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Lake George, Uganda

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This small (250 km²), shallow (mean depth 2.4 m) equatorial lake has an exceptionally constant physicochemical aquatic environment. Two outstanding features are the high relative biomass of the blue-green algae (*ca.* 95 % of the total), and the lake's 24 h rather than seasonal physiological cycle.

In open water areas the animal community is dominated by three herbivorous species feeding on the blue-green algae. Various factors interact to produce a concentric and centripetal pattern of distribution for the plankton biomass, but a centrifugal one for fishes and benthos.

The annual mean phytoplankton standing crop levels may be exceeded, but for short periods only, by those of temperate waters, while zooplankton biomass in some of the latter may even exceed those of Lake George.

Net primary productivity is adequate to withstand the cropping rates and other losses; food is not a limiting factor for the growth of herbivore populations. Day-to-day nutrient demands by the phytoplankton are met almost exclusively by intralacustrine recycling.

Introduction

Lake George, situated on the equator in Uganda at a longitude of 30° 12′ E, is one of the smallest East African Rift Valley lakes (figure 1); it has a surface area of 250 km², and a mean depth of only 2.4 m. Unlike other small lakes in the Rift Valley, Lake George is not an internal drainage basin since it is connected, by the 25 km long Kazinga Channel, to the much larger Lake Edward (of which it was a part until some 3600 years ago; Viner & Smith 1973). Despite this connection, which has important effects on its hydrological stability, Lake George is quite distinct, as a biological unit, from Lake Edward.

One of the Lake's more outstanding features is the constant dominance of its biota and biomass by, on the one hand, vacuolate blue-green algae, and on the other by herbivorous animals, in particular two species of cichlid fishes and two species of cyclopoid copepods. This seemingly obvious correlation between predators and prey posed a problem, however, because blue-green algae were thought to be indigestible by these fishes.

The extremely large populations of blue-green algae, maintained at high levels throughout the year, suggest that Lake George might provide an example of the upper limits of aquatic primary production, and thus a means of studying the features controlling such a situation.

These and several other features were among the many factors that led to the choice of Lake George as a site particularly suitable for investigation during the International Biological Programme (Greenwood & Lund 1973).

When the I.B.P. team began its studies in 1966, very little precise biological research had been carried out on Lake George. By 1973, the team had provided an overall and detailed study of the Lake such that it is now one of the most thoroughly investigated water bodies in the tropical world. The team's researches have been published in several papers (see Biblio-

graphy in this volume) and were summarized in a volume entitled 'A discussion on the biology of an equatorial lake: Lake George, Uganda', published as *Proc. R. Soc. Lond.* B **184**, 227–346 (1973). The account that follows is based principally on those sources.
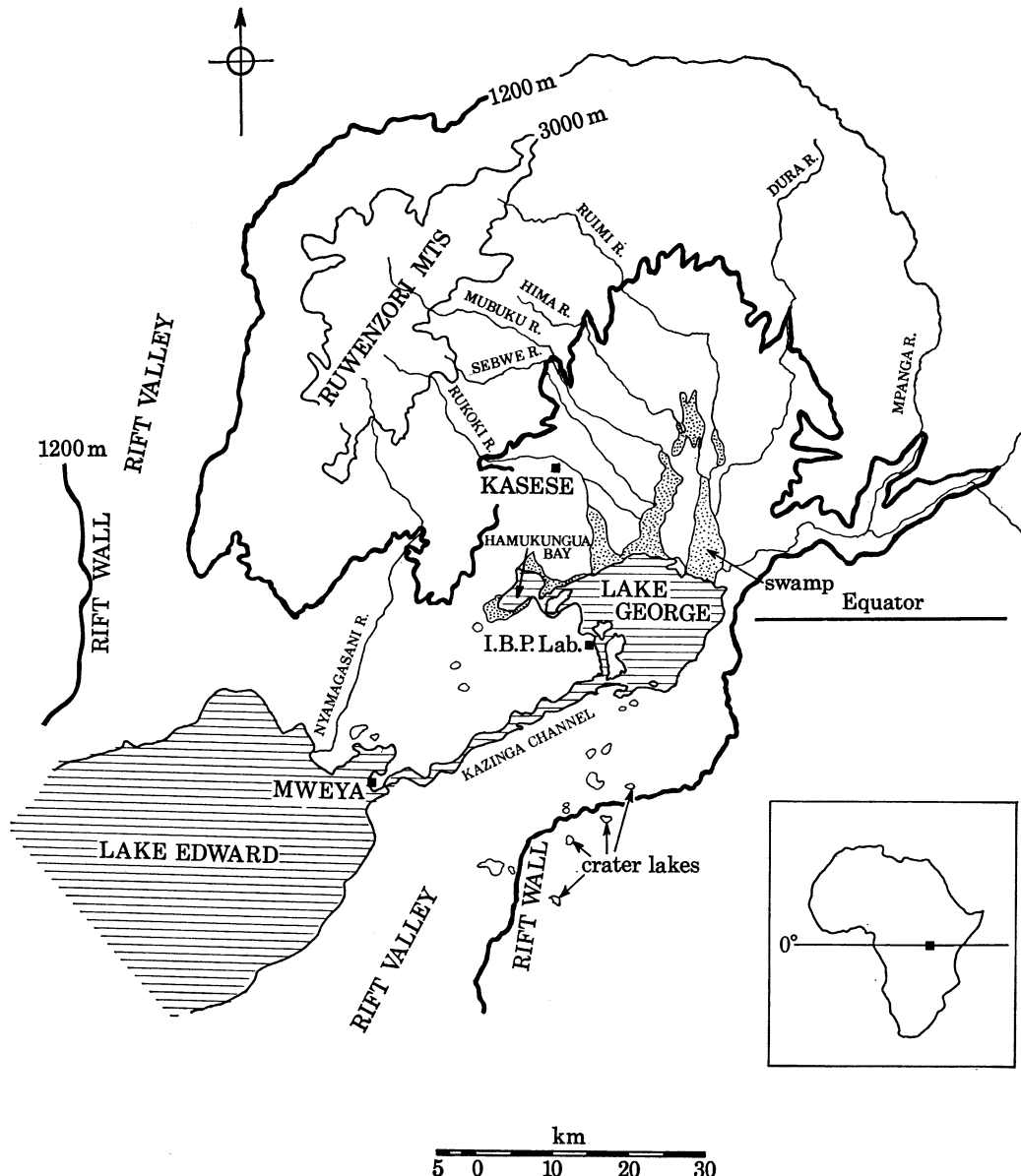

FIGURE 1. Map of Lake George and surrounding area. The inset shows the lake's position in Africa. (After Viner & Smith 1973.)

