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# AFRICA: THE FBA CONNECTION

G. Fryer & J. F. Talling

## 1. Introduction

Since its inception the F.B.A. has had an involvement with African lakes and rivers, which has been maintained throughout its history. Members of its staff have at various times worked on these waters and some of them – including the present Director, R. T. Clarke – spent several of their formative years in Africa. This pattern was set by the first officer-in-charge, R. S. A. Beauchamp, who was later to spend many years on African lakes, and by the first director, E. B. Worthington, who, when appointed, already had considerable experience of these lakes and was familiar with many of their fishes and fisheries. This connection was subsequently maintained by traffic in both directions, some members of the FBA staff later taking appointments in, or making visits to, Africa, others joining the association after service in that continent.

The attractions of African lakes and rivers (Fig. 1) are easy to appreciate. The rivers include some of the world's greatest, including the 6670 km (4145 miles) long Nile, that flows through landscapes as different as swamps and deserts, before discharging into the Mediterranean. Including some of the oldest, largest and deepest lakes of the world, African lakes display an enormous diversity in mode of origin and physiography, present distinctive physical and chemical environments, and often have extremely rich faunas and floras. Lake Victoria, with an area of c. 69 000 km$^2$, is smaller only than Lake Superior, while Tanganyika and Malawi are the world's 7th and 9th largest lakes. Lake Victoria is relatively shallow (maximum depth c. 93 m) but Tanganyika and Malawi, that lie in arms of the Great Rift, are among the deepest of lakes. Tanganyika, with a depth of 1470 m, is second only to Baikal; Malawi, at 704 m, ranks fourth in order of depth. These facts alone, taken in conjunction with their tropical settings, explain some of the peculiarities and diversity of these lakes, such as the presence of enormous oxygenless lower zones

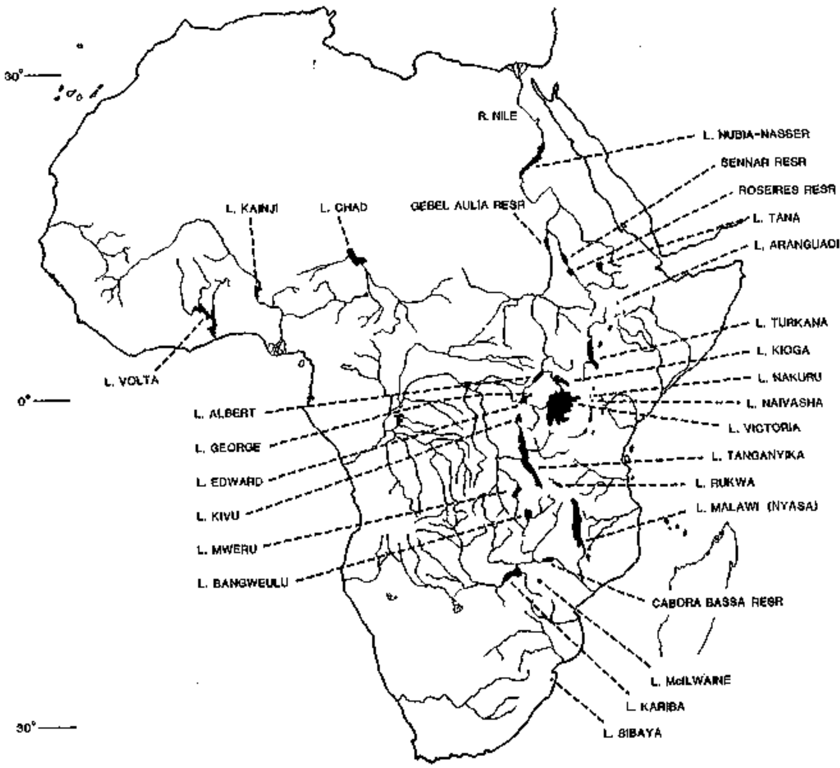


FIG. 1. Distribution of principal lakes and rivers in Africa.

