

Nilotic Lakes of the Western Rift

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Abstract The nilotic lakes associated with the Western Rift are separated from the more southerly lakes Kivu and Tanganyika by the Virunga volcanoes. They include three small lakes in the Kigezi highlands, and three large lakes, George, Edward and Albert in the valley. The small lakes have poor fish faunas (mostly introduced), and have shown major changes in their zooplankton and *Xenopus* populations over the last sixty years.

Lake George is shallow and eutrophic, with a permanent dense phytoplankton dominated by Cyanobacteria, and zooplankton dominated by *Thermocyclops* although some Cladocera are present in smaller numbers. Lake George, in common with Lake Edward, lacks the nilotic genera *Lates* and *Hydrocynus*, but both lakes have many more species of cichlids than Lake Albert.

Lakes Edward and Albert are much deeper than Lake George, and their phytoplankton is not dominated continuously by Cyanobacteria. The zooplankton associations in both lakes show changes between inshore and offshore, which in Lake Albert have been shown to be related to predation by inshore fishes. The littoral associations of invertebrates in these lakes are very diverse, particularly the insects, with, for instance, over 100 species of aquatic Coleoptera recorded from Lake Edward. Some aspects of these lakes have been little studied: the interstitial fauna of Lake Albert includes two species of Syncarida, but is otherwise unknown. Parasites and epibionts, particularly of invertebrates, are, apart from trematodes, poorly known.

1 Introduction

The western branch of the Great Rift Valley contains three major lakes forming a reservoir system stabilising the flow of the White Nile. The lakes are interconnected, and are fed by rivers from smaller lakes in the Kigezi highlands (Fig. 1). Some basic features of this system are given in Table 1. The salient biological features of these lakes are considered in sequence, starting with the highest.

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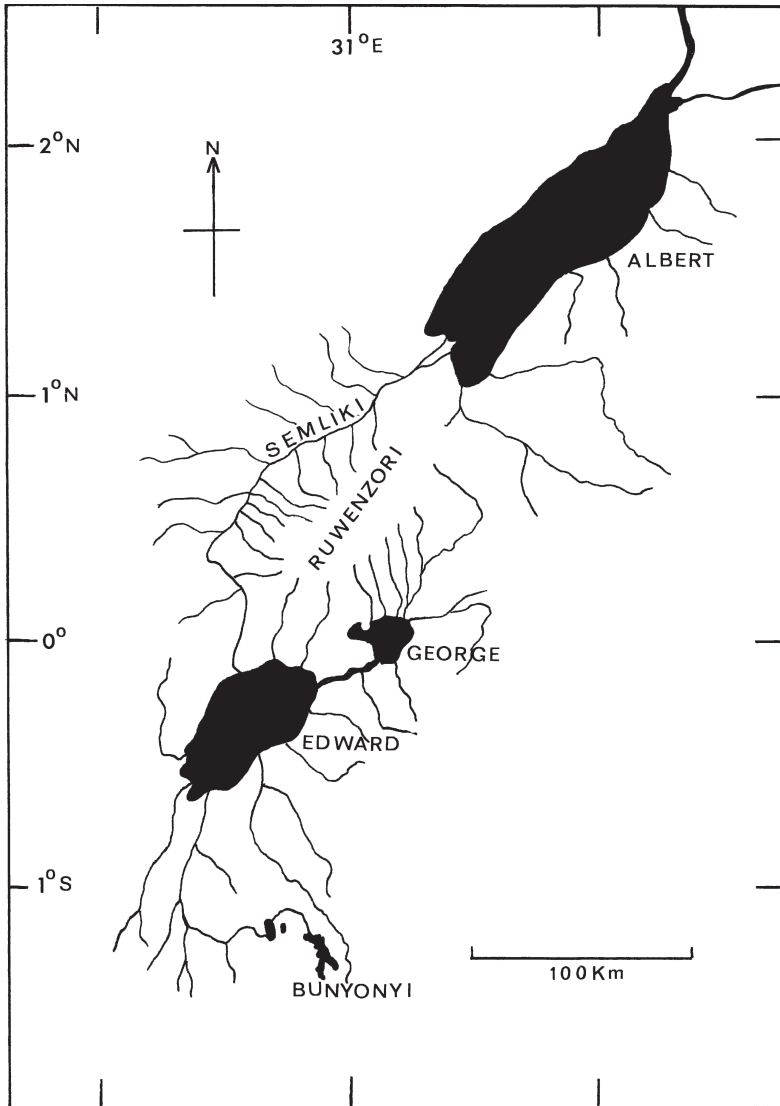


Fig. 1 Map showing connections from Lake Bunyonyi down to Lake Albert

Table 1 Basic data on lakes on the Western Rift branch of the Nile

| Lake | Altitude M | Area km ² | Max. depth M | Conductivity $\mu\text{S cm}^{-1}$ 20°C |
|----------|------------|----------------------|--------------|--|
| Bunyonyi | 1,973 | 56 | 40 | 233–286 |
| Mulehe | 1,806 | 5 | 6 | 252–260 |
| Mutanda | 1,792 | 29 | 56 | 225–235 |
| George | 913 | 250 | 3.5 | 200 |
| Edward | 912 | 2,325 | 117 | 900 |
| Albert | 619 | 5,600 | 58 | 675–735 |

2 Age and Origin

The formation of the Western Rift started in the Miocene, but the present forms of the lakes have much more recent origins. The lakes of the Kigezi highlands were formed when lava flows from the Virunga volcanoes blocked tributaries of the Rutshuru River about 18,000 years B.P.

A lake was present in the Edward basin in the early Pleistocene, and its fauna included nilotic fishes, such as *Lates* and *Hydrocynus*. These were eliminated by volcanic activity about 9,000 B.P. There appears to have been an earlier, temporary, connection with Lake Victoria, possibly via the Katonga valley and other rivers now incorporated into Lake Victoria. This connection was severed by continued uplifting of the western edge of the Victoria Basin, but before this severance a 'super-flock' of cichlids developed and formed the ancestors of the numerous species that now inhabit Lakes Victoria, Edward, George, and possibly even Lake Kivu before it was isolated by the Virunga eruptions (Snoeks, 1994). This implies that the cichlids survived the effects of volcanic activity, while the nilotic fishes did not.

Lake Albert seems to have passed through five phases: an overflowing period about 28,000 to 25,000 B.P., a closed period 25,000 to 18,000, open again 18,000 to 14,000, closed 14,000 to 12,500, and finally open with its present connection to the Nile at about 12,500 B.P. (Hamilton, 1982). The productivity of Lake Albert is thought to have increased after 5,000 B.P. due to increased flow of nutrients via the Semliki River (Hecky & Degens, 1973).

3 Lake Bunyonyi

Worthington (1932) gives a good description of Lake Bunyonyi as it was in 1931. Since that time there have been many changes. The vegetation of Lake Bunyonyi has been studied in detail by Denny (1973). The sheltered bays have extensive floating swamps of *Cyperus papyrus* and *Cladium jamaicense*, but other shores have a much wider range of plants. Particularly notable are the beds of blue flowering *Nymphaea coerulea*. Table 2 lists the species recorded by Denny. One of the interests in this list is the occurrence of particular species at an altitude of 1973 m and the fact that some, such as *Cyperus papyrus* and *Nymphaea coerulea* also occur in the Nile Delta.

In 1931, the phytoplankton was sparse, with *Botryococcus* and a few diatoms (*Synedra*), but by 1961 *Microcystis* and *Anabaenopsis* were more evident, and in 1990 the dominant forms were *Microcystis* and *Ceratium*.

