=Meito; 9=Kodiki; 10=Gawe; 11=Kochobo; 12=Kasago; 13=Opare; 14=Ajama; 15=Semere; 16=Owapet; 17=Namumbya.

as the Yala River basin on the east of Lake Victoria in Kenya. The lakes mentioned, including their surface drainage waters, form what is known as the Lake Victoria Region (LVR) system (Kaufman, 1997; Kaufman et al., 1997). Figure 1 is a map of the Lake Kyoga basin as an example of the geographical connection between satellite lakes and the main lake.

A collection of fish that was made during the initial visit to Lake Nawampasa, one of the Lake Kyoga basin satellite lakes, included taxa that had been reported as either extinct or rare in the LVR. As a result of these observations, a wider survey was designed to include most of the satellite lakes in the region with the aim of establishing the cichlid species composition of each body of water. The survey was carried out using gillnets of mesh sizes ranging from half an inch to seven inches, beach seines for relatively large satellite lakes and minnow traps for locations inaccessible by gillnets or seining. An effort was made to cover all types of habitats and seasons and to sample both diurnal and annual variations.

After capture, fish were sorted into groups of similar morphs and species were identified. At least 20 individuals of each morphotype were photographed immediately. Muscle tissue was taken from the right epaxial muscle of each of the photographed twenty individuals for molecular analysis. The tissue was then placed in a vial containing 95% ethanol. After 1 hour, the original ethanol was replaced by fresh ethanol for storage until DNA extraction. The tissue specimens were shipped to The Ohio State University for analysis. Fish specimens were then put in 10% formalin for 2 days, rinsed and dehydrated in four steps into 70% ethanol for archival. Specimens were transported to Boston University for identification, and later archived in the Harvard University Museum of Comparative Zoology.

Molecular analysis was carried out using RAPD markers (Randomly Amplified Polymorphic DNA) following the methods of Mwanja (1996) and using microsatellite markers, following Wu (1999) and Wu et al. (1999). The purpose of the analysis was to establish the genetic population structure and phylogeny of the cichlid species of the satellite lakes relative to similar species found in the main lakes. The RAPD and microsatellite techniques were chosen because of their robustness and ease of use for extensive population analysis studies. The markers also were advantageous in that they appear to reveal patterns of recent divergence better than other conventional molecular markers (Avise, 1994). This is of paramount importance for the analysis of an evolutionary young and recently disturbed system such as the LVR cichlid species complex (Kaufman, 1997).

Results

Ecological survey

Taxa ecologically similar and/or taxonomically close to many known to have disappeared from the main lakes, proved still extant in several of the satellite lakes in the LVR (Table 1). Examples of the extant species/genera obtained in surveys of the satellite lakes are shown in Table 2. Some of the satellite lakes, such as the Nabugabo lakes, contained only a small number of species as first reported (Greenwood, 1965, 1974). Others, such as the satellite lakes around Lake Kyoga, contained a variety of taxa. These taxa included both known extant species as well as several species that were morphologically similar to species or genera reminiscent of the main lakes before the establishment of the Nile perch (Greenwood, 1981; Kaufman & Wandera, unpublished). A few cichlids, such as *Astatoreochromis allaudi, Pseudocrenilabrus victoriae* and the genera *Astatotilapia* and *Paralabidochromis,* were found to be distributed widely both in the main lakes and in the satellite lakes. Most of the piscivorous cichlids, such as species of *Harpogochromis*, *Psammochromis* and *Prognathochromis*, were restricted to only a few satellite lakes.

Among the native tilapiine cichlids of the LVR, we found significant populations of the two native forms, *Oreochromis esculentus* and *Oreochromis variabilis* in several of the satellite lakes. These two species have been displaced from the main lakes. Unfortunately the surviving remnant species were also found to occur together with the closely related introduced exotic tilapiine species.

Preliminary genetic analysis

Molecular analyses of the haplochromine cichlid species of the LVR revealed that there is strong population structuring, with differentiation between the remnant populations within the main lakes and between the main lakes and associated satellite lakes (Wu, 1999). All species, both those that were widespread and the more restricted forms, were highly subdivided. Migration was estimated to be highest within lakes and lowest between the totally isolated satellite lakes.