(monimolimnia) in the two rift lakes, but not in Lake Victoria. To this can be added the different geological settings of these and other lakes, that lead to chemical differences in their waters. Their diverse origins range from tectonic folding to rifting, and even damming by the development of volcanoes, and their very varied histories may extend in some cases over several millions of years. No Cumbrian Lake District lake is more than c. 12 000 years old.

African rivers, whence came the ancestors of many of the organisms now found in the lakes, had rich faunas, and from these, in isolation, have evolved large numbers of endemic lacustrine species. Of these, fishes of the family Cichlidae are the most outstanding. Work still in progress suggests that both lakes Victoria and Malawi may each hold from 300 to as many as 500 species of endemic cichlids. This, plus the



presence of many non-cichlid fishes, makes them by far the richest lacustrine fish faunas in the world. Their principal rival is Lake Tanganyika where, although there may be fewer, but still many, species, the end-points of evolution are represented by the most highly differentiated forms. Nor are cichlid fishes the only organisms to display such explosive evolution. The gastropod molluscs, prawns, crabs, copepods, ostracods, non-cichlid fishes and others of Lake Tanganyika in particular make this lake one of the richest repositories of endemic animals in the world, whose attraction to students of evolution is obvious.

The fishes of these lakes, many of which display remarkable habits, are however more than elements in field laboratories of evolution. To the peoples of Africa they are, like the water of the lakes itself, a natural resource of immense importance. Correctly exploited, they represent a renewable source of proteinaceous food of incalculable value, and it was with a view to obtaining information on how exploitation might best be done that much of the early work on African lakes was directed. Such work cannot be restricted to a study of the fishes themselves. It demands knowledge of the hydrological regimes that prevail in the different lakes, that may affect migrations and reproductive cycles; of the algae that form the basis of many food chains; of the chemical environment that determines to a large extent the behaviour of algal populations; and of the invertebrates that eat the algae, or other invertebrates, that ultimately contribute directly or indirectly to the diets of fishes, or are sometimes parasitic on them. It also requires much general information about the fishes: where they live, what they eat, what conditions they can and cannot tolerate, where they spawn, how fast they grow, how long they live, and information of many other kinds. To all these topics past and present members of the FBA staff have contributed. The following sections deal with the background and nature of the work involved.

It is not the intention to produce here a complete bibliography of papers on African material written by FBA staff and by those with close connections with the Association, but merely to give some idea of the scope and range of what has been accomplished. The papers cited, however, cover much of the work or include references to related, uncited, papers. That the work of others is largely uncited is not to be taken as indicating that it is unimportant; the omissions merely reflect the limited objectives of this article.

## 2. General and multidisciplinary surveys

Although it is convenient, in later sections, to separate some components of freshwater science in Africa, a large part in its development was played by general and multidisciplinary surveys. Shortly before he became the first Director of the FBA, E. B. Worthington was influential in several of these. The work of the 1927–8 fisheries survey of Lake Victoria (Graham 1929) extended to aspects of general limnology (e.g. Worthington 1930), and pre-dated the German Sunda Expedition of 1928–9 which is widely regarded as the base-line study of tropical limnology. At this time (1929) another worker soon to be active in the infant FBA, Penelope Jenkin, made a general survey of the Rift Valley lakes of Kenya, with some remarkable results from the alkaline soda lakes (Jenkin 1929, 1932, 1936, 1957).

The most influential single expedition was the Cambridge Expedition to the East African Lakes of 1930–1, led by Worthington. From it emerged not only descriptions of lakes and taxonomic accounts but also quantitatively-based studies of relationships between populations and environmental conditions, in the spirit of the then-young science of ecology. Examples include accounts of the diurnal migrations of zooplankton (Worthington & Ricardo 1936) and, from the late L. C. Beadle, of the physical and chemical characteristics of swamps and lake waters in relation to biological distributions. In later years Beadle was a frequent visitor to the Windermere Laboratory, member of the FBA Council, and author of the best general book on African inland waters.