The zooplankton has also shown dramatic changes. In 1931, *Daphnia curvirostris*, *D. laevis*, *Ceriodaphnia reticulata* and *Metadiaptomus aethiopicus* were present, but by 1962 all these species had disappeared, and *Thermocyclops* had increased (Green, 1965a). Samples taken in 1975, 1990 and 2001 have not contained any *Metadiaptomus*, *Daphnia laevis* or *Ceriodaphnia reticulata*. However a single

Table 2 Macrophytes recorded from Lake Bunyonyi, altitude 1973 m (after Denny, 1973)

| Emergent species | Floating-leaved species |
|----------------------------------|------------------------------------|
| <i>Carex pseudocyperus</i> | <i>Lemna minor</i> |
| <i>Cladium jamaicense</i> | <i>Nymphaea caerulea</i> |
| <i>Crassocephalum vitellinum</i> | |
| <i>Cyperus immensus</i> | <i>Potamogeton x bunyonyiensis</i> |
| ..nudicaulis | ..thunbergii |
| ..papyrus | <i>Spirodela polyrhiza</i> |
| <i>Hydrocotyle mannii</i> | |
| ..ranunculoides | |
| <i>Leersia hexandra</i> | |
| <i>Mentha aquatica</i> | |
| <i>Phragmites australis</i> | Submerged species |
| ..mauritanus | <i>Ceratophyllum demersum</i> |
| <i>Polygonum pulchrum</i> | <i>Chara</i> sp. |
| ..salicifolium | <i>Hydrilla verticillata</i> |
| <i>Pycnostachys coerulea</i> | <i>Lagarosiphon</i> sp. |
| <i>Pycnus lanceus</i> | <i>Potamogeton pectinatus</i> |
| <i>Rumex abyssinicus</i> | ..schweinfurthii |
| <i>Scirpus costatus</i> | <i>Utricularia vulgaris</i> |
| <i>Thelypteris squamigera</i> | |
| <i>Typha latifolia</i> | |

specimen of *D. curvirostris* was found in 1990 among thousands of *Moina micrura* and *Thermocyclops*. In 2001, no *Daphnia* were found, in spite of an intensive search (Green, personal observation). The presence of a single *D. curvirostris* in the 1990 samples indicates a very small population persisting somewhere in the lake, perhaps mainly as resting eggs, which hatch at irregular intervals. The hatchlings would provide a mechanism for testing the suitability of the environment. If they survive and reproduce they could produce a significant population, but this does not appear to have happened yet.

When Worthington & Ricardo (1936) studied the vertical migration of zooplankton in Lake Bunyonyi they found that juvenile *Caridina nilotica* formed, numerically, about 0.4% of the mid-lake plankton. The adults were found among vegetation around the margins of the lake. Gordon (1933) described the extraordinary variation in the rostrum of *Caridina* in Lake Bunyonyi. In some individuals the rostrum was shorter than the eye, and lacked either dorsal or ventral teeth. In others the rostrum was several times the length of the eye and bore numerous ventral as well as dorsal teeth. Intermediates between these extremes were also found. Gordon (1933) regarded all the forms as variants of *C. nilotica*. A recent study (Richard & Clark, 2005) has re-described *C. nilotica*, and separates all the Bunyonyi forms from it, describing four new species: *C. bunyonyiensis*, *C. gordonae*, *C. pseudonilotica*, and *C. subventralis*. Some of these species are probably not confined to Lake Bunyonyi, because Green (1965a) found wide variation in the rostrum of *Caridina* in Lake Mutanda resembling the range found by Gordon. The question of the range of variation in *Caridina nilotica* will require the application of molecular methods before it is settled.

Lake Bunyonyi was originally fishless, but in 1919 the small catfish *Clarias carsonii* was introduced, and by 1928 dried fish were being exported from the lake to Kampala. *Oreochromis niloticus* was introduced into the lake in 1928, and various other introductions are listed in the Annual report of the East African Fisheries Research Organisation for 1953. They include *Oreochromis esculentus* and some Lake Victoria '*Haplochromis*'. None of these later introductions produced a sustainable fishery. The latest introduction is the crayfish *Procambarus clarkii*, which is now abundant.

Not least of the changes in Lake Bunyonyi are those found in the clawed toads of the genus *Xenopus* (Tinsley, 1981). In 1925, a sample of 86 *Xenopus* from Lake Bunyonyi contained 85 *X. laevis bunyoniensis* and one *X. wittei*. Other samples taken between 1925 and 1935 contained only *X. laevis bunyoniensis*, but in 1972 only *X. wittei* was found.

In 1931, *Xenopus* was abundant in L. Bunyonyi, and Worthington records it as part of the food chain leading to otters (*Lutra macullicollis* and *Aonyx congica phillipsi*). The former species was abundant in the open lake, while the latter, much larger, species was found in the swamps. Both species are now rare in the lake.

These biological changes have taken place against the background of a permanently stratified lake, with a lack of oxygen below about 7 m from the surface (Denny, 1972). There is some evidence that phosphate has increased in the lake. Talling and Talling (1965) recorded $93 \mu\text{g l}^{-1} \text{PO}_4 \text{P}$ at a depth of 35 m in 1961, while Denny (1972) found $480 \mu\text{g l}^{-1}$ at 30 m and $610 \mu\text{g l}^{-1}$ at 37 m. Eutrophication, caused by the expanding human population, could explain the changes in the phytoplankton, and possibly, the zooplankton, but the changes in the *Xenopus* population may be more related to the retreat, or even extinction of one species in response to invasion by other species. The otters were probably reduced by hunting for their fur.

4 Lake Mulehe

Lake Mulehe is the smallest and shallowest of the Kigezi lakes. Its surface is about 14 m above that of Lake Mutanda. Water drains through a swamp into Lake Mutanda, and this flow is sometimes visible as a blue-green patch on the eastern side of that lake. In 1961, the phytoplankton was dominated by *Melosira*, together with *Synedra*, *Oscillatoria* and *Coelastrum* (J. Talling, personal communication). In 1975, *Melosira* was accompanied by *Microcystis* and *Pediastrum*, and in 1990, the dominant forms were *Microcystis* and *Ceratium*.

The zooplankton showed little change between 1962 and 1990. The only noteworthy event was the disappearance of *Ceriodaphnia reticulata* between 1962 and 1975 (Green, 1976). In 1962, Lake Mulehe had the most productive fishery of the Kigezi lakes. About 30 canoes were operating, and producing good catches of introduced *Oreochromis*. In 1990 only three canoes were operating, and the catches were poor. Carp (*Cyprinus carpio*) have been introduced into the lake, and, according to the local people, flourished for a few years, but are now scarce.

Xenopus population changes in Lake Mulehe parallel those in Lake Bunyonyi. In 1934 all the specimens collected were *X. laevis bunyoniensis*, but in 1975 this species had disappeared and was replaced by two other species: *X. wittei* and *X. vestitus*. These two species can be distinguished by their pigmentation and their differing calls (Kobel et al., 1996). Both were sometimes found in the same trap set in Lake Mulehe, and probably invaded the lake from the nearby mountain ridges, where they occur in small water bodies (Tinsley, 1981).

5 Lake Mutanda

Lake Mutanda is the deepest of the Kigezi lakes. It receives water from the Ruhezaminda River, which drains from the Ruhuma Swamp, which in turn receives the outflow from Lake Bunyonyi. Water also flows from Lake Mulehe through a swamp into Lake Mutanda.

The River Kaku flows out of Lake Mutanda and joins the Rutshuru, which eventually flows into the southern end of Lake Edward.

In 1962 the phytoplankton of Lake Mutanda contained the desmids *Staurastrum* and *Closterium*, together with *Pediastrum* and *Coelastrum*, but in 1990 the dominant form was *Ceratium* accompanied by small amounts of *Microcystis*, and by 2001 *Microcystis* was dominant. These changes are consistent with eutrophication.