Table 1. Estimates of the number of cichlid fishes contained in the LVR satellite lakes based on our field survey data from 1990 to 1997. The table also shows the occurrence of the Nile perch, *Lates niloticus* in LVR

	Haplocromines	Tilapiines		Nile perch
Lake Victoria Basin				
Main Lake		Native	Introduced	
Lake Victoria	>100	1	4	Dominant
Nabugabo lakes				
Lake Nabugabo	<5	0	4	Dominant
Lake Manywa	<5	1	0	Absent
Lake Kayanja	<5	1	2	Absent
Kioki lakes				
Lake Kachera	>20	1	4	Absent
Lake Kijanebalola	>20	1	4	Absent
Lake Mburo	>20	1	4	Absent
Lake Kyoga Basin				
Main Lake				
Lake Kyoga	<50	0	4	Dominant
Satellite lakes				
Lake Nawampasa	>60	2	3	Absent
Lake Lemwa	>50	2	2	Absent
Lake Bisina	>30	2	4	Rare
Lake Nyaguo	>50	2	2	Absent
Lake Nakuwa	<5	0	4	Dominant
Lake Nyasala	<30	1	4	Dominant
Lake Edward-George System				
Main Lakes				
Lake Edward	~50	3	2	Absent
Lake George	>40	3	1	Absent
Satellite lakes				
Lake Saka	>30	0	1	Absent
Lake Kabaleka	>40	3	1	Absent

Table 2. List of examples of taxa extinct from the main Lakes Victoria and Kyoga but still extant in satellite lakes

Taxa	Main lakes;	Satellite lakes
Allochromis	Extinct	present (Kyoga lakes)
Harpagochromis	Extinct	present (Nabugabo, Kyoga and Kioki lakes)
Astatotilapia latifasciata	Extinct	present (Kyoga lakes)
Prognathochromis	Extinct	present (Nabugabo, Kyoga and Kioki lakes)
Lipochromis	Extinct	present (Kyoga lakes)
Pyxichromis	Extinct	present (Kyoga lakes)
Haplochromis annectidens	Absent	rare (Nabugabo lakes)
Haplochromis obliquidens	Extinct	absent
Haplochromis lividus	Extinct	absent
Tridontochromis	Extinct	only one extant species (Kyoga lakes)
Prognathochromis perrieri	Extinct	absent

Table 3. Preliminary genetic analysis of cichlid fishes of satellite lakes species in comparison to similar species of the main lakes based on RAPD (for tilapiine species) and microsatellite markers (for haplochromine species). This results are extracted from Mwanja (1996), Wu et al. (1999) and Wu (1999)

Genetic attribute/ Species or species complex	Polymorphism	Heterozygosity	Allelic diversity	Population Subdivision
Tilapiine Complex				
Native				
O. esculentus	Higher	Higher	Higher	Higher
O. variabilis	Equivalent	Equivalent	Higher	Higher
Non indigenous				
O. leucostictus	Higher	High	Higher	Lower
O. niloticus	Lower	Lower	Higher	Higher
T. rendalii	Equivalent	Lower	Higher	Higher
T. zilli	Equivalent	High	Higher	Equivalent
Haplochromine complex				
Haplochromine spp.	Higher	Higher	Higher	Higher
Astatoreochromis alluadi	Lower	Equivalent	Equivalent	Higher
Astatotilapia spp.	Higher	Higher	Higher	Higher

Genetic diversity has not been depleted in these species. The majority of species exhibited high within-population heterozygosity and allelic diversity (Table 3). Among the tilapiine species of the LVR, we found evidence of genetic interaction between the native and introduced species (Mwanja et al., 1995; Mwanja, 1996). Tilapiine swamp forms such as *Oreochromis leucostictus* were found to be less differentiated than strict lacustrine species like *O. esculentus*.

Discussion

Although previous studies (Sage et al., 1984; Meyer et al., 1990) revealed limited genetic differences between various Lake Victoria haplochromine species, new sets of molecular markers (microsatellite DNA markers) designed in our laboratory can differentiate populations and species even at a guild or sibling level. These molecular markers have already been used to examine a series of phylogenetic and macroevolutionary questions in the haplochromine cichlids (Wu 1999). Whether the species that we have found in the small water bodies of the LVR are of recent origin, or reflect long-term historical patterns in the LVR is of great importance in elucidating evolutionary and hydrological processes that have shaped the LVR system. Among the tilapiine cichlids, which form a sister group to the haplochromine species, significant populations of the two native forms remain in satellite lakes, even though they have been largely displaced from the main lakes of the region. Batjakas et al. (1997) postulated that limnological changes in the main lakes, from a diatom-dominated ecosystem to one dominated by cyanobacteria, may account for the displacement of the ngege (*Oreochromis esculentus*), the originally most important commercial species, from the main lakes. This could explain its current relegation to the minor satellite lakes that tend to be less eutrophic, and less dominated by cyanobacterial phytoplankton.

Minor satellite lakes versus *large lakes*

On the macroevolutionary level, a question of major interest to us concerns the historical nature of satellite lakes in relation to their role in species radiation and recolonization events that followed the several desiccation phases in the LVR. The results of our ecological survey and preliminary phylogenetic analysis show that satellite lakes contain most but not all major morphotypes known to be or to have existed in the larger lakes (Greenwood, 1981). Most common among these satellite lakes are poorly differentiated morphotypes thought to be basal in evolution to more derived taxa known from the larger lakes (Kaufman et al., in prep). These findings have led us to propose two hypotheses (though not mutually exclusive) of the role played by minor lakes in evolution of cichlid fishes.

