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# UNIQUE OPPORTUNITIES FOR RESEARCH IN THE GREAT LAKES OF CENTRAL AFRICA

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MOST of the tropical fresh water in the world occurs in Africa. In Central Africa there are the ancient and deep Lakes Tanganyika and Nyasa, the more recent natural Lakes Bangweulu and Mweru, the modern hydro-electric dam Lake Kariba, and other smaller yet important bodies of water such as Mweru-wa-Ntipa. All provide numerous problems for hydrobiological research. We have been concerned primarily with fish, since research on these lakes has generally been related to Government fisheries research programmes. The purpose of this article is to direct attention to some research opportunities which we believe to be unique, and also to indicate major problems which require investigation. They are grouped under four major headings; basic productivity, evolution, systematics and population dynamics.

## Basic Productivity

Little is known of many aspects of productivity in the tropics; but it seems from work in tropical seas[1] that a relatively high level of production can persist throughout the year on a small nutrient budget due to rapid successions in the cycle of assimilation, consumption, death or excretion and remineralization. In Lakes Tanganyika and Nyasa where the euphotic zone is generally deep, some areas are highly productive and provide an ideal situation for the investigation of the rate of biochemical processes where light and temperature are not major limiting factors. Little or nothing is known of the influence of bottom muds on the nutrient balance of shallow and deep tropical lakes, while the chemistry of inflows and outflows has never been examined in detail.

The annual cycle of water-levels, and of temperature and oxygen stratification patterns in relation to meteorological conditions, is known for some Central African lakes, and wind-generated seiches have been recorded at the surface and on the thermoclines (internal or temperature seiche) of the deeper lakes. Recent work[2,3] indicates that, in Lakes Tanganyika and Nyasa, water movements associated with internal seiches such as upwelling and turbulence near the thermocline interfaces may be primarily responsible for the supply of nutrients to the euphotic zone. Because of their morphometry and characteristic winds, these two lakes provide ideal subjects for the investigation of internal seiches in large freshwater bodies. Investigation of the form, magnitudes and seasonal variations of the seiches will, however, require very considerable expansion of present hydrographic sampling programmes.

Investigations of the production of the biota of many lakes in this area have only just begun. Investigations of phytoplankton production and the abundance of certain elements of the invertebrate fauna of bottom deposits are being carried out on Lake Kariba sponsored by the Nuffield Foundation, but only limited work in this field has been done on the other great lakes. There is consequently opportunity for extensive investigations of the ecology and production of planktonic and sessile algae, bacteria, invertebrates of the littoral, limnetic and benthic zones and of lake muds; and into the interrelationships of these microscopic elements with the chemical constituents of the water masses and with the vertebrates at the summit of the food chain.

Some phenomena of particular interest to marine biologists occur also in certain of these lakes, where they are reproduced in miniature and readily accessible for examination. Examples are: the patterns of wave and water movements, the diurnal vertical migrations of zooplankton and fish (in Lake Tanganyika, the range of migration often exceeds 100 m), exclusion effects of dense phytoplankton patches on fish and cycles of successive dominance of species in some phytoplankton populations.

Fish production in the great lakes has been examined extensively because of its economic importance. However, relatively very little is known of the biology and physiology—the characteristics of breeding, feeding and growth—of even the commonest and most important fish species. Ecological relationships between economically important fish, predator–prey relationships, fish distribution and migration provide unlimited fields for investigation. In some areas, the fish ecosystems are unexploited and virgin, and unique opportunities still exist to study the ecology, population dynamics and evolution of these ancient and complex faunal communities, a chance which has largely been lost in the widely lamented case of the African terrestrial mammals.

## Evolution

Lakes in the African rift valleys are unusually old. Lake Tanganyika may have existed, in various forms, since the Pliocene, and Lake Nyasa since the lower Pleistocene. With long isolation, this has resulted in large, endemic species flocks of fishes, mostly belonging to the family Cichlidae, and indeed the great majority of fish in these lakes have evolved there. These faunas, and those of some tropical rivers which have even larger numbers of fish species, may be remarkably diverse only in comparison with the relatively impoverished waters of Europe and North America[4]. The great lakes, however, are unique in the predominance of a single family showing in each lake a wide range of adaptive radiation.

