I. INTRODUCTION

II. POLLUTION

- Atmospheric

- Nutrient enhancement

- Euthrophication

- Anoxia/stratification

III. OVERFISHING

IV. EXOTIC INTRODUCTIONS

I. **INTRODUCTION**

Lake Victoria is in central Africa, second only to Lakes Superior and Baikal in size, Victoria's equatorial location, recent formation and opportunistic colonization by the cichlid tribe Haplochromini provide a young, continuing evolutionary radiation. P.H. Greenwood, the scientist most familiar with the assemblage, eventually recognized that the extreme plasticity of these fish would cloud any phylogenetic relations because of intra-species, morphological and habitat range overlaps, and that more definitive methods would have to be found. The resultant radiation, as described by Greenwood (1981), contains 29 genera and two subgenera. 1992 estimates of the total number of pre-catastrophe species and subspecies, range from 800-1,000 species.

Recent, extensive gene sequencing of these cichlid fishes has raised questions about the conventional notion of speciation as a process of accruing genetic variation (Sturmbauer and Meyer, 1992). Sturmbauer and Meyer demonstrated separation of the processes of genetic and morphological variation. Relative "directions" of these two processes need not be related in any way and the rates obviously need not be the same. Examples of "living fossil" species which have remained physically unchanged can be said to be in morphological stasis. They provide a contrast to the well documented trend for genetic variation to accrue over time.

The newly formed Lake Victoria underwent a founder event like few documented to date. While many families of fishes were present, only the cichlids underwent this rapid "diversification". Cichlids are secondary freshwater fishes, i.e., they have evolved from marine ancestors, and all Haplochromis
(sensu lato) are maternal mouth-brooders. Inherent physical and behavioral predispositions amounted to unique qualifications for the exploitation of opportunity presented by the creation of

this new ecosystem. Phenotypic plasticity is exhibited to a high degree by all Haplochromines (indeed all cichlids), and so the ancestral Haplochromine may have been very plastic itself. Commonly derived Haplochromine traits are behavioral and physical plasticity, territoriality, tolerance of a high dissolved mineral content, and parental brood care.

Since its formation the lake expanded to an area about twice its present size, allowing those species that survived low water to colonize new habitat as it became flooded. Although not mentioned in the literature, I believe that this second dispersal event had profound impact on the phylogeny of the lake's cichlids. The decline of high water to today's level resulted in fragmentation of the freshwater ecosystem as ponds and swamps became isolated from the main lake at different points in time. These sequentially created demes provide a series of evolutionary events.

Agricultural pollution and localized over fishing began in the 1930's and increased with time. Fertilizer runoff continued to pour into the lake at an ever increasing rate. Even so, it was not until the 1950's, fully twenty years later that euthrophication took hold. Meanwhile, the subsistence fishery of the three riparian nations - Kenya, Uganda and Tanzania - continued unchecked.

According to Graham (1929), mesh sizes were continuously reduced in response to declining catches. Ngege (Oreochromis esculentus), the target species, was decimated. However, over-fishing was selective enough that only one species, the ngege was threatened.

Between the late 1950's and into the 1960's a series of seventeen introductions of Lates (Nile Perch) took place. Again, it took a long time to dramatically impact the system. As recently as 1970, open water trawls contained less than 5%
Lates
. In the early 1970's, however, the perch population exploded. By 1974, catch ratios had jumped to 98%
Lates
in the northern end of the lake. The perch population "explosion" at the northern end of the lake began, as a team of Dutch scientists in Tanzania, arrived in the extreme southern portion of the lake in 1976.

The ecological situation in the lake can be summed up as follows: The deep water (below 50') is devoid of fish, open water is occupied by two species Lates and Rastrineobola, and (an endemic, pelagic minnow). The periphery of the lake is reasonably intact. Rocky outcrops, dense papyrus vegetation and occasionally sand provide refuge from the perch.

II. **POLLUTION**

1. Atmospheric

Acid rain was probably the earliest pollution affecting the lake. The industrialization of Europe and its relatively upwind position has resulted in the deposition of significant amounts of sulfurous compounds in Africa. Sulfur is an element known to be metabolized by bacteria and critical to their existence. Scientists believe that Lake Victoria was sulfur limited. With unlimited organic detritus to fuel it and the addition of a virtually absent key limiting factor, bacterial population were no longer held in check.

2. Nutrient Enhancement

Artificial nutrient enhancement is to blame for the warping of this ecosystem's phytoplankton community. Lake Victoria has always been murkier than most with Secchi depths of one to two meters. It supported life all the way to the bottom, was isothermic and well mixed. Early scientists performed extensive deep and open water trawl surveys. This is perhaps some of the best sampled habitat with 130 species described so far. Unfortunately, almost all of them are already extinct. An entire fauna was lost.