During 1938–40 a founder member of the FBA staff, R.S.A. Beauchamp, made pioneer studies of the hydrography of the two deepest African lakes, Tanganyika and Nyasa (later Malawi). He established the basic characteristics of persistent thermal stratification and deoxygenation of the long-isolated deeper layers (Beauchamp 1939, 1940, 1953). Another staff-member, Rosemary Lowe, later added biological information for L. Malawi in the course of an investigation of fish biology (Lowe 1952), but it was not until the 1953–5 survey of this lake by the Joint Fisheries Research Organization that information covering hydrography, chemistry, plankton, zoobenthos, and fish could be assembled simultaneously (Jackson, Harding, Iles & Fryer 1963). Two participants in this survey, D. Harding and G. Fryer, had previously gained practical experience as research students at the Windermere Laboratory, to which Fryer later returned as a staff member, after working successively in Malawi, Zambia and Uganda. Harding remained longer in Africa, and provided invaluable information on the hydrography, chemistry and fisheries of Lake Kariba during the crucial early years of impoundment.

A one-time contemporary of Harding and Fryer at Windermere in the early 1950's, J. F. Talling joined a research group at the then University College of Khartoum, the Hydrobiological Research Unit. Led by the late J. Rzóska, a truly incomparable figure in African hydrobiology (Talling 1985a), this group and its successors were responsible for a wide-ranging survey of the hydrobiology of the Nile (Rzóska 1976). Talling's contributions concerned especially the physical and chemical environment and the population dynamics and primary production of phytoplankton. Some of his later work, after joining the FBA staff in 1958, involved surveys of similar scope on lakes in East Africa carried out from bases in Uganda and Ethiopia. Details can be found in Talling (1963, 1965a, b), Talling & Talling (1965), and Baxter et al. (1965).



A new supportive role of the FBA in African limnology developed between 1966 and 1973 as part of its contribution to the International Biological Programme (IBP). The scientific result was a well-integrated and multidisciplinary survey of environmental conditions, populations, and production processes in Lake George, Uganda (summarized in Lund & Greenwood 1973, Greenwood 1976, Burgis 1978). The work was carried out by the Royal Society African Freshwater Biological Team, for which aspects of training, management, and general advice were provided by staff of the FBA. In another IBP-linked study, on L. Chilwa in Malawi, a future member of the FBA staff – M. T. Furse – was active in work on fish populations (Furse et al. 1979). A few years later the FBA supported the final phase of another survey, set up by the Overseas Development Administration, London, of Lake Turkana in Kenya. Although centred upon the fishery, this provided a wealth of other information on one of the most distinctive African lakes (Hopson 1982). Support on a smaller scale has been given by the FBA, ever since its inception, to a variety of initiatives concerning African fresh waters. Material from various African studies has been worked up at Windermere by visiting scientists; Edna Lind's publications on African desmids provide an example. In many instances its library resources have helped to make up for a deficiency of literature in the continent itself. They have made possible some broad surveys of African topics, which still continue.

## 3. The physical environment

Many of the distinctive features of tropical lakes can be traced to the magnitude and time-relations of their energy income. Given the absence of a very pronounced winter-summer alternation, the fundamental characteristic of temperature-density layering might be expected to be less developed and seasonally less regular than in temperate lakes. This was broadly the experience from the expedition surveys of 1927–8 and 1930–1 (e.g. Worthington 1930). However Worthington & Beadle (1932) commented upon the existence of a sharp thermocline in L. Edward, although they were mistaken in supposing it to be the first such tropical record. Later Beauchamp (1939, 1940, 1953) radically extended knowledge of temperature stratification in the very deep tropical lakes Tanganyika and Malawi, showing that it could be indefinitely prolonged although subject to seasonal cycles susceptible to the wind regime.