There are interesting examples of parallel development in the different lakes, for example, the bizarre scale-eating habit of Tanganyika *Plecodus*, and Nyasa *Corematodus* and *Genyochromis*. It has been suggested that both allopatric and sympatric speciation have been responsible for the adaptive radiation[5,6], but most recent opinion favours the effectiveness of intra-lacustrine geographical barriers in isolating fish populations. The majority of species are shore or bottom dwellers, and in general are confined to particular types of habitat. In these deep lakes the anaerobic hypolimnion commences at depths between 150 and 250 m, and is often found within several hundred metres from shore, especially in Lake Nyasa. This effectively bars migration of shore and bottom dwelling species. Any long movements must be linear, and discontinuous arrangements of habitat types along the shoreline may result in series of completely isolated fish communities. The ecology of littoral fish species has been studied at Nkata Bay on Lake Nyasa, but no comparable work has been published in respect of Lake Tanganyika where the situation is essentially similar. In off-shore and pelagic areas, species flocks in which the closely related members are not spatially isolated present a special problem; most striking of these are the predatory cichlids *Bathybates* in Lake Tanganyika (7 species), and *Rhamphocromis* (8 spp.) and *Diplotaxodon* (12 spp.) in Lake Nyasa. Investigation is required of the biological, ecological and geographical isolating mechanisms which maintain distinctions between closely allied species, and these lakes provide perhaps the finest natural laboratory in this field.

Degree of speciation has also been correlated with the presence or absence of the extremely voracious predators *Hydrocyon* and *Lates*, and evidence has been gathered from several lakes and rivers[7]. The problem of the restrictive effect of predation on speciation has wide ecological implications, and its investigation would be rewarding.

Ecological investigations of these species flocks cannot be divorced from comparative ethological studies, which are also necessary in the field of epigamic behaviour in relation to speciation and genetic isolation. No work of this type has been carried out in these lakes, though the foundation has been established for such a study on a family basis[8]. The Cichlidae are ideal for such investigations in that they show well-marked ritualistic behaviour centred on a mating site; while the small size, circumscribed territories and preference for clear water of many of the rock-dwelling species render them particularly suitable for aquarium investigations.

The remarkable variety of fish in Lakes Nyasa and Tanganyika exemplifies the morphological variation characteristic of the tropics in other phyla, and may provide many clues to the mechanisms controlling differentiation and the rate at which it can proceed.

## Systematics

Our knowledge of fish systematics in the African great lakes is still very incomplete, though a good background has been given by the works of several taxonomists[9–11]. In Lake Tanganyika there are 242 described species and in Lake Nyasa 225, of which 136 and 190 respectively are Cichlidae. The taxonomy of the Lake Tanganyika Cichlidae has recently been revised but the cichlid fauna of Lake Nyasa requires revision, and the very heterogeneous genus *Haplochromis*, to which 112 Nyasan species are assigned, requires redefinition, in which case a number of new genera will have to be erected. The relationships between the faunas of Lake Nyasa and the Zambezi, and of Lake Tanganyika, and the Congo and Nile require investigation. Lake Victoria, grouped rather with the East than the Central African lakes, does not enter this discussion, though from the points of view of cichlid speciation and evolution[12] it is of considerable interest.

In the opinion of certain zoogeographers[13], the African fish fauna evolved in tropical Africa and spread outwards as geomorphological and tectonic events permitted the passage of fish between lake and river systems. In some areas, the same events isolated this fauna, of common phylogenetic origin, in widely differing environments. It is therefore not surprising that considerable morphological variation is found among allopatric populations.

Interesting problems are posed by the polymorphism of some fish species. In Lake Nyasa, three of the commonest species of the rocky shores are polymorphic[6], and striking cases of colour polymorphism have been found in collections from northern shores of Lake Tanganyika. Other cases, perhaps many, are likely to be found on more exhaustive collecting.