The crustacean zooplankton of Lake Mutanda in 1962 was remarkably similar to that of Lake Bunyonyi in 1931 (Green, 1965a). Three species of *Daphnia* were present, together with *Ceriodaphnia reticulata* and *Metadiaptomus aethiopicus*, all of which disappeared between 1962 and 1975 (Green, 1976), reflecting the change in Lake Bunyonyi between 1931 and 1962. These crustaceans have not re-appeared in samples taken in 1990 and 2001. The crustacean zooplankton of both Lakes Bunyonyi and Mutanda have converged to a simplified version, dominated by *Thermocyclops oblongatus* and *Moina micrura*, which is similar to that found in Lake Mulehe in 1962.

Lake Mutanda has also had introductions of various fish, including *Oreochromis* and *Cyprinus* but none has developed into a long-term sustainable fishery. The *Xenopus* population in Lake Mutanda has also changed, from *X. laevis bunyoniensis* in 1934 to *X. vestitus* in 1969, although a single *X. laevis bunyoniensis* was found together with 218 *X. vestitus* in 1975 (Tinsley, 1981). Originally all three lakes were populated by *X. laevis bunyoniensis*, but this species was replaced by *X. wittei* in Lake Bunyonyi, and *X. vestitus* in Lake Mutanda, while both species invaded Lake Mulehe.

6 Lake George

The Western Rift is interrupted by the Virunga volcanoes, separating the drainages to the Congo and the Nile. The first insight of this was gained by Speke (1863) who wrote "I found these hills to be the great turn point of the Central African

watershed". Lake George, a truly equatorial lake, bisected by the equator, was studied intensively by an IBP team between 1966 and 1972. Their results were summarised by Greenwood (1976), based mainly on papers published by the team (e.g. Burgis et al., 1973; Lock, 1973; Viner & Smith, 1973; Ganf, 1974a, b).

The remarkable feature of Lake George is the lack of any marked seasonal change (Ganf & Viner, 1973). During the six years of the IBP study the level did not vary by more than 0.1 m. Beadle (1981) attributed this to the structure of the outlet to the Semliki River from Lake Edward, where rocks form a barrier which acts like a spillway, maintaining a constant lake level. Table 1 shows that the conductivity of Lake George is much lower than that of Lake Edward. This difference is maintained by the slow flow in the 30 km long Kazinga Channel, mainly towards Lake Edward. While the outflow to the Semliki prevents the level from rising, the constant supply of water via streams from the Ruwenzori Mountains prevents the level of Lake George from falling. These streams supply approximately 2.8 times the mean volume of Lake George per year (Viner & Smith, 1973), giving a theoretical retention time of 130 days.

Another unchanging aspect of Lake George is the consistently large population of Cyanobacteria (*Microcystis* and *Anabaenopsis*), which form 70–80% of the phytoplankton. The general lack of seasonality includes solar radiation and the species composition of both phytoplankton and zooplankton. In contrast, diurnal changes are marked. On a typical day the 2.5 m water column starts with a uniform temperature of 25°C. By 14.00 h the top 30 cm can reach up to 35°C. Oxygen concentration in the water column at dawn is near 100% saturation, but by 16.00 h the top 20 cm may reach 230% saturation. The stratification usually breaks down near dusk under the influence of evening breezes. The Cyanobacteria tend to be evenly distributed in the water column at dawn, but by mid-afternoon there is a reduction in the numbers near the surface and an increase near the bottom. The even distribution is restored when the sun goes down.

The zooplankton of Lake George shows no marked seasonal changes, either in composition or abundance. *Thermocyclops crassus* forms about 80% of the zooplankton biomass, while the cladocerans, *Moina micrura*, *Daphnia barbata* and *Ceriodaphnia cornuta* are relatively minor constituents in the open water (Burgis, 1973). Figure 2 compares the standing crop biomass of *T. crassus* in Lake George with that of *Cyclops abyssorum* in a temperate eutrophic lake in Scotland. The relative stability of the Lake George population contrasts strongly with the sharp seasonal peak in Loch Leven.

The horizontal distributions of both phytoplankton and zooplankton are influenced by wind induced water movements. Figure 3 shows that both are most abundant in midlake and show more or less concentric reductions towards the lake margins (Burgis et al., 1973).

The macrophytic vegetation of Lake George was studied in detail by Lock (1973). He listed 53 species from the lake margins and surrounding swamps, but recorded no submerged macrophytes in the main body of the lake. The reduction of light penetration by the dense phytoplankton is thought to be the main factor restricting rooted macrophytes to the margins of the lake. Free floating macrophytes

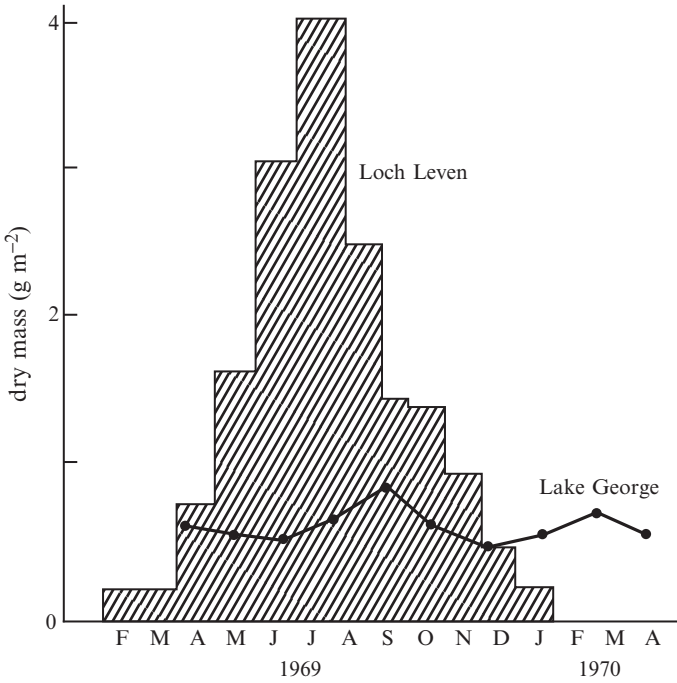


Fig. 2 Standing crop biomass of *Thermocyclops crassus* in Lake George, compared with that of *Cyclops abyssorum* in Loch Leven, Scotland (after Burgis, 1974)

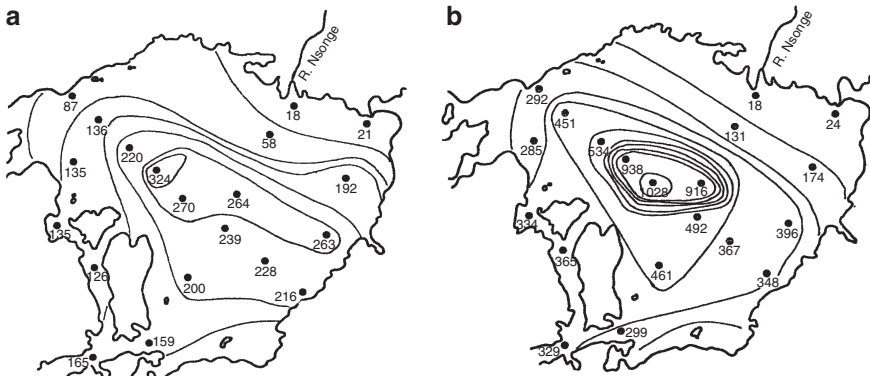


Fig. 3 Biomass density of plankton at 20 sites around Lake George on 9 December 1969. A – phytoplankton as μg chlorophyll a per litre; contours at $50\mu\text{g}$ intervals. B – zooplankton as μg dry mass per litre; contours at $100\mu\text{g}$ intervals (after Burgis et al., 1973)

are not restricted by phytoplankton, and on Lake George *Pistia stratiotes* formed the basis of a plant community that could result in the formation of small floating islands. Clumps of *Pistia* became overgrown by *Hydrocotyle ranunculoides*, and the duckweeds *Lemna* and *Spirodela* grew between the *Pistia* plants. In Hamukungu Bay the community developed further, with the additions of *Enhydra fluctuans*, *Leersia hexandra*, *Ludwigia stolonifera* and *Marsilea minuta*. These floating islands were however very small in comparison to those found on Lake Kioga, where the islands incorporate substantial amounts of Papyrus, and are strong enough to support fishermen.