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It was not until after 1950, when expedition-type work was yielding to locally based effort, that seasonal dynamics of stratification were followed closely over a series of annual cycles. In L. Malawi Harding (in Jackson et al. 1963) initiated records that were continued by other members of the Joint Fisheries Research Organization, and in L. Victoria Talling (1966) extended earlier work by Fish. The Victoria sequences in particular showed how the seasonal temperature-density cycle underlay many other cycles, chemical and biological. A comparison of many African waters (Talling 1969) showed that although latitude is the overall decisive factor for seasonal heat storage, the similar seasonal incidence of vertical mixing in various lakes of East and Central Africa is related to the common influence of the South-East Trade Winds. Another factor affecting thermal stratification is altitude; the stratification conditions in a variety of elevated East African lakes were explored by Talling with collaborators in the university of Addis Ababa (Baxter *et al.* 1965). From this work more intensive and seasonal studies of stratification were developed by the university group.

A finer resolution than the seasonal time-scale is necessary to capture much important physical behaviour. Thus the day-night variation of solar radiation input often generates a diurnal or diel pattern of temperature-density stratification, especially important in productive shallow waters which lack a deeper long-term stratification but are metabolically active. Such a water, the Kavirondo (Winam, Nyanza) Gulf of L. Victoria, attracted the attention of Worthington in 1927 and led to the first detailed study in limnology of a tropical diel cycle (Worthington 1930). Much later, in 1953–6, Talling (1957a) was also drawn into work on diel behaviour in shallow productive waters of the Upper Nile and L. Victoria. In some of these the absorbed solar energy input set up both daily density barriers and photosynthetic reactions in the medium ($+O_2$, $-CO_2$), with interaction between the two. The same was true of patterns of diel change in L. George, studied by the IBP team and shown to form part of the most important and pervasive system of temporal change in this waterbody.

Partly associated with these diel studies, and partly independently, attention has been given to underwater light penetration with its controlling variables (Talling 1957a, b, 1965a; Ganf 1974b) and to wind-induced currents (Viner & Smith 1973). These physical features can determine the light-dependent photosynthesis of phytoplankton and spatial distributions of its biomass. In rivers, water flow by gravity-induced currents is predominant, and was shown by Talling and co-workers to determine the overall space-time aspects of phytoplankton development in the Nile (Prowse & Talling 1958, Talling & Rzóska 1967, Talling 1976b, 1985b).

## 4. The chemical environment

Almost every ecological study on African fresh waters has paid attention to, and often provided new information on, the chemical composition of the medium. Thus Worthington in 1927–8 investigated the pH and 'alkaline reserve' (alkalinity) of lakes Victoria and Albert. However relatively few studies have obtained and systematically compared analyses from a wide variety of African waters, or traced the geochemical or biological origin of the variation encountered, or tried to assess the biological consequences of such variation. In these respects the work of Beadle from the 1930–1 expedition to East African lakes was a landmark. It documented, more clearly than before, the enormous range of ionic content and relative ionic composition of African lakes. Particularly striking were the soda lakes surrounded by precipitated salts, with a peculiar flora and fauna, often rich in quantity but limited in diversity.



The Nile (Talling 1976a, 1980) is an example of a river-system which drains geochemically distinct areas and in which the chemical composition of water changes during its passage downstream. Such change was traced by Talling (1957b) over a distance of some 2500 km between L. Victoria and Khartoum. It included distinctive contributions from tributaries and the extensive Sudd swamps, with implications for water quality even in distant Egypt (Talling 1980). A third source of chemical modification, spatially and seasonally, is the growth of phytoplankton within sectors of longer water-retention. The chemical dynamics of this biological situation were separately studied in the White Nile (Prowse & Talling 1958) and Blue Nile (Talling & Rzóska 1967).