THE BIOLOGY OF LAKE GEORGE

The equatorial situation of Lake George provides a climatic régime resulting in an exceptionally unvaried physico-chemical aquatic environment, a stability that is further enhanced by local geomorphological features, in particular the close proximity of the 5000 m high Ruwenzori range (see figure 1; also Viner & Smith 1973).

An important effect of these mountains is not only to supply the lake with its principal affluent rivers, but also, because of the vast catchment area involved, the high rainfall on the mountains, and the melt-water from glaciers and snow, to provide both a high run-off and a continuous flow of water through the lake. In effect, the mean flushing rate of these streams is equal to 2.8 times the mean lake volume annually (Viner & Smith 1973). These continuous affluents, although varying in flow at any one time by an order of magnitude, offset the effects of the two annual dry seasons both by maintaining an almost stable lake level and by providing a continuous supply of primary nutrients to the lake. It is calculated that the annual import of NH_4- and NO_3-nitrogen to the lake is 1153 tonnes from the affluent streams but only 277 t from direct rainfall; the figures for PO_4-phosphorus are 182 and 119 t for the two sources respectively.

Since the flow of run-off water varies seasonally, the quantity of nutrients coming into the lake will also show some variation; likewise, nutrients contained in the direct rainfall on the lake surface will also vary, being greatest during the biannual wet seasons (April–May and October–November). Yet, despite these fluctuations there are no correlated changes in the concentration of the phytoplankton. An apparent explanation for this anomaly lies in the importance to the phytoplankton community of nutrients recycled within the lake. On the basis of laboratory measurements for the amount of ammonia and phosphate excreted by the zooplankton, it was calculated that 3300 t of nitrogen and 640 t of phosphorus are provided from this source annually; to this can be added the much smaller quantity of 220 t of ammonia excreted annually by the herbivorous fishes *Tilapia nilotica* and *Haplochromis nigripinnis* (Ganf & Viner 1973; Ganf & Blažka 1974). These totals are well in excess of those derived from rainfall and run-off inflow, and seem to meet the day-to-day requirements of the phytoplankton.

It is the opinion of Ganf & Viner (1973) that if such recycling were halted, the ecological stability of the lake would be upset to the point where the size of the phytoplankton community would be much more closely governed by the inflow of nutrients from outside the lake. The contribution of nutrients released as decomposition products from the thick bottom sediments of the lake is relatively insignificant. The upper 5 cm of these sediments are frequently disturbed by water movements, and ammonia and phosphate originating there are readily transported to the overlying water. However, as compared with concentrations of these substances at depths between 5 and 15 cm, those in the upper layer are extremely low (figure 2) and are proportionately similar to those in the algae. This implies that little decomposition takes place in the upper 5 cm and, since the concentrations of ammonia and phosphate fall off at depths below 15 cm, the principal zone of decomposition in the sediments is between those depths (Ganf & Viner 1973).

Other aspects of nutrient recycling may be considered briefly (see Ganf & Viner 1973 for details). Carbon is recycled via algal respiration, and large quantities of organic carbon (10–15 mg l^{-1}) probably originate from the phytoplankton, either through extracellular excretion or by mechanical loss of mucilage from the colonial blue-green algae. Dissolved organic nitrogen is also found in some quantity (0.5–0.8 mg l^{-1}), and probably originates in the same way. Ammonia may be released as a result of algae below the euphotic zone having excess amounts of oxidized nitrogen relative to the amount of photosynthetically fixed carbon skeletons available for protein metabolism.

There is considerable indirect evidence that both nitrogen and phosphorus in Lake George are in short supply relative to the potential demands from the phytoplankton. During the day

concentrations of dissolved inorganic phosphate never rise above $2 \ \mu g \ l^{-1}$; nitrite and nitrate nitrogen are usually undetectable (Ganf & Viner 1973). Thus it seems likely that supplies of these nutrients are utilized as soon as they become available to the phytoplankton.

In assessing the nutrient budget of the lake particular attention was paid to establishing a water budget, a very necessary datum too when assessing the amount of planktonic material flushed out through the lake's major effluent, the Kazinga Channel (see p. 375). Since the greatest amount of the Lake George biomass is incorporated in the plankton (see table 2), especially the phytoplankton, it is essential to have figures for this loss when estimating production rates.
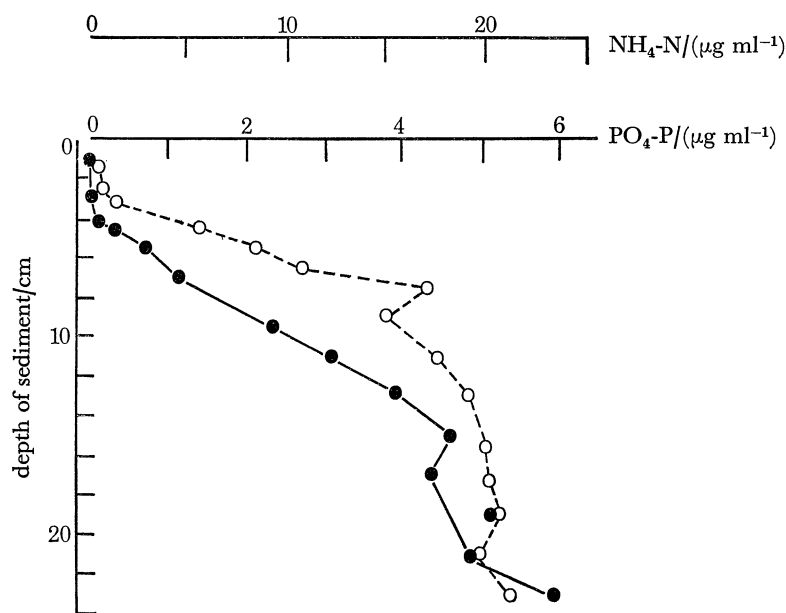

FIGURE 2. Depth distribution of soluble, i.e. water washable, PO_4-phosphorous and NH_3-nitrogen in mud sediment columns taken from the centre of Lake George. The sharp increase in concentration below ca. 5 cm indicates the depth to which turbulence frequently penetrates. O- - -O, NH_4-N; ●——●, PO_4-P. (From Ganf & Viner 1973.)

TABLE 1. ANNUAL WATER BALANCE OF LAKE GEORGE

	$10^6 \ m^3$	inflow proportions	% of total
inflow	1948	1. Ruwenzori mountains	57
rainfall on lake	205	2. Eastern Plateau	38
total to lake	2153		
evaporation from lake	456		
hence discharge down Kazinga Channel	1697		

After Viner & Smith (1973).