In recent years *Pistia* has diminished in abundance on Lake George (Mary Morris, personal communication). This may be due in part to heavy metal pollution from the Kasese mines which lie about 9 km north of the lake (Denny et al., 1995). There have also been fluctuations in the hippopotamus population, partly caused by an outbreak of anthrax. These population changes are reflected in variations in erosion of the shoreline, and when populations are low there are increases in the floating grasses along the Kazinga channel.

Along the northern shore of Lake George, where rivers descend from the Rwenzori, there are extensive swamps. The largest of the swamps, with an area over 100 km², has six inflowing rivers, and is dominated by *Cyperus papyrus*, but in the centre has a wet *Ficus* forest, which appears to be floating, with water visible between the trees, when viewed from the air. We know nothing of the microflora and fauna of this area.

The invertebrate fauna of the marginal vegetation has not been examined, but the benthos in the main lake has been studied by Darlington (1977). Most of the lake bottom is covered with a layer of soft organic mud, inhabited by larval Diptera. Two species of *Chaoborus* are the most abundant (McGowan, 1974), while several species of chironomid larvae, including *Procladius brevipetiolatus* and *Chironomus imicola*, are also widespread. Oligochaetes, ostracods and hydracarinae are also present, but have not been identified. Only one mollusc, *Melanooides tuberculata*, is present in the main body of the lake, but along the Kazinga Channel there are twelve additional species, including three lamellibranchs: *Mutela rostrata*, *Corbicula africana* and *Sphaerium victoriae* (Mandahl-Barth, 1954). In shallow water the presence of *Hippopotamus* can limit the numbers of molluscs: Mandahl-Barth found that whenever his dredge was filled with hippopotamus dung it contained no molluscs, or at most a few *Melanooides*.

Table 3 shows the mean densities of benthic invertebrates in midlake and inshore. There is a clear differentiation of the faunas, with ostracods most abundant in midlake, and oligochaetes, hydracarinae, *Tanytus* larvae and *Melanooides* more abundant inshore.

The fishes of Lake George have been studied by Greenwood (1973), Dunn (1975) and Gwahaba (1973, 1975). The overall list of fish species includes 33 species, 21 of which are cichlids. The feeding habits of these cichlids are diverse. The two most important species feed on phytoplankton. By far the most numerous species is *Enterochromis nigripinnis*, with approximately 30,000 fish per hectare (biomass ca 6 g m²). The much larger *Oreochromis niloticus* was less evenly distributed,

Table 3 Lake George: comparison of midlake and inshore benthic invertebrates (data from Darlington, 1977)

| | Mean no./m ² | | % Total biomass | |
|-----------------------------------|-------------------------|---------|-----------------|---------|
| | Midlake | Inshore | Midlake | Inshore |
| <i>Chaoborus</i> , larvae & pupae | 3,825 | 2,136 | 34 | 14 |
| <i>Procladius brevipeiolatus</i> | 1,537 | 4,417 | 17 | 12 |
| <i>Tanytus</i> sp. | – | 1,357 | – | 17 |
| <i>Chironomus imicola</i> | 657 | 289 | 18 | 4 |
| Oligochaetes | 1,234 | 6,177 | 18 | 41 |
| Ostracods | 12,218 | 375 | 9 | <1 |
| <i>Daphnia barbata</i> | 5,889 | 318 | 2 | <1 |
| Copepods | 2,143 | 1,559 | 1 | <1 |
| <i>Melanoides tuberculata</i> | – | 72 | – | 8 |
| Hydracarinae | – | 303 | – | 4 |

with about 75 fish per hectare (biomass 2.5 g) in midlake, and 900 fish per hectare inshore, with a biomass of 12 g m². This inshore biomass formed the basis of a commercial fishery, which flourished during the 1960's, with a factory dedicated to preparation and marketing. As commercial fishing intensified, the size of the fish gradually decreased, but the numbers caught increased, probably because smaller meshed nets were used. This process could not continue indefinitely, and eventually the factory closed, and now lies in ruins.

Other cichlids utilise a range of different foods available in Lake George (Dunn, 1975). For instance: *Yssichromis pappenheimi* preys on zooplankton, *Labrochromis mylodon* preys on molluscs (mainly *Melanoides*), while *Lipochromis taurinus* feeds on the embryos and fry of other cichlids. Perhaps the most interesting of the Lake George cichlids is *Thoracochromis petronius*. This species is almost confined to the Kashaka Crater Bay, where it feeds on insects in a rocky marginal area; a habitat not found elsewhere in the lake.

An occasional feature of the ecology of Lake George is the occurrence of storm driven deoxygenation. This does not affect the whole lake, but can result in substantial mortality of fish. Gwahaba (1973) records a storm in September 1971, which killed about 150,000 *Oreochromis niloticus*, but he estimated at that time this was only 4% of the total biomass of that species. Such fish kills do not occur every year, so the fish populations are not seriously endangered by this form of mortality.

Another potential threat to the fishes in Lake George is the copper mine at Kilembe to the north of the lake. The mine opened in 1959 and closed in 1978, but during that period the tailings gave rise to metal enriched soil deposits which were washed towards Lake George during the wet season. Denny et al. (1995) showed that copper and cobalt were passing into the lake through the swamps along its northern border. The concentrations of these metals were highest in the north in both sediments and plankton. There are some indications that this pollution may be diminishing. Denny et al. found a copper concentration of 749 µg g⁻¹ and cobalt at 89 µg g⁻¹ in sediment near the northern edge of the lake in September 1992.

At the same place in 2000 Lwanga et al. (2003) found copper at $270 \mu\text{g g}^{-1}$ and cobalt at $57 \mu\text{g g}^{-1}$. This may indicate that the pollution washing out from the tailings is diminishing with time since the mine closed in 1978.

Lwanga et al. (2003) also showed that heavy metals were passing through the food chain, and accumulating in fish livers. *Oreochromis leucostictus* had the highest concentration ($189 \mu\text{g g}^{-1}$ dry weight) of copper in its liver, but only $0.2 \mu\text{g g}^{-1}$ dry weight in its flesh (muscle). These figures indicate that the flesh would be safe for a man to eat, but not the liver. A comparison of these data with earlier data from Denny et al. (1995) shows that here again there has been a decrease. In April 1991 the livers of *O. leucostictus* had a copper concentration of $571 \mu\text{g g}^{-1}$ dry weight, while in May 2000 the figure was $189 \mu\text{g g}^{-1}$. This decrease is similar to that in the sediments, and indicates that, as long as the mining does not resume, the pollution will gradually diminish. Recent work by Hartwig et al. (2005) and Owor et al. (2007) shows that most of the contaminants settle soon after entering the lake, and that at present Lake George is highly resilient.

7 Lake Edward

Lake Edward is the deepest of the lakes in the western group of Nile sources. Damas (1937) described it as 'a veritable paradise', and contrasted the abundance of life with the relative poverty he had seen on Lake Kivu, 150 km to the south. The relatively high conductivity (ca $900 \mu\text{s cm}^{-1}$) of Lake Edward is not easy to explain (Lehman, 2002), and is only one of the marked contrasts with Lake George. The conductivity of Lake George is kept low by inflowing streams from the Rwenzori, and a net outflow via the Kazinga Channel to Lake Edward. The sources of the extra ions in Lake Edward have not yet been precisely identified. The saline crater lakes around the northern end of the lake are probably relevant, but underground seepage into the lake has not been established. The elevated conductivity of Lake Edward is not sufficient to induce any marked reduction in biodiversity of either plants or animals.