Seasonal and vertical changes in a very different habitat, the offshore waters of L. Victoria, were studied by J. F. and I. B. Talling during a secondment (1960–1) from Windermere to the East African Freshwater Fisheries Laboratory at Jinja, Uganda. Although here the major ions varied very little, fractions of inorganic carbon, nitrogen, phosphorus and silicon were depleted in the upper layers during phases of phytoplankton growth and accumulated in the lower during phases of stronger thermal stratification. Deoxygenation in the lower layers also led to the transfer and accumulation of $Fe^{2+}$ and $Mn^{2+}$. Such a huge lake is far from horizontally homogeneous, and the tendency towards enhanced biological production (e.g. of diatoms) in the inshore channels left its mark in the nutrient (e.g. Si) depletion there.

Yet more contrasting situations of nutrient supply and depletion were disclosed by work supported by the FBA in the decade 1966–76, involving the surveys of lakes George and Turkana. The shallow, productive and frequently mixed waters of L. George showed an indefinitely prolonged depletion of inorganic nitrogen and phosphorus (Viner 1977), with pronounced accumulations only below the sediment-water interface. In L. Turkana (Harbott, in Hopson 1982) the crucial supply factor was the seasonal floodwater (rich in nitrate) from the main northern tributary of the Omo River, which led to a decided north-south chemical polarization of this elongate and moderately saline lake.

In 1960–1 the Tallings took the opportunity to sample African lakes as widely as possible, then systematically to assemble and analyze the findings with those of other workers. The result (Talling & Talling 1965) has often been used as a reference compilation. An example in graphical form is shown in Fig. 2. More recently a survey of chemical variation, in Ethiopian inland waters, has been made by Wood & Talling. Both these regional overviews illustrate chemical and biological trends along a gradient of increasing salinity, with $HCO_3^-$ plus $CO_3^{2-}$ dominant among the anions.

## 5. Phytoplankton ecology and primary production

The chemical diversity of the medium, outlined above, is one source of special interest in the ecology of African phytoplankton. This was recognised from the results of the early expeditions to East Africa in which Jenkin and Beadle participated, showing major floristic changes along salinity and alkalinity gradients. Such differentiation was briefly taken up in later chemical surveys (Talling & Talling 1966) and more systematically for diatoms by Gasse, Talling & Kilham (1983). Thus species of the genus *Melosira* are important phytoplankters in most African lakes of relatively low alkalinity and salinity, whereas a few chemical specialists (such as the blue-green *Spirulina fusiformis ('platensis'))* are characteristic of soda lakes (see Figs 2, 3b). There is further conspicuous variation of a quantitative kind in biomass development, which is influenced by the quantities of nutrient elements available externally and those incorporated in the algal crops (Talling 1981).

There is also a fundamental interest in the regulation of population dynamics in tropical waters where temperatures are consistently high and there is no winter radiation check to growth. In Africa the necessary longer term studies developed after 1950 at several universities and fisheries research institutes. After earlier work on Nile phytoplankton from the University of Khartoum (Prowse & Talling 1958, Talling & Rzóska 1967), and by courtesy of the East African (now Uganda) Freshwater Fisheries Research Organization, Talling was able to make a limited study on seasonality in L. Victoria (Talling 1957c), and then a more extensive one during 1960–1 (Talling 1962, 1966) when a visiting worker from the FBA. Building upon earlier studies (reviewed in Talling 1986) he found that the incidence of vertical mixing, and re-stratification, was the master-factor behind seasonal changes of phytoplankton abundance. However individual species displayed a variety of patterns of cyclic fluctuation, with the strongest contrast between certain diatoms and blue-green algae. Diatoms (Fig. 3a) responded positively to enhanced mixing and provided an interesting comparison with the spring diatom maximum in Windermere (Talling 1965b). Numerous co-existing