An annual water balance for Lake George is given in table 1. The outflow volume based on these figures is equivalent to a flow rate of $53.5 \ m^3 \ s^{-1}$.

The hydrodynamic interrelationships of Lake George, the Kazinga Channel and the various sources of water input are complicated. They may be summarized by saying that the Channel is, in effect, a lake rather than a river, and that because of the slight (1 m) slope between Lakes George and Edward, it plays an important role in damping out sharp fluctuations in flow rate. Consequently Lake George is maintained as a lake rather than an expanded river

which, in view of the large volume of water passing into its basin, it would become if the Channel were not such an efficient governor. As it is, the balance of climatic and hydrological factors maintains the lake level with variations of only ± 0.1 m of its 2.4 m mean depth (and this despite an annual flushing rate of 2.8 times the lake volume; Viner & Smith 1973). Given this flushing rate it was estimated that the minimum amount of material that must be fixed annually by the plankton (95 % algae, see below) is, in tonnes dry mass 73000; carbon 25000; nitrogen 3400; phosphorus 220; chlorophyll a 300. Expressed in another way, the daily fixation must be at a rate of 200, 70, 9.2, 0.6 and 0.8 t for the materials respectively. These are estimates of minimum values because no account is taken of losses through grazing or permanent sedimentation (Viner & Smith 1973).

Figures relating to these latter demands and losses on carbon were made by the team (see Moriarty et al. 1973). The total daily intake of phytoplankton over the whole lake by the principal herbivores was calculated to be 34 mg carbon (C) m^{-2} for the fishes (*Tilapia nilotica* and *Haplochromis nigripinnis*), 504 mg C m^{-2} for *Thermocyclops hyalinus* the principal herbivorous zooplankter, and a total daily ingestion by the benthos of 1 g C m^{-2}.

About 300 mg C m^{-2} d^{-1} of the carbon requirements of the benthos could be supplied from the faeces of the planktonic herbivores; the remaining 700 mg must be derived from the phytoplankton, either directly or through decomposers. Thus, in addition to a daily loss of *ca.* 540 mg C m^{-2} by direct grazing on the phytoplankton, these organisms must also supply 700 mg C m^{-2} d^{-1} for the herbivores, giving a necessary minimum total of 1240 mg C m^{-2} d^{-1} net primary production to meet these demands alone.

Work carried out by members of the I.B.P. team (Moriarty 1973; Moriarty & Moriarty 1973; Moriarty et al. 1973) has shown that, contrary to an earlier opinion (Fish 1952), ingested blue-green algae can be digested and assimilated by herbivorous species of fish. Indeed, these plants are the principal elements in the diet of *T. nilotica* and *H. nigripinnis*, the major constituents in the ichthyomass, of which they together comprise *ca.* 60 %, or 8.3 g (f.m.) m^{-2}. Mr M. P. Tevlin, another team member, showed that copepodites and adults of *Thermocyclops hyalinus* are also able to digest and assimilate blue-green algae, and that, as with the fishes, these algae are the chief constituents of the diet (Tevlin, in Moriarty et al. 1973).

Moriarty's (1973) research on *T. nilotica* and *H. nigripinnis* shows that digestion of the algae takes place in the intestine, but only after acid lysis of the algal cells has occurred in the stomach. The lowest but apparently the optimal pH recorded from the stomach of *T. nilotica* is 1.4; at higher pH values lysis is less efficient, and little digestion occurs when the algae are subjected to acid concentrations at or above pH 2.0. Acid secretion in the stomach of these species follows a diel cycle closely associated with the feeding cycle, beginning at dawn and continuing until sunset, by which time the lowest pH values are reached uniformly throughout the stomach. When feeding starts the stomach is contracted and most of the first food taken passes straight into the intestine; since no acid lysis occurs, the blue-green algae are undigested and are excreted in the faeces, apparently undamaged. Later in the cycle, as the stomach expands and the pH is lowered, increasing numbers of blue-green algae are lysed and subsequently digested.

In laboratory experiments it was shown that *T. nilotica* assimilated an average of *ca.* 43 % of ingested carbon when fed on lake phytoplankton (which contains blue-green algae, diatoms and green algae); under similar conditions *H. nigripinnis* assimilated *ca.* 60 % of ingested carbon. Much higher levels of assimilation are recorded when these fishes are fed with monospecific

cultures of ^{14}C labelled algae. For example, *T. nilotica* can assimilate 70–80 % of ingested carbon derived from the blue-green algae *Microcystis* sp. and *Anabaena* sp., the diatom *Nitzschia* sp., and the green alga *Chlorella* sp.; *Haplochromis nigripinnis* assimilated similar proportions of carbon from *Microcystis* sp. (see Moriarty *et al.* (1973) for a more detailed account and further references).

Using monospecific cultures of labelled *Microcystis*, Tevlin showed that adult and copepodite *Thermocyclops hyalinus* can assimilate *ca.* 35 % of ingested carbon, and the nauplii about 58 %. Since in the lake *T. hyalinus* feed almost exclusively on *Microcystis*, these figures are probably a reasonably close approximation to those obtaining in nature (Moriarty *et al.* 1973).

THE PHYTOPLANKTON

The phytoplankton dominates the biomass (and bioeconomy) of Lake George to a remarkable extent. More than 95 % of the total biomass (equal to a mean standing crop of 48 g C m^{-2}) is derived from the phytoplankton, which in turn comprises some 99 % of the total plankton (including it must be noted the planktonic stages of the dipteran *Chaoborus*).

Dominating the phytoplankton are the blue-green algae (constituting about 80 % of its biomass). The reasons for the success of blue-green algae in Lake George are not easily established, especially when comparisons are made with other shallow lakes, or shallow regions of deeper lakes, in east Africa (see discussion in Burgis *et al.* 1973).

Among the blue-green algae, the large colonial types such as *Microcystis* and *Aphanocapsa* predominate, with filamentous forms like *Anabaenopsis* and *Lyngbya* also well represented (Burgis *et al.* 1973). Diatoms, except for *Synedra berolinensis* and sometimes *Melosira* sp. are poorly represented, a point of particular interest when it is known that other east African lakes are diatom dominated. Two factors may confer greater biological advantage to the heterocystic blue-green algae in Lake George. First there is their ability to fix molecular nitrogen in an environment where concentrations of inorganic nitrogen are very low (< 10 μg NH_3-N l^{-1}). Second, the relative density imparted to these algae by their gas vacuoles may increase the chances of their remaining in the euphotic zone (or regaining entrance to it) under the conditions of minimal turbulence obtaining during the long daily period of thermal stratification in the water column (see Ganf, in Burgis *et al.* 1973).