Verbeke (1957) described three major associations of marginal vegetation around Lake Edward, but also pointed out that variation was considerable. The Lemneto-Pistietum is typical of calm water down to a metre in depth. A typical association would include *Lemna*, *Azolla*, *Pistia*, *Ceratophyllum* and *Utricularia*. Additional forms such as *Jussiaea repens* and *Hydrocotyle ranunculoides*, interweave to bind the association together. In deeper water, around 2 m, the association includes *Ceratophyllum*, *Vallisneria* and *Najas*, and in the deepest vegetated zone *Potamogeton pectinatus* becomes dominant.

The invertebrates associated with the aquatic macrophytes in Lake Edward are considered in detail by Verbeke (1957), and his work should be consulted for a thorough systematic and quantitative account. Some generalisations emerge: Fig. 4 shows the relative abundance of major groups. The shallow water is dominated by carnivorous water beetles (Dytiscidae), but this is also the zone where mosquitoes

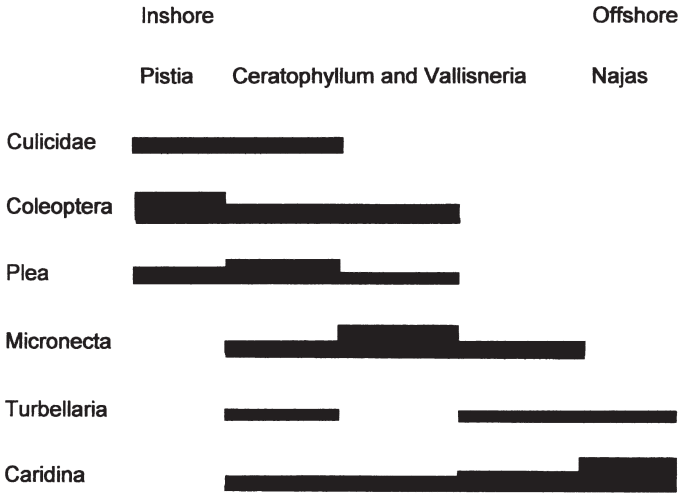


Fig. 4 Zonation of invertebrates in relation to vegetation in shallow water around Lake Edward (based on data from Verbeke, 1957)

(Culicidae) are most abundant. The middle zone has an abundance of *Micronecta*, while the deeper vegetation is populated mainly by *Caridina*. An outstanding feature of the invertebrate associations in the marginal vegetation of Lake Edward is the richness of coleopteran species. Guignot (1957) records 69 species of Haliplidae and Dytiscidae from the lake, while Balfour-Browne (1950) adds 41 species of Palpicornia (Hydrophilidae, etc.), and Brinck (1955–1956) adds five species of Gyrinidae. It is possible that these numbers may increase, because the present records are from a relatively limited number of sites around the lake.

Aquatic Hemiptera are also abundant in Lake Edward: at least 30 species have been recorded (Poisson, 1949). The genera best represented are the notonectid, *Anisops* (6 spp.), and the corixid, *Micronecta* (6 spp.). These are relatively small forms, but also present is the giant *Lethocerus cordofanus* (= *Belostoma nilotica*), ranging up to 80 mm in length.

Mosquito larvae also flourish in the shallow marginal waters. Wolfs (1957) records 13 species, including three of *Anopheles* and five of *Culex*. The larvae of *Taeniorhynchus* have their siphons modified to pierce plant tissues, and the two species found in Lake Edward are well known to be associated with *Pistia stratiotes* (Hopkins, 1952), and the larva of *T. africanus* has also been found attached to the underside of *Lemna* (Connal, 1928–1929). The margins of Lake Edward also have a range of Trichoptera. Jacquemart (1957) lists 15 species, some of which occurred mainly near river outflows. This number of species is lower than that found in Lake Albert (24), but higher than in Lake Kivu (7). The Trichoptera play a small role in the food web of Lake Edward, but they do form part of the diet of several species of fish, such as *Barbus altianus*, *Clarias gariepinus*, *Mormyrus caschive* and *Astatotilapia nubila*. The Ephemeroptera of Lake Edward have not been studied in detail, but Verbeke (1957) found that *Povilla* larvae were important in the diet of several fish species.

Table 4 Ostracoda in Lakes Edward and George (data from Lowndes, 1936; Klie, 1944; Lindroth, 1953 with nomenclature according to Martens, 1984)

| | Edward | George |
|---------------------------------|--------|--------|
| <i>Physocypria capensis</i> | + | – |
| .. <i>bullata</i> | + | – |
| <i>Candonopsis africana</i> | + | – |
| <i>Cypris decaryi</i> | + | – |
| .. <i>latissima</i> | + | + |
| <i>Hemicypris fossulata</i> | + | + |
| <i>Heterocypris congenera</i> | + | – |
| .. <i>obliqua</i> | + | + |
| <i>Strandesia unicolor</i> | + | – |
| <i>Stenocypris stagnalis</i> | + | – |
| .. <i>junodi</i> | + | – |
| <i>Cypridopsis affinis</i> | + | – |
| <i>Sarscypridopsis clavata</i> | + | – |
| .. <i>pygmaea</i> | + | – |
| <i>Zonocypris glabra</i> | + | – |
| <i>Oncocypris worthingtoni</i> | + | + |
| <i>Cyprretta tenuicauda</i> | – | + |
| <i>Centrocypris horrida</i> | – | + |
| <i>Limnocythere michaelsoni</i> | + | – |
| .. <i>coelebs</i> | + | – |

Entering deeper water, beyond the limits of rooted vegetation, there is a marked change in the fauna. Chironomid larvae become important, and the larvae of *Chaoborus anomalus* are numerous, migrating up and down in the water column, and emerging in enormous numbers of adults at regular intervals through the year. Below 40m the fauna diminishes. No molluscs occur below this depth, although a few ostracods range down to 50m. The ostracods of Lake Edward so far recorded are more diverse than those known from Lake George (Table 4) but there is a need for further study of this group in this part of the Nile, particularly in Lake Albert.

The phytoplankton of Lake Edward is much sparser than in Lake George, but still has a high proportion of Cyanobacteria, including *Microcystis flos-aquae*, *Anabaenopsis tanganyicae* and *Lyngbya lagerheimii* (Rich, 1933). A more characteristic feature found by Rich was the abundance of the diatom *Surirella biseriata*. Examination of the sediments of Lake Edward shows that diatoms were much more abundant in the past, but the main species was *Stephanodiscus damasii* (Gasse et al., 1983).

The zooplankton of Lake Edward differs from Lake George in the presence of *Daphnia longispina* and *D. monacha* instead of *D. barbata* (Green, 1971). *Diaphanosoma excisum* and *Ceriodaphnia cornuta* also form significant parts of the cladoceran zooplankton, which shows changes in composition in deeper water (Fig. 5). *Moina micrura* is important inshore, and decreases in deeper water, while