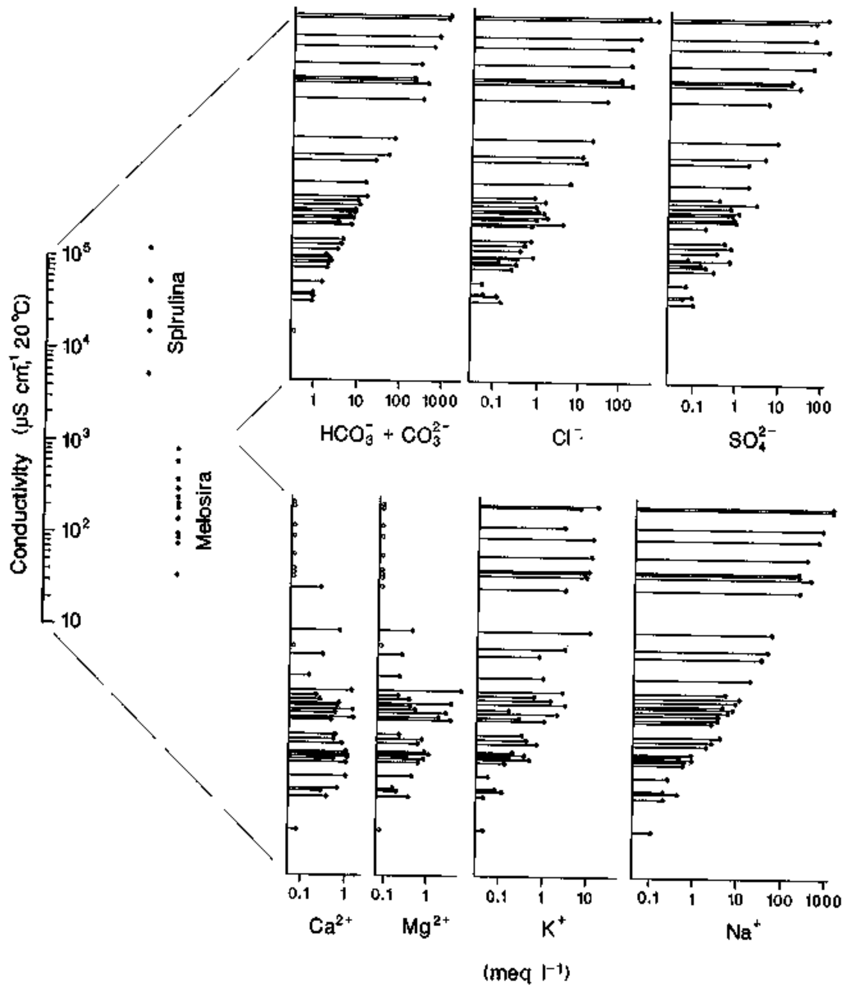



FIG. 2. Analyses of African lake waters arranged on a salinity-related scale of ascending conductivity, to show concentrations of major anions and cations and the prominent occurrence in phytoplankton of the diatom *Melosira* spp. and the blue-green *Spirulina fusiformis* (*S. platensis* auct.).
Adapted from Talling & Talling (1965) and Wood & Talling (unpublished).