Nitrogen is not usually limiting to fresh water systems (Hecky and Kilham 1988) and indeed, it does not appear to be a limiting factor in the Victoria basis. The nitrogen to phosphorous ration (N:P) is extremely important to phytoplankton. The lake's water prior to massive fertilizer runoff was dominated by two or three diatom species. The massive input of fertilizer into the system has resulted in the displacement of diatoms by blue-green algae. Nitrogen may become more limited in tropical lakes with extensive blue-green fixation.

Each organism has an optimal N:P, which is dependent upon the physiological availability of each of the two elements. In similar fashion, ascending trophic levels employ highly specific enzymes in the digestion of their food. Any shift in the amino acid profile could render a food source useless, severing the food chain.

At this point Lake Victoria is a "runaway enviro-chemical train". Secchi disc visibility has dropped to 0.2 meters and turbidity has increased by three orders of magnitude (Kaufman 1991). The inherent stability of a diverse ecosystem has been exchanged for a few simplified processes and with a crumbling food web ecosystem stability is decreasing. While it is possible to extrapolate data and make short-range predictions about an individual element, it is generally not useful to do so because the large number and complexity of variables make correct, realistic, quantitative predictions virtually impossible.

3. Euthrophication

Euthrophication is the most serious threat to the Lake Victoria ichthyofauna. The process is a self-complicating one as increased turbidity implies increased sedimentation fuelling the biological oxygen demand. Decomposition consumes oxygen until there is no oxygen left. Biological oxygen demand in Lake Victoria is such that there is no oxygen left.

The lake's bed reveals a pattern of variably cyclic, seasonal anoxic episodes. Further evidence is provided by the fish themselves. Many species exhibit an efficiency upgrade in the form of ultra-fine gill structure.

4. Anoxia/Stratification

Initially, the Nile Perch was believed to have a higher oxygen requirement than its cichlid prey. This led to the predicted existence of a low oxygen refuge layer immediately atop the oxycline. Confirmation of this refugium has been provided by sonar scan and a camera equipped, remotely operated vehicle. It is now known, from testing the oxygen requirements of Lates retrieved from the lake in 1991, that the perch is capable of surviving with a little as two to three percent dissolved oxygen while the cichlids need only one to two percent. Additionally, the perch has been filmed (in situ), making forays through the low oxygen refugia a short distance into the anoxic zone.

Seasonal and localized anoxia has been well documented throughout the history of the lake, but historically it has been temporary. Now the seasonal winds are insufficient to overcome the severe anoxic stratification. Anoxia has become permanent. While permanent stratification has profound implications of its own, it is a chronic problem by nature and one which is well studied in other, deeper lakes. A more acute problem is the continuing expansion of the eutrophic zone relentlessly squeezing the entire ecosystem closer and closer to the surface.

A physical separation between the lower, anoxic bottom water and the oxygenated upper layer produces a pronounced boundary layer. The fluid dynamics of these two bodies of stratified water allow for vertical fluctuations and tilting of the oxycline. Driven by the wind, sudden, upward shifts suffocate massive schools of fishes which have been found, undecomposed, strewn across the bottom as well as hanging lens-like in mid water.

The permanency of the stratification implies a separation of waters. Nutrients lost to the depths are essentially gone. This has the effect of increasing the loss of trace elements in an already limited system. Fortunately, the native prawn (Caridina nilotica), has been observed functioning in the depths without measurable oxygen. As the only known facultative anaerobe in the lake, this shrimp represents the only organism recovering nutrients from the benthos and therefore is a key species if the lake is ever to recover.

III. **OVERFISHING**

While one Haplochromis and one Labeo species have been over fished in the past, no endemics are being over fished now. Instead, it is the perch which is being over exploited. This is good news for the remaining ichthyofauna and has even sparked discussion of controlled reintroductions. The down side will be the economic loss to those countries harvesting and processing the perch. Unfortunately, the governments of those countries, dependant upon the import capital it provides, are planning for long term, large scale stocking of the perch in order to prop-up the fishery.

IV. **EXOTICS**

1. Lates sp. (Nile Perch)

A. Predator

The Lates present in the lake today keys out to no know Lates species (Kaufman pres. Com.). The numerous introductions of the perch in Kenyan and Ugandan waters were almost certainly of two or more species. The Lates present today is apparently a hybrid. However, it may have evolved phenotypically since entering the lake. This massive, “gape-and-suck” predator is alien to this habitat. The endemic fauna evolved without such a threat. Consequently, instinctive avoidance behavior is poorly developed within the endemic flocks. Lates does exist in other cichlid-dominated lakes. In Lake Tanganyika, for instance, Haplochromines coevolved with Lates, which occupies a top predatory niche.