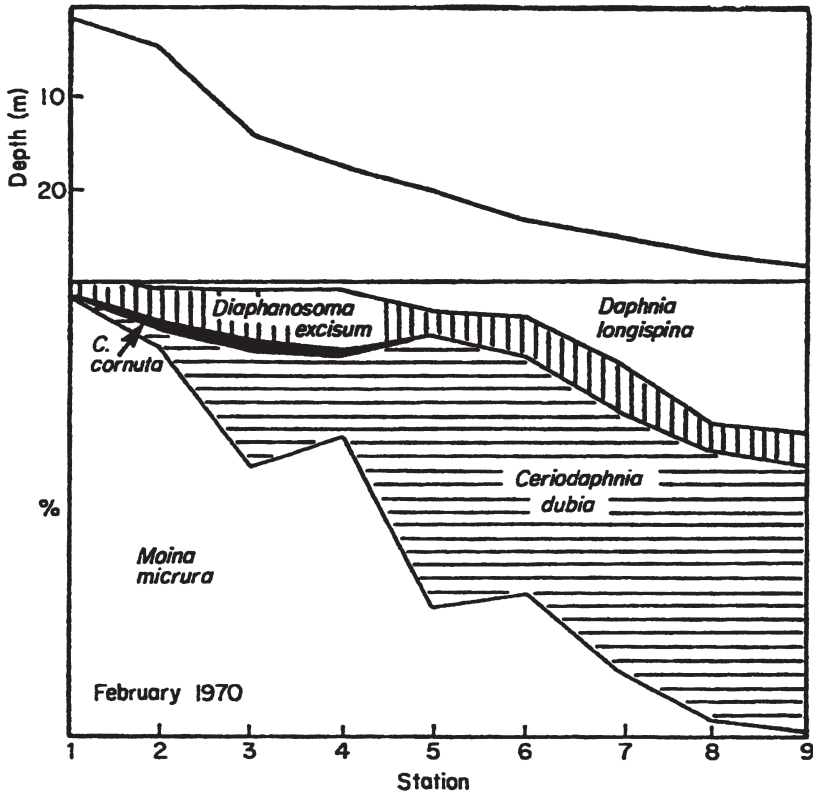


Fig. 5 Variation in the percentage composition of the planktonic Cladocera in Lake Edward in relation to depth (after Green, 1971)

Table 5 Lake Edward: numbers of zooplankters in vertical hauls at four stations from the Uganda shore, 3 November 1962

| Depth (m) | 8.5 | | 19 | | 24.5 | | 29.5 | |
|---------------|--------------------|----|--------------------|------|--------------------|-----|--------------------|-----|
| | No. m ² | % | No. m ² | % | No. m ² | % | No. m ² | % |
| Cladocera | 5,416 | 6 | 20,786 | 30 | 59,586 | 36 | 78,956 | 28 |
| Cyclopoida | 55,712 | 60 | 36,127 | 51 | 67,137 | 40 | 119,837 | 43 |
| Nauplii | 29,637 | 32 | 13,150 | 18.6 | 38,349 | 23 | 77,487 | 28 |
| Rotifera | 1,471 | 2 | 141 | 0.2 | 622 | 0.4 | 1,273 | 0.4 |
| Chaoborus lv. | 0 | | 240 | 0.3 | 467 | 0.3 | 1,951 | 0.7 |

Daphnia longispina and *Ceriodaphnia dubia* become more abundant. The relative importance of the major groups of zooplankton is shown in Table 5. Cyclopoids, mostly *Thermocyclops oblongatus* and *Mesocyclops* spp. are the most abundant group throughout, but the Cladocera steadily increase in numbers in the deeper water. These samples were taken from relatively shallow water, which probably

had oxygen available down to the bottom. Below 40m there is no oxygen in Lake Edward, and in a series of samples taken in March 1964 by Prof. L. Beadle, no Cladocera were found in vertical hauls between 70 and 50m, but in the top 30m *Daphnia longispina*, *D. monacha* and *Ceriodaphnia dubia* were abundant.

The young of many species of fish feed on zooplankton, but in Lake Edward a specialised zooplanktivore has arisen in a genus normally found among vegetation in shallow water. Adults of *Aplocheilichthys pelagicus* live in deep open water, and feed on *Daphnia*, *Ceriodaphnia*, cyclopoids and *Chaoborus* (Worthington, 1932). There has also been a radiation of cichlids in Lake Edward, resulting in about 60 species, one of which, *Yssichromis pappenheimi* (which also extends into Lake George) feeds on zooplankton. The general impression of the cichlid radiation in Lake Edward is of a muted version of the explosive radiation that occurred in Lake Victoria, with, for instance, only one piscivore and only one paedophage.

The non-cichlid fishes of Lake Edward are more remarkable for those missing, rather than those present. The absentees include genera such as *Lates*, *Alestes*, *Citharinus*, and *Hydrocynus*. Some of these have been found as fossils within the Lake Edward catchment, and their extinction has been attributed to volcanic activity about 8,000–10,000 years ago. They were prevented from recolonising the lake from Lake Albert by the waterfalls on the Semliki River. A similar fate eliminated the Nile Crocodile from Lakes Edward and George, but in recent years crocodiles have appeared in both lakes and the Kazinga Channel. It is not known if they made their own way there via the Semliki, following forest clearance along its banks, or whether they were introduced by man.

8 Lake Albert

Lake Albert has a larger surface area than Lake Edward, but is not so deep (cf. Table 1).

The water temperature varies between 27°C and 29°C, and thermal stratification is limited. During the windiest period, from May to August the water is well mixed to the bottom of the lake. In calmer periods some stratification occurs, but without sharp thermoclines (Evans, 1997). During these periods the oxygen in deep water is reduced, but rarely falls to zero: so for much of the year aerobic life is possible in the deepest parts of the lake.

The seasonal and spatial distribution of the phytoplankton in Lake Albert has been studied by Evans (1997). He listed about 75 species, but found the diatoms *Stephanodiscus* (*Cyclostephanos*?) and *Nitzschia* were dominant for most of the year, over most of the lake.

Anabaena flos-aquae showed seasonal and regional peaks of abundance, particularly in the northern half of the lake. Evans considered that phosphate was not limiting, but, based on data provided by Holden (1963), nitrogen deficiency was limiting the growth of the phytoplankton.

The zooplankton of Lake Albert shows great spatial and temporal variation. Figure 6 gives a simplified view of the spatial variation of cladocerans based on annual means. In midlake *Daphnia monacha* is the most abundant cladoceran, but also occurs in smaller numbers at inshore sampling sites. The distribution of this species and the helmeted form, *D. lumholtzi* was considered in detail by Green (1967a). The main conclusion was that inshore fish predation was the major factor governing the distributions of the two forms; in particular the absence of intense predation