Although much progress in fish taxonomy has been made in Central Africa in the past two decades, the adverse consequences of classification by comparison of morphological features, often referring to extremely few specimens, are still felt. These 'morphological species' were described by early systematists who were unable to collect their own material. Some later systematists, although conducting their own collecting expeditions, had limited experience of African ecological conditions and lacked appreciation of the scope of variability within the species unit. Hence the 'discovery' and description of so many 'museum species'. Past experience therefore indicates that systematists should be resident, have facilities to collect and house long series of specimens, and be able also to examine the ecology of each fish in its region and the geomorphological factors affecting its distribution. Correct taxonomic interpretation of all essential specific features, including the range of morphological variation, can then be made.

In invertebrate investigations, very little has been done in any of the lakes except Lake Tanganyika. At present some workers are revising the taxonomy of the Mollusca of Lake Nyasa, the first major study of this group in that Lake since 1896. Much entomological work remains to be done, particularly with regard to *Diptera* and *Coleoptera*[14].

## Population Dynamics

There is a real need for analyses of freshwater fish populations in the major fisheries of tropical Africa to determine rational levels of exploitation. In recent years, several fisheries have suffered economic over-fishing and possibly biological over-fishing due to lack in basic knowledge which could guide management, as well as to increased fishing effort by the indigenous populations who desire to replace the old bartering economy with a cash economy. The introduction of efficient synthetic nets has made this effort more effective. From statistical analyses, theoretical models can be developed which predict changes in the fish stocks at different levels of exploitation. Examination of *Tilapia esculenta* populations in Lake Victoria[15] indicates that the population dynamics of a tropical fish species are amenable to conventional techniques of analysis, but some parameters used in estimates of the dynamics of population structure such as growth, recruitment rate, and natural mortality are influenced here by factors which do not obtain in higher latitudes. For example, there are typically no large seasonal environment changes in the tropics, and fish growth in lakes often continues without marked seasonal growth checks. Similarly, breeding may continue throughout the year. Estimations of 'year classes' or of recruitment frequency will therefore require special treatment. Natural fluctuations in tropical fish populations appear to be more marked than in temperate zones. The ability to recover rapidly after severe loss, and also to take advantage of improved ecological conditions by rapid numerical increase, appears characteristic of some fisheries.

Interactions between fish species themselves probably play a large part in the natural balance of the populations, particularly in predator–prey relationships and density-dependent phenomena. In the benign physical environment of the tropics, the relative importance of predation in natural mortality may be greater than in temperate latitudes. This balance can very easily be upset by selective fishing gear. For example, selective fishing for the important Kariba *Tilapia mossambica* has resulted in great decrease in *Tilapia* stocks, due probably to the relative increase of the predator *Hydrocyon* which feeds on young or small fish and was not selected-against by the gear used. Again, ring-netting in north Lake Tanganyika for Nile perch (*Lates*) and sardine caused the virtual disappearance of the slow-growing predator perch there and a great increase in sardine. These results in both fisheries occurred after about three years' fishing effort.

Not only are there many opportunities for investigations in each lake, but there is also need for comparisons between the lakes. This is particularly pressing in view of the several current proposals for transfer of some fish species to other lakes, such as the plankton feeding *Clupeidae* of Lake Tanganyika to Lake Kariba. The place of the *Clupeidae* in other lakes is taken by various species of plankton feeding *Engraulicypris*, and detailed studies of the ecology of all lacustrine plankton feeders should be undertaken before transfer. Nile perch (*Lates*) have recently been accidentally introduced into Lake Victoria. Transfers of alien fish can have disastrous effects if undertaken in a random way without preparatory study.

## Research Facilities in Central Africa

Some facilities are provided by research branches of Government Departments in Tanzania, Zambia, Rhodesia and Malawi. In Rhodesia there is also the University College in Salisbury, and the Lake Kariba Fisheries Research Institute. The East African Freshwater Fisheries Research Organization, Jinja, Uganda, has also done work on Lake Tanganyika. Research facilities are in general meagre in relation to the vast area and research opportunities. The realization of these opportunities, unique in many respects, will contribute not only to original knowledge but also to the economic development of Central Africa.

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