The first of these is that the satellite lakes are residual ponds, left behind with large portions of the biological species diversity when the main lakes receded during extensive desiccation periods. The second is that the satellite lakes can act both as nursery beds for cichlid species and as dispersal way stations that can facilitate dispersal at the end of periods of desiccation, to later re-supply Great Lakes.

Whatever the explanation, there is no doubt that the minor lakes are currently playing a covert role as refugia for endemic species ravaged by the dramatic human impact on the LVR since the beginning of the 20th century. The satellite lakes present the only manageable natural refuge that can guarantee persistence of the most vulnerable forms or species. The results of molecular analysis show that the resident populations of satellite lakes are highly differentiated between lakes. Thus, it would be a good policy to maintain and manage various satellite lakes as independent evolutionary units. Transfer of fish species between satellite lakes should only be done after a careful analysis of the genetic and ecological implications of such actions. Such conservative management practices will ensure the integrity of the isolated populations, enabling them to continue to evolve without further anthropogenic pressures.

The ecological and evolutionary importance of minor lakes

The importance of cichlid fishes in the minor lakes was first considered by Greenwood in several of his papers (for example, Greenwood, 1974, 1981). Among the lakes on which Greenwood worked were the Nabugabo lakes west of Lake Victoria. He found that these minor lakes were not as speciose as Lake Victoria and to be different markedly in species composition. He suggested that several of the species endemic to the Nabugabo system might be evolutionary precursors to species in the larger lakes. Greenwood concluded that minor lakes act as nursery beds, delivering new prototypes that move into the larger systems, where they act as the prototypes that radiate into the stock of species in the wider systems.

Our recent discovery of a cichlid fauna in satellite lakes in the LVR equivalent to a significant proportion of the extinct taxa of the large Lakes Kyoga and Victoria, has led us to suppose a broader role for satellite lakes than envisioned by Greenwood. Minor satellite lakes act not only as nursery beds of prototypes for the larger lakes, but also as critical refugia for diverse ecological types and genetic lineages. The high number and large variety of satellite lakes in the LVR presents opportunities for radiation almost similar to what a large lake may offer, if not more; as such, the pace of generation of species in satellite lakes may be similar to that in large lakes. Meanwhile, their sheltered habitats offer protection to species similar to those in the greater systems, largely isolated from the anthropogenic changes that the big lakes have been experiencing. We think small lakes have often been part of the ontogenetic speciation cycles of big lakes (Kaufman, 1997). Remembering that this is so may help explain some of the faunal peculiarities of these systems. Research continues on the evolutionary analysis of these recent discoveries using both morphological and molecular tools to elucidate the evolutionary history of the main lakes and their satellite lakes.

Introduction of Nile perch and non-indigenous tilapiine fishes into the LVR left little room for refuge by the native cichlid species, especially in the large lakes. However, in only a few of the minor lakes, such as Lake Nabugabo in the Lake Victoria basin and Lake Nyasala in the Lake Kyoga basin, has the Nile perch been able to establish, take over and exert its 'extinction machinery' on the endemic fauna. In some of the minor lakes, such as Lake Bisina in the Lake Kyoga Basin, the Nile perch initially flourished following introduction from the 1960s up to the mid 1980s, but has since declined apparently due to selective fishing pressure. We are finding, as with the main lakes with Nile perch, an appearance of a possible resurgence by the original native cichlid species in locations where Nile perch has become rare or absent. Such situations provide us with a set of natural experiments on the effect of the Nile perch and/or other factors that are thought to have contributed to species loss across the LVR. Such studies are necessary if we are to establish the status of various species and develop realistic management options for all compartments of the indigenous fauna.

Tracing the impact of limnological changes on particular fish species and on overall fish genetic diversity over a larger time scale (i.e. since the last major desiccation period) could be enhanced by studies of these various satellite lakes. Any connection identified could then be extended to the large lakes and if cautiously applied, can be monitored to predict threats to fish fauna in the region. Changes in the limnology of small lakes are more likely to be easier to discern and assess than in the larger systems.

Certainly large lakes are more diverse and limnologically more variable compared to the satellite lakes, but the two systems also have a lot in common including similar fish fauna groups. For example, Lake Kyoga basin lakes, both the main and the multitude of satellite lakes, are thought of as a single continuous swamp. Satellite lakes may, therefore, provide reliable reference points concerning changes that may have occurred more widely in the LVR. In practice, these smaller lakes offer management options with respect to the simultaneous management of fisheries and preservation of species biodiversity, since they can be closed to fishing and monitored more easily.

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