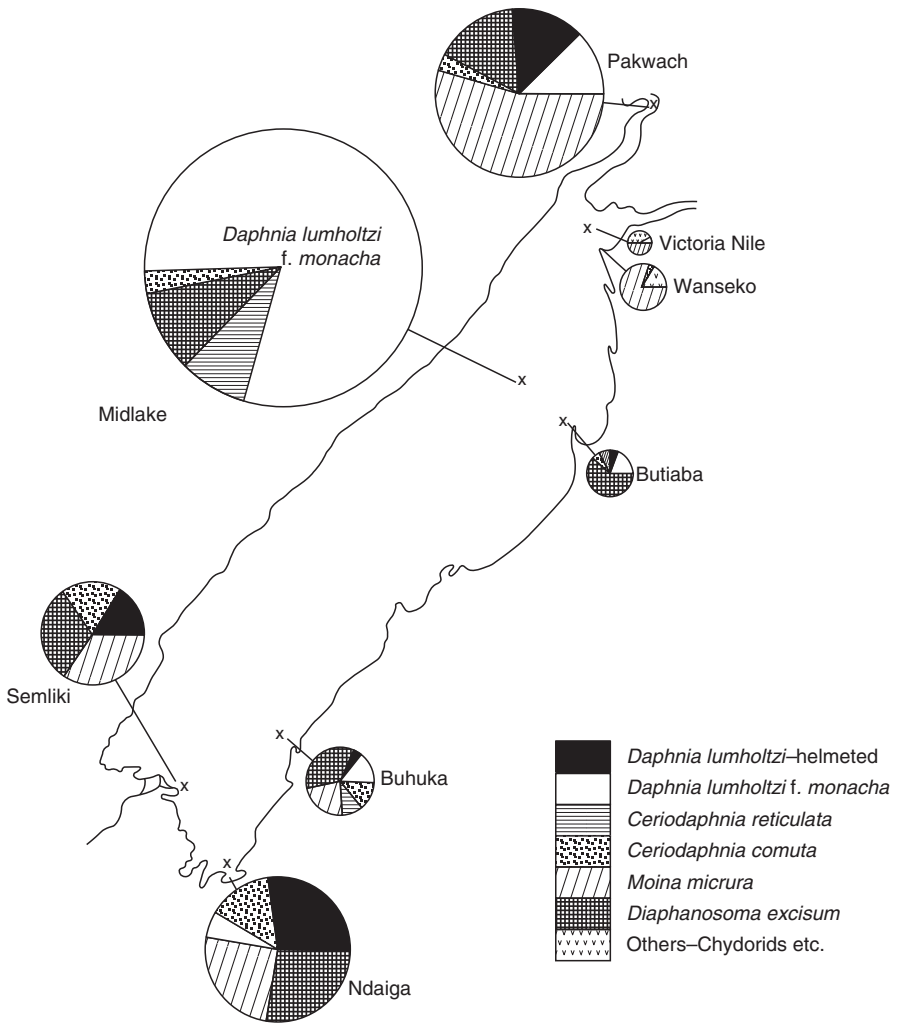


Fig. 6 Total Cladocera and their mean annual percentage composition at eight sites in Lake Albert. The area of each circle is proportional to the number of Cladocera under 1 m² (after Green, 1971)

in midlake allows the development of large numbers of *D. monacha*. The large population of daphnids in midlake helps to explain (by competitive elimination) why there are so few rotifers in the open water. Rotifers are much more abundant inshore, where cladocerans are sparser, as at the mouth of the Semliki River (Green, 1967b). Plankton samples taken along transects of the lake show that the cladoceran zooplankton can be divided into an offshore group: *Daphnia monacha* and *Ceriodaphnia reticulata*, and an inshore group: *Moina micrura* and *Daphnia lumholtzi*. Overlapping these two groups were *Diaphanosoma excisum* and *Ceriodaphnia cornuta*. Lehman et al. (1998) have shown that *Diaphanosoma mongolianum* is also present: this may explain the wide overlap by *Diaphanosoma* of the inshore and offshore groups. Diaptomids are rare in Lake Albert, with few records of *Thermodiaptomus galebi* (Lehman et al., 1998).

In addition to the large population of *Daphnia monacha* in midlake there are even larger numbers of cyclopoid copepods. *Thermocyclops (neglectus)* and *Mesocyclops (aequatorialis and ogunnus)* are both present (Lehman et al., 1998), and, including all the copepodid stages, can number up to 370,000 m⁻². These form the main food of the small cyprinid fish *Mesobola bredoi*, which is endemic to the lake (Howes, 1984). A notable feature of the midlake plankton of Lake Albert is the consistent presence of young *Caridina nilotica*, in numbers ranging up to 15,000 m⁻². Adult *Caridina* are abundant inshore near the outer edges of the vegetated zone, but the larval forms become truly pelagic and occur in large numbers 20 km from the shore. In the same region the larvae of *Chaoborus anomalus* are present, ranging up to 2,000 m⁻².

Caridina forms a major part of the diet of the Tiger Fish, *Hydrocynus forskalii*, in offshore waters, but inshore, particularly in the lagoons, this fish is mainly piscivorous, including at least six species of fish in its diet (Holden, 1970). Its larger relative, *Hydrocynus vittatus* is scarcer, but preys on fish, mainly in the southern shallows of the lake. *Hydrocynus* forms part of a food chain exploited by native fishermen. They use bundles of grass and brushwood to entrap small *Haplochromis*, which act as bait to catch *Hydrocynus*, which in turn are used as live bait on large hooks to catch large *Lates*. In Lake Albert a female *Lates* averages about 27 kg, but can get up to 90 kg, while males average about half the weight of the females.

Lates niloticus is the top predatory fish in Lake Albert, but can fall prey to large crocodiles. Baker (1866) records his men recovering half of a fish, weighing 50 pounds, the other 50 pounds having been bitten off by a crocodile.

Figure 7 presents a simplified food web for Lake Albert. The groups enclosed in boxes each have an estimated number of species; these indicate that a complete food web would be extremely complicated. The molluscs for instance include both gastropods and lamellibranches with their very different feeding methods. The insects are even more complicated, with an estimated 200 species, ranging from mosquito larvae to predatory coleopterans. The diagram shows only a representative sample of 10 species of fish. At present about 46 fish species are known from Lake Albert, and their diets range from phytoplankton through zooplankton, insect larvae, molluscs and other species of fish.

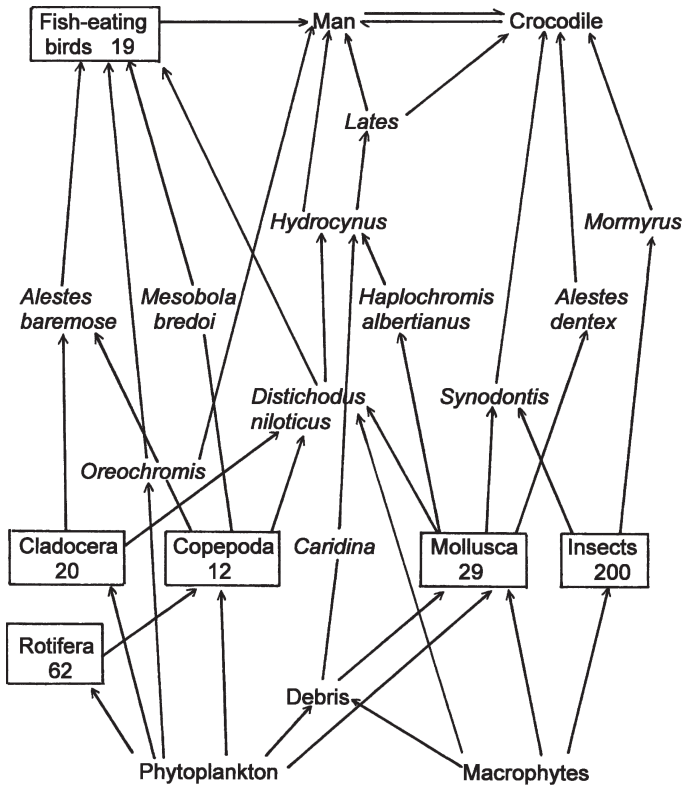


Fig. 7 Simplified food web for Lake Albert, indicating the major links, many minor links are omitted, and only 10 of the 46 species of fish are included. The numbers in boxes estimate the number of species, and, hence, links (original)

Complications in the food web are also introduced by changes in diet with age. This is most spectacularly shown in *Crocodylus niloticus*. Cott (1961) showed that young crocodiles eat a lot of insects, including giant aquatic Hemiptera, predatory Coleoptera, and Odonata (particularly *Brachythemis leucosticta* in Lake Albert). As the crocodile grows it includes larger animals in its diet. When 2–3 m in length it feeds mainly on fish, but also includes molluscs, reptiles, birds and mammals. The last group becomes increasingly important as the crocodile grows beyond 4 m in length. Over all animal groups Cott lists about 200 species as prey of *C. niloticus*, making any food web into an indecipherable tangle.

The benthos of Lake Albert has not been studied in detail, but the data available at present indicate that it may contain more species than Lake Edward. There are more species of molluscs and Trichoptera in Lake Albert, and Guignot (1957) records 92 species of Haliplidae and Dytiscidae in the lake, while Lake Edward has 69.