The pattern of thermal stratification, which has a considerable effect on the primary producers, is a product of interaction between the solar, temperature and wind régimes, while the solar régime itself also effects the patterns of photosynthetic activity in the primary producers.

Incident solar energy varies during the year by only ± 13 % of the daily mean of 1970 J cm^{-2}, and may be considered a constant environmental factor (although individual days can show differences as great as 860 and 2760 J cm^{-2} (Viner & Smith 1973)). The depth distribution of solar energy within the lake is sharply attenuated, with considerable amounts lost through scattering and absorption by the great amount of suspended material (particularly the phytoplankton), and by the pigmentation of the water. Because the phytoplankton has such a profound influence on light penetration even slight changes in phytoplankton population sizes can have significant effects on the depth of the euphotic zone and hence on photosynthesis. A rough indication of light penetration may be gained from the fact that Secchi disk readings ranged from 26 to 46 cm (see also Ganf 1974*a*). This extremely poor light penetration is undoubtedly the major factor in restricting submerged macrophytes to those parts of the lake near and in

river mouths where algal populations are sparse and consequently the water is very clear (see Lock 1973).

The absence of seasonal decreases in solar radiation means that air temperatures are uniformly high throughout the year and, consequently, so is the water temperature. The lower layers of the water column are the most constant thermally, remaining at temperatures of 23–25 °C. The surface water temperature rises progressively during the day, reaching a maximum at about 15h00. Water turbulence during this part of the day is minimal and insufficient to transfer the surface heat gain to the whole column; extreme stratification results. Since the mean peak surface temperature is *ca.* 30 °C (although temperatures of 35 °C have been recorded) a vertical thermal gradient can develop in the water column which, it will be recalled, has an average depth of 2.4 m.

Between 17h00 and 19h00 the surface waters cool and turbulence is created by the consequent convection currents and by wind action. On most days the column is thus completely mixed, becoming isothermal during the night when the net heat gain of the day is, on average, lost. A heat budget for Lake George has been calculated, and gives an energy intake of $26 \text{ kJ cm}^{-2} \text{ d}^{-1}$.

At dawn (07h00) the phytoplankton is uniformly distributed in the water column, but with the onset of thermal stratification (*ca.* 10h00) it tends to sink; by about 16h00 the highest algal concentrations are found below the euphotic zone. Redistribution occurs after sunset (*ca.* 19h00) when stratification begins to break down. Ganf (in Burgis *et al.* 1973) has suggested that the uniform vertical distribution of phytoplankton during isothermal periods is due to turbulence in the water column, but that during periods of stratification the distribution is a function of an organism's excess density. The buoyancy, for example, of diatoms and algae other than blue-greens is such that they would sink during periods of minimal turbulence. The relative density of gas-vacuolated blue-green algae, however, is such that under these conditions there is both an increased probability of their remaining in the euphotic zone and of their reentering it once they have passed below it. Diatoms and other algae would have to await the return of turbulence to be carried back into the euphotic zone.

The probability that blue-green algae spend relatively longer periods in the euphotic zone than do other algae, and their ability to survive periods of low oxygen and nutrient availability may be critical factors in accounting for their dominance in Lake George.

The depth and the turbulence cycles of Lake George result in an accumulation of settled but viable phytoplankton in the superficial sediments of the lake. When these sediments are stirred into the water, as happens during strong winds, the algae are resuspended. Samples taken in the water column on such occasions show no significant increase of chlorophytes and diatoms, but the numbers of *Microcystis* and other blue-green algae show a two- to sevenfold increase. Furthermore, most of the blue-greens are still viable, although their relative viability decreases noticeably with their depth in the sediments.

The amount of algal material added to the water column from the sediments, and its viability, depends, of course, on the depth to which the sediments are disturbed. Stirring to a depth of only 8 cm (a not uncommon occurrence) will double the standing crop of algae in the water (Viner & Smith 1973; Burgis *et al.* 1973). The blue-green algae of the mud, particularly those in the upper 10 cm, must therefore be considered as an integral part of the column metabolism.

Diurnal and longer term oscillations in phytoplankton biomass show marked fluctuations, but there is an overall stability at the level of *ca.* 30 g C m^{-2} (see figure 3; also discussion in Ganf & Viner 1973).

The team's researches indicate that short-term variations have a greater influence on the ecological stability of Lake George than do any seasonal trends.

Particularly important factors affecting the positive or negative value to be attached to the specific rate of community increase during any 24 h period are the climatic events of the previous 24 h. Very slight changes can result in negative production rates (see table 2, in Ganf & Viner 1973). For example, wind-induced turbulence has a pronounced influence on the concentration of chlorophyll a in the water column and thus upon the minimum vertical extinction coefficient of photosynthetically active sunlight. In other words, the magnitude of net production is not simply a function of daily fluctuations in solar radiation, but is related also to the mixing régime of the water column.
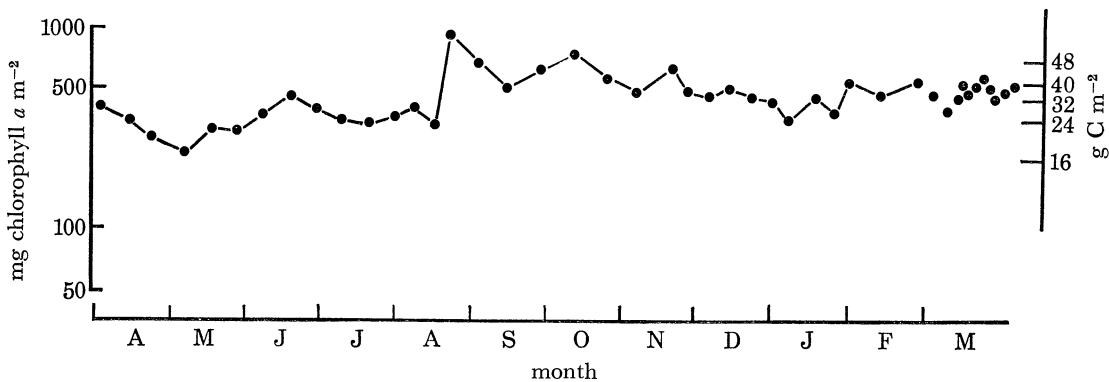

FIGURE 3. Seasonal variation in the phytoplankton biomass; sampling frequency 10 days April to February, but reduced to 2 days February to March. Each point represents the mean of twenty sites weighted for depth and area. Biomass is given as chlorophyll a (left) or carbon (right). (After Ganf & Viner 1973.)