B. Prey

Haplochromines, in general, are gregarious, opportunistic, precocious, even inquisitive fishes. They do well in captive propagation so well that administrative networking is proving the only challenge to conservation efforts. Aside from an over abundance of progeny.

Haplochromis, like many cichlids genera are typically territorial. This trait, more than any other, has left the cichlids vulnerable to predation. Additionally, all Lake Victorian Haplochromines are sexually dimorphic, maternal mouth-brooders. This reproductive specialization and its associated isolating mechanics (e.g., egg spots), have proven divergence potential, particularly during mate selection. As one might imagine however, mouth-brooding has exacerbated the affects of predation, because when Lates eat the mother it also consumes the next generation.

2. Oreochromis nilotica

A. Competition

Inter-specific competition, when not mutually exclusive, implies a slight variation in niches (Ricklefs, 1993). Indeed, the concepts of the niche and competition are inseparable. Goldschmidt and others have gone one step further to time ecological segregation of a niche to reproductive isolation. Behavioral plasticity facilitates the breakdown of this and other isolations mechanisms in captivity. In situ behavioral observations are inadequate at this point to shed definite light on the situation but it is believed that competition as well as a relatively rigid social structure prevent these isolation breakdowns in nature.

B. Out-breeding/and Genetic Heterogeneity

Hybridization and its results have been observed not only in captivity, but also in the lake, especially with the Tilapiine Oreochromis. Oreochromis collected in Uganda in 1982 are pheno-typically intermediate between the endemic
O. esculentus
and the exotic
O. nilotica
. Personal observations lead me to conclude that this aggressive hybrid is better suited to Lake Victoria today then either of its parent species. Selective forces present in today's lake are quite different from those under which the endemics evolved. Consequently, the most appropriate traits from each parent species are being selected for. The "new and improved"
Orechromis sp
. will presumably become "fixed" as gene pool fluctuations settle out.

REFERENCES

Fryer, G. & T.D. Iles, 1972. The Cichlid Fishes of the Great Lakes of Africa, TFH Pub.

Goldschmidt, T. 1991. Egg Mimics in Haplochromine Cichlids (Pisces, Perciformes) from

Lake Victoria. Ethology 88: 177-190.

Goldschmidt, T., F. Witte, & J. de Visser, 1990. Ecological Segregation of

Zooplanktivorous Haplochromine Species (Pisces: Cichlidae) from Lake Victoria, Oikos 58: 343-355.

Goldschmidt, T., F. Witte, 1990. Reproductive Strategies of Zooplanktivorous

Haplochromine Cichlids (Pisces) from Lake Victoria Before the Nile Perch Boom, Oikos 58: 356-368.

Graham, M.A. 1929. The Victoria Nyanza and its Fisheries, Crown Agent for the Colonies. London.

Greenwood, P.H. 1981. The Haplochromine Fishes of the East African Lakes. Cornell Univ. Press.

Hert, E. 1991. Female Choice Based on Egg-spots in Pseudotropheus aurora. Burgess 1976, a Rock-dwelling Cichlid of Lake Malawi, Africa, and Journal of Fish Biology 38: 951-953.

Hert, E. 1992. Homing and Home-site Fidelity in Rock-dwelling Cichlids (Pisces: Teleostei) of Lake Malawi, Africa, Environmental Biology of Fishes 33: 229-237.

Kaufman, L.S. 1992. Catastrophic Change in Species-Rich Freshwater Ecosystems: The Lessons of East African Cichlid Fishes: Single Ancestor for the Species Flocks in Lake

Victoria, Nature.

Ricklefs, R.E. 1993. The Economy of Nature, W.H. Freeman. New York

Sturmbauer, C. & A. Meyer. 1992. Genetic Divergence, Speciation and Morphological Stasis in a Lineage of African Cichlid Fishers, Nature 358: 578-581.

West-Eberhard, M.J. 1989. Phenotypic Plasticity and the Origins of Diversity, Annu. Rev. Ecol. Syst. 20: 249-278.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas & N. Bouton. 1992. The Destruction of the Endemic Species Flock: Quantitative Data on the Decline of the Haplochromine Cichlids of Lake Victoria, Environmental Biology of Fishes 34: 1-28.

Witte, F. & M.J.P. van Oijen. 1990. Taxonomy Ecology and Fishery of Lake Victoria Haplochromine Trophic Groups, Zoologische Verhandelingen. National Natuurhistorisch Museum, Leiden.

Lates

-Predator

-Prey

Oreochromis

-Competition

-Hybridization