One feature that may enhance the biodiversity in Lake Albert is the development of sandspits along the eastern shore. These produce sheltered bays, some of which become lagoons, more or less separated from the main body of the lake, providing vegetated areas for fish and amphibians, which in turn provide food for a great diversity of birds. Reptiles are also common in the lagoons. The snakes include *Natriciteres olivacea*, *Grayia smythii* and *Naja melanoleuca*; the last two species frequently feeding on fish. When Worthington studied Lake Albert in 1931, the large turtle *Trionyx triunguis* was quite abundant, but is now rarer. The smaller *Pelusios chapini* (recently separated from *P. subniger*), also occurs in Lake Albert, but it is shy, elusive, and rarely seen. The Nile Monitor lizard, *Varanus niloticus*, swims well, and is common around the lake, acting as predator, scavenger and robber of crocodile nests. The last activity carries some risk, and *Varanus* has been found in crocodile stomachs.

The most widespread and abundant frog around the lagoons is *Dicroglossus occipitalis*, a large species, capable of prodigious leaps in the shallow water, and liable to eat anything that it can swallow, including smaller frogs.

The sandspits also provide a habitat that has been little studied in Lake Albert: the interstitial. A small start was made in 1962 by digging a hole near the waters edge on Kaiso spit. The water accumulating in the hole was passed through a plankton net and two species of Syncarida were found. They were originally described as species of *Parabathynella* (Green, 1964), but, in a detailed revision of the Parabathynellidae, Schminke (1973) placed them in separate, newly created, genera, so that they are now known as *Cteniobathynella bakeri* and *Heterodontobathynella niniana*, but nothing more is known of their biology and distribution. Another indication of the greater diversity of animal species in Lake Albert compared to Lake Edward is found in the Crustacea parasitic on fish. Table 6 compares the two lakes; a part of the difference is probably due to the absence of some hosts from Lake Edward. For instance, *Opistholernaea longa* is specific to fish of the genus *Lates*, and *Lamproglena hemprichii* occurs on *Hydrocynus*. Both these fish hosts are absent from Lake Edward. For a detailed discussion of the biology and distribution of parasitic Crustacea in the inland waters of Africa see Fryer (1968).

Table 6 Parasitic Crustacea in Lakes Albert and Edward (data from Fryer, 1968)

| | Lake Albert | Lake Edward |
|-----------------------------|-------------|-------------|
| <i>Ergasilus kandti</i> | + | – |
| <i>Lamproglena monodi</i> | + | + |
| .. <i>elongata</i> | + | – |
| .. <i>hemprichii</i> | + | – |
| <i>Lernaea barnimiana</i> | + | + |
| <i>Opistholernaea longa</i> | + | – |
| <i>Argulus africanus</i> | – | + |
| .. <i>rhypidiophorus</i> | + | + |
| .. <i>cunningtoni</i> | + | – |
| <i>Dolops ranarum</i> | + | + |

Table 7 Branchiura parasitic on fishes in Lake Albert, and occurrence of the epibiotic peritrich, *Epistylis* (Ep)

| Fish host | <i>Argulus cunningtoni</i> | <i>Argulus rhipidiophorus</i> | <i>Dolops ranarum</i> |
|-----------------------------------|--------------------------------|-----------------------------------|---------------------------|
| <i>Hydrocynus lineatus</i> | – | + | – |
| <i>..forskali</i> | – | + | – |
| <i>Alestes baremose</i> | – | + | – |
| <i>Bagrus bayad</i> | + | + | + |
| <i>..docmak</i> | – | – | + (Ep) |
| <i>Disticodus niloticus</i> | + | – | – |
| <i>Auchenoglanis occidentalis</i> | + | – | + (Ep) |
| <i>Labeo horie</i> | + (Ep) | – | – |
| <i>Synodontis schall</i> | + | + | + |
| <i>Clarias lazera</i> | + | + | + (Ep) |
| <i>Lates niloticus</i> | + (Ep) | + (Ep) | + (Ep) |

A final complication in assessing faunal diversity is the existence of parasites and epibionts. Comparative data on parasites in the lakes of the western rift have not been assembled, although there are scattered records in the literature, and Tinsley (1981) gives a good account of the parasites found in *Xenopus* in the Kigezi lakes.

Peritrich ciliates are often found attached to other organisms, both animals and plants. In Lake Albert a species of *Epistylis* was found attached to both *Argulus* and *Dolops*, which in turn were attached to fish. Table 7 shows that *Argulus* and *Dolops* occur on a wide range of fish, and although *Epistylis* is not restricted by the fish host, it does occur more frequently on *Dolops* than on *Argulus*. The two species of *Argulus* sometimes occur on the same individual fish, together with *Dolops*, and on one large *Lates* all three were found together with the copepod *Lernaea barnimiana* (Fig. 8). This copepod anchors its head into the tissues of the fish, and its elongated body projects outside. A 'necklace' of peritrichs was found around the body of the copepod near the point at which it emerged from the host. This phenomenon has been noted by other workers on parasitic copepods (Cunnington, 1914; Capart, 1944; Fryer, 1956), but the peritrichs were not identified. The specimens from *Lernaea* in Lake Albert were studied alive, and found to be a remarkably large species of *Rhabdostyla*, with a body length of about 500 µm instead of the more usual 50 to 80 µm (Green, 1965b). Examination of other 'necklaces' from other parts of Africa show that other genera, such as *Epistylis*, are often involved, and sometimes more than one species of peritrich can be found on a single parasitic copepod. Similar infestations of peritrichs can also occur on free-living flatworms, annelids, molluscs, crustaceans and insects. If a study was made of the epibionts of invertebrates in Lake Albert one would expect to find at least 40–50 species, and, in view of the findings by Lust (1950) in Germany, a good proportion would occur on the aquatic Coleoptera and Hemiptera, which together number over 100 species in the lake.

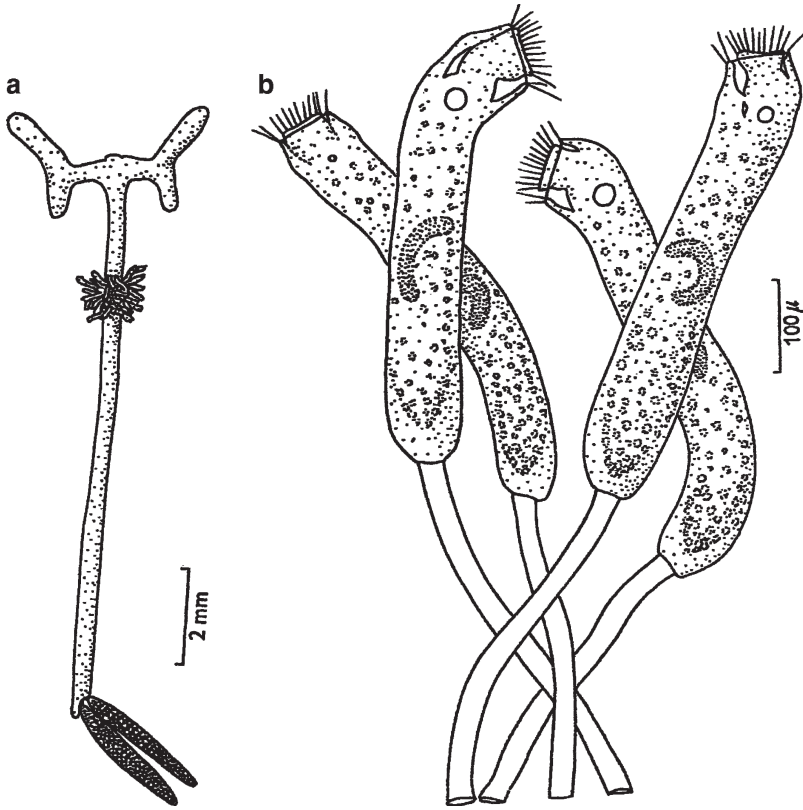


Fig. 8 A, Adult female *Lernaean barnimiana*, a parasite of *Lates niloticus* from Lake Albert; note the 'necklace' of peritrichs. B, The peritrich *Rhabdostyla elongata*, zooids in open feeding condition (after Green, 1965b)

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