On a lake-wide basis the horizontal distribution of phytoplankton shows a clearly concentric pattern, with the greatest concentration of biomass near the lake centre, and very much lower densities near the shore, particularly in the region of the two major affluent rivers. For instance, on one day the phytoplankton density (measured as grams of chlorophyll a per litre) was 324 near lake centre, only 18–21 near the rivers, and from 87 to 216 at other shore localities. This pattern shows some seasonal variation in detail and it is affected by the intensity of flow through the lake, but no matter how great the distortion, the biomass is always highest near the centre (see figures 13 and 14 in Burgis et al. 1973).

Probably the most important factor in bringing about this concentric distribution in non-motile organisms is the pattern of wind-induced water movement in the shallow, near circular lake basin (see Viner & Smith 1973). Another factor probably reinforcing this primary and physical one is the greater predation pressure on the phytoplankton in regions near the lake edge (see below, p. 385).

A similar concentric pattern is seen in the distribution of the zooplankton (Burgis et al. 1973; Burgis 1974). Despite the motility of the zooplankters, these small organisms offer but slight resistance to water currents, and as they contribute substantially to the diet of many fishes, the same two factors as affect the phytoplankton are operational here as well.

The zooplankton

The zooplankton community is dominated by two species of cyclopoid copepods, *Thermocyclops hyalinus* and *Mesocyclops leuckarti*, the former species providing up to 68 % of the total crustacean biomass (Burgis 1974, in which figures given in Burgis *et al.* 1973, are corrected). Three species of *Cladocera* are found in the open waters, but occur in relatively very low numbers.

Adults and copepodites of cyclopoid copepods are raptorial feeders and thus are better able, than are filter feeders, to utilize the large elements of the phytoplankton which predominate in Lake George. The cyclopoid nauplii, however, are filter feeders and it is possible that population sizes of *Thermocyclops* and *Mesocyclops* are limited by this fact; that is, food supplies are a limiting factor for the nauplii but not for other developmental stages. There may also be heavier predation on the nauplii by the young instars of the dipteran *Chaoborus*, and by *Mesocyclops leuckarti*. The scarcity of suitably sized algal particles may partly explain why the other herbivorous zooplankters (all small filter feeders) are not more abundant in the lake (Burgis *et al.* 1973).

A characteristic feature of the crustacean zooplankton in Lake George is the small size of its constituent individuals; the largest cladoceran, *Daphnia barbata* is little more than 1 mm in length. This phenomenon may be, as Hrbáček (1962) suggested, a consequence of the heavy predation pressure on large individuals (Burgis *et al.* 1973). Certainly zooplankton forms the major element in the diet of most young fishes, in individuals of at least one fish species throughout their life span, and in the diet of larval *Chaoborus*. Larval *Chaoborus* are a peculiar element in the zooplankton because, although functionally planktonic predators, the insects are also a major constituent of the benthic biomass; third and fourth instar larvae bury into suitable substrates by day, and emerge into the water column by night to feed.

The annual mean standing crop of all Crustacea in the zooplankton has been calculated (for 1969–70) as 828 mg (d.m.) or 364 mg C m^{-2}, and that of the dominant *T. hyalinus* as 559 mg (d.m.) or 246 mg C m^{-2}. The annual mean production of this species is estimated at 44 mg, or 19.6 mg C m^{-2} d^{-1}. This figure, together with the annual mean biomass, suggests that given a steady-state population, about 8 % of the *T. hyalinus* biomass is produced, and lost, each day.

Distribution of the animal biomass

No clear-cut pattern of horizontal distribution can be determined for the zoobenthos as a whole (see figure 4). As this figure shows, some elements have a high biomass in mid-lake, others inshore and yet others have their greatest biomass in the intermediate zones of the lake. These various patterns are probably to be correlated with the distribution of the different substrate types, and the ecological requirements of particular benthic organisms. The open waters of the central lake region have a soft, unstable and largely deoxygenated mud bottom; inshore substrates are firmer and more varied. The distribution of chironomid insect larvae, for instance, may reflect these substrate difference since once the short-lived initial planktonic phase is passed, the larvae would have difficulty in settling successfully on the unstable mud of the mid-lake region.

A concentric horizontal distribution is apparent in the figures obtained for the ichthyomass, but here the higher figures occur inshore, possibly a reflection of the greater variety of microhabitats in those regions and of the fact that the majority of fish species breed inshore (Burgis *et al.* 1973).
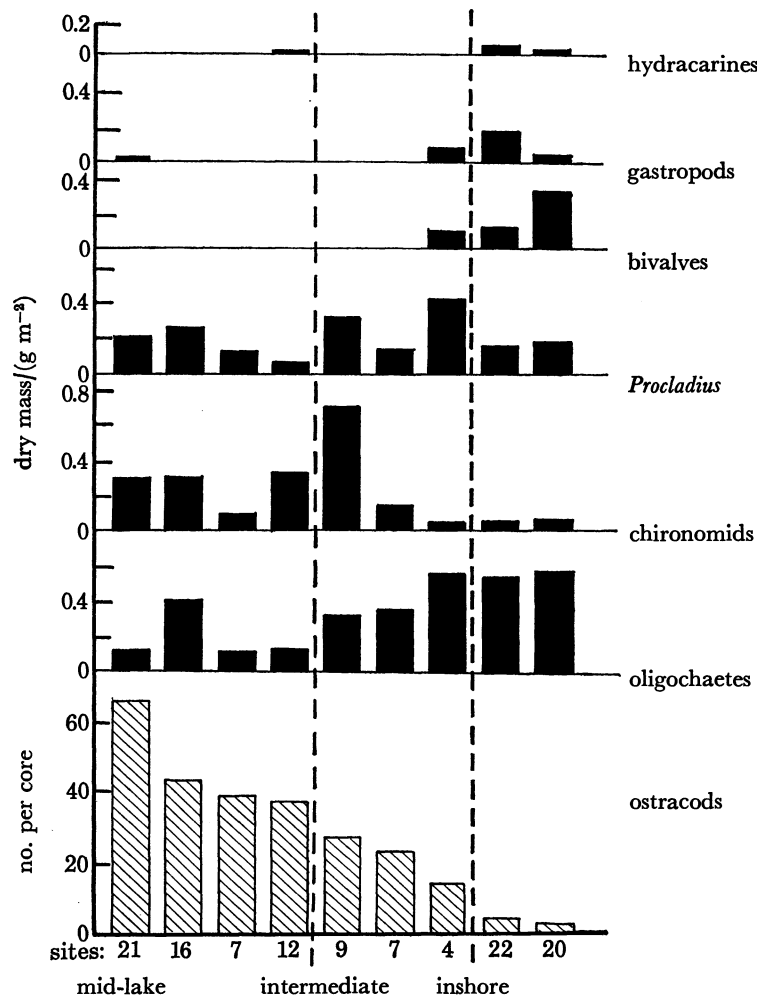
384   P. H. GREENWOOD

FIGURE 4. Biomass of the main components of the benthic mud fauna at nine sites in Lake George
(site numbers given on horizontal axis). (From Burgis *et al.* 1973.)

The populations of the fishes (expressed as 10^3 individuals per hectare), however, show an exceptional area in the overall pattern, because the lowest density (13×10^3 fish ha^{-1}) is found in the northeastern region of the lake where the river Nsonge enters.

The increased variety of inshore substrates and the associated diversification of its benthos provide a trophically more varied area than does the mid-lake region. For this reason it is not surprising to find a greater diversity of fish species close inshore than in mid-lake.

THE FISHES OF LAKE GEORGE

Both ecologically and in terms of biomass the fish fauna (a total of 29 species) is dominated by members of the percoid family Cichlidae, in particular by the fifteen species of the genus *Haplochromis* (Burgis *et al.* 1973; Moriarty *et al.* 1973; Greenwood 1973). Apart from one exceptional species, no *Haplochromis* individuals exceed an adult length of 12 cm, yet of the fishes with lake-wide distribution (10 species, including three with mean adult masses of 0.5 to 10.0 kg) the *Haplochromis* comprise some 59 % of the total ichthyomass (or 9.32 g (f.m.) m^{-2}). The other cichlids of lake-wide distribution, *Tilapia nilotica* and *T. leucosticta*, comprise about

23 % of the ichthyomass (or 2.9 and 0.6 g (f.m.) m^{-2} respectively). The greatest proportion of the total ichthyomass is contributed by the two herbivorous cichlids, *T. nilotica* and *H. nigripinnis* which feed principally on blue-green algae (Burgis *et al.* 1973; Moriarty *et al.* 1973).

The open waters of the lake are populated by three carnivorous *Haplochromis* species in addition to the herbivores mentioned above. One of these species is essentially insectivorous, one is a piscivore feeding mainly on other *Haplochromis*, and one a specialized zooplankton feeder (Burgis *et al.* 1973; Greenwood 1973). Adults of the piscivore reach a length of 25 cm and are the largest *Haplochromis* in the lake.

Inshore, the *Haplochromis* species show a wider range of trophic specializations and include detritus feeders, piscivorous predators, insectivores, mollusc eaters and a species feeding on 'Aufwuchs' (Greenwood 1973; Burgis *et al.* 1973). Most of these species show facultative feeding habits and most show age-related changes in diet. With few exceptions (e.g. the large piscivore), inshore *Haplochromis* species are confined to that region of the lake. All the *Haplochromis* species, irrespective of their feeding habits and distribution, breed in the inshore areas of the lake, and show no marked seasonality in their breeding patterns.

Of the fish species belonging to families other than the Cichlidae, four have a lake-wide distribution and nine are virtually confined to the inshore regions. As adults, three species of the former category are essentially piscivorous predators and one is an insectivore feeding mainly on dipterous larvae and emergents. Four of the inshore species feed almost exclusively on chironomid larvae from the benthos; four others also feed on insect larvae from this source but do include in their diets a greater variety of dipterous larvae. The young of all three species, like the young cichlids, prey on the zooplankton, especially the crustaceans, but the impact of this predation has not been quantified. (For more detailed accounts of food and feeding habits, see Moriarty *et al.* 1973.)

Studies made on the gut contents of certain fishes show that among herbivores there is probably some selection based on the size and perhaps the shape of the food organisms; adult *T. nilotica*, for example, show a marked positive selection for the colonial blue-green alga *Microcystis*, the filamentous blue-green *Lyngbya*, and the colonial diatom *Synedra*. The fry of *Haplochromis nigripinnis* (whose adults are herbivorous) positively select larger elements of the zooplankton such as the cladocerans *Daphnia* and *Moina*. As adults these fishes ingest mainly the large colonial species of blue-green algae; the diatoms ingested are trapped in the mucilaginous sheaths of these algae (Moriarty *et al.* 1973).

Individuals of the principal piscivorous fish species (*Haplochromis squamipinnis*) are mainly insectivorous when < 10 cm long but become progressively more piscivorous until at lengths over 20 cm the diet is entirely of fish and includes the young of *Tilapia* and, more particularly, young of *Haplochromis* (which regrettably, could rarely be identified to species).

The other piscivorous fish predators (*Bagrus docmac*, *Clarias lazera* and *Protopterus aethiopicus*) are all larger than *H. squamipinnis* and thus take larger prey, but *Haplochromis* are still the predominant food items.

Predation on the open-water zoobenthos is mainly through one species, *Haplochromis angustifrons*, which feeds on ostracods and chironomid larvae (Moriarty *et al.* 1973). Inshore there are more fish species feeding on the zoobenthos but the predation pressure is more widely dispersed.

Predation by adult fishes on zooplankton, especially in the mid-lake region, is relatively slight as compared with that by the planktonic larval stages of the dipteran *Chaoborus*. However,

the demands on this food source by juvenile fishes both inshore and in the open waters may be considerably higher, and could affect the size characteristics of the zooplankters (see above, p. 383).

Some preliminary estimates have been made of the ichthyomass in Lake George. The mean for the entire lake is 22.7 g (f.m.) m^{-2}, but there are pronounced differences in the ichthyomass at different localities; for example, at one site on the north shore the mean figure for 5 months in 1971 was 90.5 g (f.m.) m^{-2}, but in centre lake for the same period it was only 6.3 g (f.m.) m^{-2} (Burgis *et al.* 1973).

As many as 4000 t of fish are removed each year by the commercial fishery on the Lake; for the decade 1960–70 the annual catch ranged from 1.7 to 4.1 10^3 t (see figure 11 in Burgis *et al.* 1973; also Gwahaba 1973). Approximately 80 % of this catch is *Tilapia nilotica*. Fish-eating birds (especially pelicans, cormorants and darters) are probably also important predators on the fishes but unfortunately their effect could not be quantified.

The macrophytes

There are over 60 km^2 of swamps associated with the waters of Lake George, especially along the northern shore of the lake; in most swamp areas up to 97 % of the plant biomass is papyrus (*Cyperus papyrus*). Tentative estimates of the plant biomass in these swamps range from 2.5 to 4.5 kg (d.m.) m^{-2} (Thompson, in Burgis *et al.* 1973). Submerged macrophytes (*Ceratophyllum, Nymphaea, Utricularia*) occur only in the mouth and lagoons of the Nsonge river, where the water is clear; emergent vegetation, consisting mainly of the swamp grass *Paspalidium geminatum*, is sparse and of restricted occurrence (Lock 1973). The floating Nile cabbage (*Pistia stratiotes*) is particularly abundant in bays on the western side of the lake; it has a clear-cut seasonal periodicity probably related to its cycle of seasonal reproduction (Thompson, in Burgis *et al.* 1973).

Conclusion

The work of the I.B.P. team has clearly established that the biological processes within Lake George are little affected by seasonal changes. Instead, diurnal changes in solar radiation, temperature, oxygen saturation and pH values have far greater effects on the flora and fauna. The lake can, in fact, be said to have a 24 h physiological cycle rather than the seasonal cycles characteristic of lakes in other latitudes and probably of other lakes in the tropics. Such a diel rhythm is, of course, well established for terrestrial situations in the tropics, but has not been established before in any major aquatic habitat.

TABLE 2. MEAN STANDING CROP BIOMASS IN THE OPEN WATERS OF LAKE GEORGE

depth of the water column = 2.25 m

	g C m^{-2}
phytoplankton	46.800
zooplankton (Crustacea)	0.488
Chaoborus (planktonic and benthic)	0.214
benthos (excluding *Chaoborus*)	0.305
herbivorous fishes	0.885
carnivorous fishes	0.483
total	49.175

The seasonal constancy of the lake is certainly a factor in its sustained productivity. Although the mean levels of phyto- and especially zooplankton biomass (see table 2, and figure 3) in the lake may be equalled or exceeded by peak levels in temperate lakes, those concentrations are maintained for only short periods (see Burgis *et al.* (1973) for comparative figures).

The concentration of phytoplankton in Lake George, even when compared with that in other tropical lakes, is high. For example, the phytoplankton concentration (as measured by chlorophyll *a*) in Lake George ranges from 150 to 350 mg m^{-3}; in off-shore areas of Lake Victoria it rarely exceeds 5 mg m^{-3}, and in shallow bays of that lake it reaches values of 15–20 mg m^{-3}. Higher figures, however, have been recorded from such tropical lakes as Aranguati in Ethiopia (917–2170 mg m^{-3}; Talling, Wood, Prosser & Baxter 1973).

The dominance of the phytoplankton biomass in Lake George is striking: 95 % of the total biomass and 99 % of the plankton biomass. In Lake Maggiore for example the phytoplankton forms 73 % of the total plankton biomass (both on the basis of the annual mean and at peak abundance), and in a reservoir near London it formed 79 % of the annual mean total plankton biomass (Burgis *et al.* 1973).
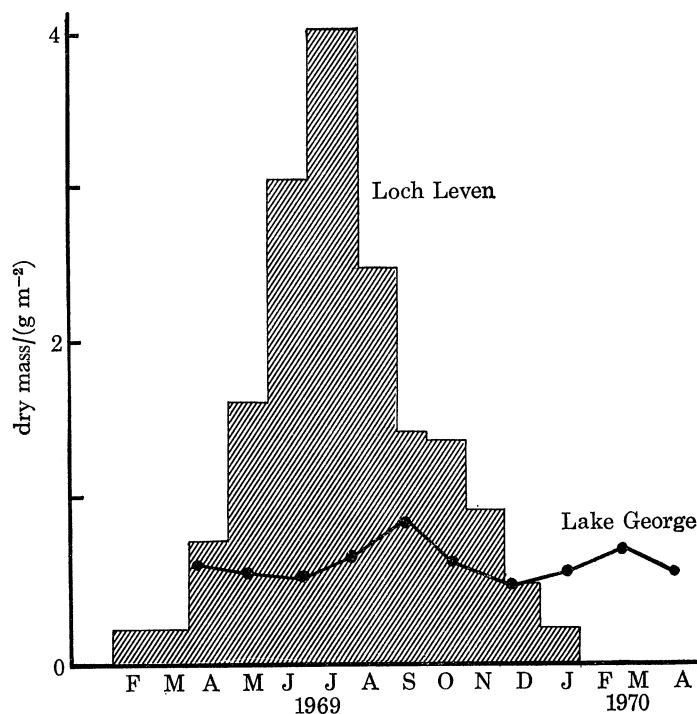

FIGURE 5. The standing crop biomass of *Thermocyclops hyalinus* in Lake George (●—●—●) compared with that of *Cyclops strenuus abyssorum*, the dominant zooplankter in Loch Leven, Scotland. (After Burgis 1974.)

Zooplankton biomass in Lake George is not particularly high even when compared with that in temperate lakes; for example as compared with Loch Leven, the mean standing crop biomass of the dominant Lake George zooplankter (*Thermocyclops hyalinus*) is much below that of its counterpart (*Cyclops strenuus*) in Loch Leven (see figure 5). In Lake Chad, one of the few tropical lakes for which figures are available, the zooplankton biomass (0.25–1.5 g (d.m.) m^{-2}) is comparable with that in Lake George (Burgis *et al.* 1973; Burgis 1974).

The few available figures for benthic biomass suggest that this parameter too is not exceptionally high in Lake George (0.74 g (d.m.) m^{-2}), and it can be lower than in Lake Chad (0.4–3.2 g (d.m.) m^{-2} depending on locality).

The mean ichthyomass, 22.7 g (f.m.) m^{-2}, is comparable with that obtained from sewage lagoons in Britain, and from the large man-made Lake Kariba in Zambia. In certain parts of Lake George, however, much higher figures (up to 100 g (f.m.) m^{-2}) have been obtained. These are comparable with the ichthyomass derived from fish-ponds under intensive cultivation (see Burgis et al. (1973) for details and references).

It is clear that in Lake George most of the photosynthetically fixed energy flow is through the primary producers, and that relatively little is transferred to the higher trophic levels (Ganf & Viner 1973). The team's researches (see especially Moriarty et al. 1973) indicate that the fauna is unlikely to be food-limited; from this point of view the system is inefficient in the transfer of solar energy from the primary to the other trophic levels.

The feedback loops established between the phyto- and zooplankton in nutrient recycling (see above, p. 377) are of considerable importance to the lake's economy. A supply of nutrients is continually maintained for the primary producers, while grazing by certain fish species and by the zooplankton prevents the build-up of excessive algal crops that could deoxygenate the water column overnight (see Ganf & Viner 1973; Ganf 1974 b, c). In this aspect of energy transfer and redistribution the lake can be considered efficient.

The density of chlorophyll a in Lake George suggests that it is an eutrophic lake, yet ambient concentrations of dissolved inorganic nitrogen and phosphorus are very low (< 10 μg NH$_3$-N l^{-1} and < 2 μg PO$_4$-P l^{-1}; Ganf 1974c). However, as Brylinsky & Mann (1973) point out, nutrient dynamics are more relevant to production than are nutrient concentrations. Ganf & Blažka (1974) have shown that the zooplankton excrete more nitrogen and phosphorus annually than enters the lake from other sources; the annual loading of inorganic phosphorus is 1.28 g m^{-2} and that of inorganic nitrogen (NO$_3$+NO$_2$+NH$_3$) is 11.2 g m^{-2}. When these figures are analysed on Vollenweider's scheme for determining eutrophication, Lake George would rate as a highly eutrophic lake. Thus, to quote Ganf (1974c) '...even under conditions of very little human interference, large eutrophic phytoplankton crops are likely to develop, where catchment areas provide substantial quantities of nutrients which may be recycled many times within the lake before passing out'.

It is difficult to pin-point Lake George in any scheme of general lake comparisons (see Ganf & Viner 1973). Superficially, it would seem to be a stable ecosystem, yet the occurrence of such phenomena as sudden but localized fish kills (Ganf & Viner 1973) show that the lake is easily upset by slightly adverse ecological changes. The relative long-term stability of the equatorial climate may thus have allowed the biota to evolve a delicate equilibrium with the environment such that small environmental changes may have extreme effects on the biota. Alternatively, there are many aspects of the lake's ecology that suggest it should be placed high in a continuum of lake types that show progressively reduced ranges of environmental influences.

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Discussion

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Dr Greenwood has emphasized that the most remarkable general feature of this lake is the overall stability of both physicochemical conditions in the water and the rate of production. He indicated that one of the regulators of this stability is the continuation throughout the year of the copious inflows from the high and glaciated Rwenzori Mountains. I should like to add that, though there are in fact considerable seasonal fluctuations of inflow, the water level did not vary by more than 0.1 m during the six years of the I.B.P. project. Even during previous unusually wet seasons the level has never, so far as we know, risen by as much as 1 m, and we have good reason to suppose that conditions in this lake have changed very little over the past fifty years. The level of no other African lake so far investigated is as stable as this, and most are subject to vastly greater seasonal and longer-term fluctuations (5 m and more) with consequent periodic flooding of large areas of land which often cause considerable increases in the rate of production. L. Chad is a notable example. I would think that this apparently unique feature in the hydrology of L. George is mainly due to the nature of the outlet into the R. Semliki from L. Edward, which acts as a hydrological 'buffer'. The water flows out over a rocky barrier

sloping steeply on the far side, thus forming a natural spillway which rapidly compensates for a rise in water level.

I would, however, suggest that the dominant regulator of production is the very regular wind régime. The daily winds stirring the very shallow water to the bottom ensure that diurnal stratification very rarely lasts long enough to alter the generally rather constant and homogeneous conditions in the water. The rare 'fishkills' mentioned by Dr Greenwood are caused by unusual calm periods for several days with consequent continuation of stratification and rapid depletion of oxygen, and catastrophic results when the wind returns.

These generally very stable features of L. George are thus due to a combination of circumstances which are not associated with any other lake so far investigated. I believe that the resulting simplification of the ecosystem has made it a manageable and particularly suitable object for a relatively short-term research project.

Mary J. Burgis (*City of London Polytechnic, Old Castle Street, London E1*)

I think there can be no doubt that without the stimulus of the I.B.P. and the initiative of the U.K.-P.F. Committee there would not have been a detailed freshwater project in equatorial East Africa.

I wish to make one or two points relative to the questions posed by Professor Clapham this morning, particularly since he asked for comments relevant to the future. First, with regard to preliminary preparations: it speaks for itself when I tell you that we spent the first six months of our time in Uganda as building labourers constructing our own laboratory and living quarters. Repetition of such a situation could be avoided by having someone, with authority to act, on the spot during the planning phase. Nothing happens if authority is 6500 km away. However, I cannot stress too strongly that one of the principle reasons why this initial difficulty was not a disaster was the flexibility of the Royal Society in allowing us to make our own decisions as to procedure and expenditure. Had they bound us with red tape and bureaucracy the project would never have got off the ground at all and we were most appreciative of their trust.

My second point concerns communication. One thing I am sure that the I.B.P. has shown most clearly is that ecosystem studies can only be tackled by groups of researchers working cooperatively. However, cooperation depends on communication. Even in a close-knit group such as that at Lake George it is possible for individuals to maintain a remarkable degree of isolation, and many research groups are much less closely bound together. When, as in many cases, members are scattered across several institutions at least one strongly motivated, and often rigorous, coordinator is essential. I am impressed by the degree of coordination achieved within the P.T. section since they appear to have succeeded in not only producing integrated results from numerous parts of one project but also in placing the whole within the context of comparisons on a world-wide basis. In my experience the communication necessary to make such comparisons possible can only be achieved at small working and discussion meetings (national or international) of those actually involved in the work.

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A fragment of Royal Society history: in 1902 Council was informed about the very serious outbreak of sleeping sickness in Uganda. Lord Lister was President, and the matter was referred to the Malaria Committee. The Society also had a Tsetse Fly Committee but at that time, of course, no one knew that sleeping sickness was transmitted by the tsetse fly. Later in 1902 the

Society decided to send a team to Uganda but it proved impossible to find a senior and experienced investigator who was willing to go to Uganda. The Society therefore appointed three young men (G. C. Low, C. Christy and A. Castellani). They established a laboratory in Uganda and, with the assistance of David Bruce, determined for the first time that sleeping sickness was caused by a trypanosome transmitted by tsetse flies. In 1911 the Society appointed a 28-year-old protozoologist to join the team at the Society's laboratory at Mpumu. She was Muriel Robertson, who stayed there until 1914, was one of the first ladies to be elected a Fellow of the Royal Society, and died only two years ago, aged 90. I hope Mary Burgis will feel encouraged by this earlier example of a Royal Society team in Uganda!