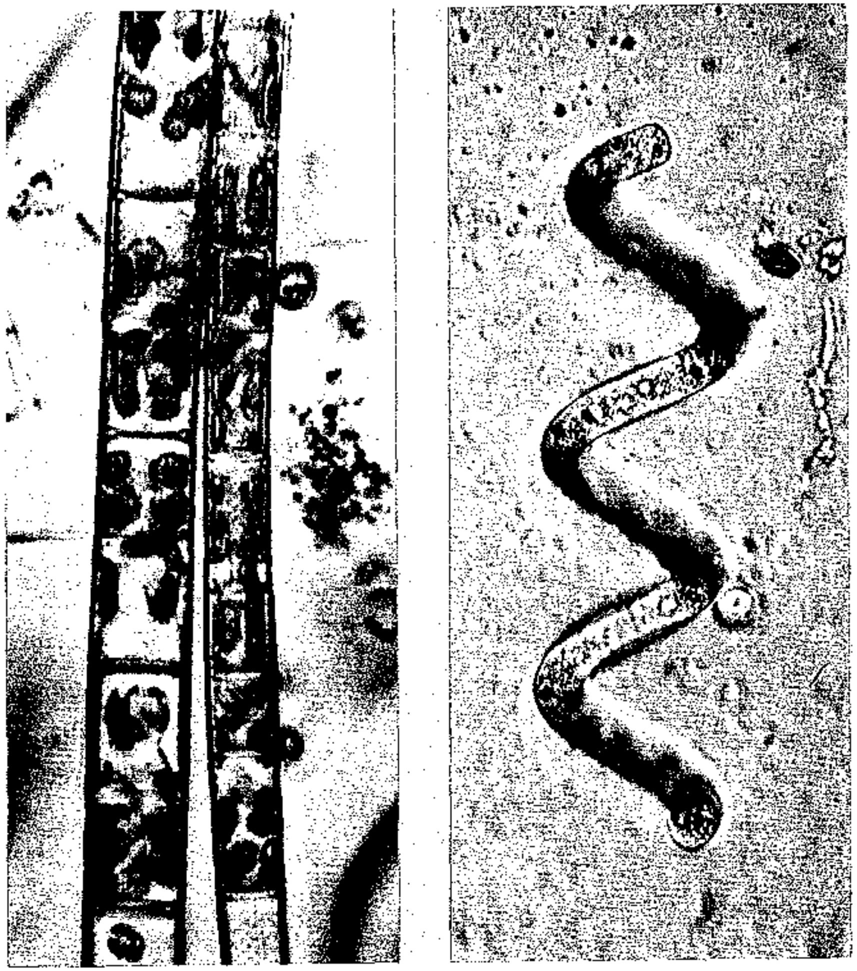


FIG. 3. Phytoplankters typical of lakes of low and of high alkalinity and salinity: (a) *Melosira nyassensis* var. *victoriae* from the Mwanza Gulf of Lake Victoria (b) *Spirulina fusiformis* (*S. platensis* auct.) from Lake Nakuru, Kenya.

green algae, including conspicuous desmids, showed only small amplitudes of variation in abundance. Such a limited variability was also found by Ganf (1974a), in the IBP study, to predominate in the algal populations of L. George where mixing is frequent over the time-scale of population growth. Over the history of this lake's development,



however, algal changes have been considerable as shown by a study of diatom remains in the sediments (Haworth 1977). The various patterns of phytoplankton seasonality in Africa have recently been surveyed by Talling (1985b), who distinguished between *hydrographic regulation* by water-column characteristics and *hydrological regulation* by influences of water input-output. In examples already mentioned, hydrological regulation of phytoplankton development is clearly seen in the flowing and impounded waters of the Nile (Prowse & Talling 1958, Talling & Rzóska 1967), and also in L. Turkana subject to annual influxes of river flood-water (Harbott, in Hopson 1982).

The tropical situation, and the variety of fresh waters, lend special interest to the photosynthetic conversion of solar energy for phytoplankton production. Evidence for intense activity in productive waters is provided by diel patterns of oxygen variation, whose analysis has been used to obtain estimates of rates per unit area (Talling 1957a, Ganf 1975). More discrimination is possible by experimental measurements on population samples exposed in situ. The earliest such experiments in Africa, including some in 1929 on L. Nakuru by Jenkin (1936), were intended as a sort of bioassay of underwater light penetration. Those directed towards the magnitude and regulation of photosynthetic productivity were begun near Khartoum by Talling in 1953 (Prowse & Talling 1958) and later extended to various Nile headwaters and adjacent lakes (Talling 1957a, 1965a, Talling et al. 1973). One striking feature was the generally high level – under favourable light conditions – of specific activity per unit biomass, whether assessed from cell volume or chlorophyll *a* content. Another was the varied photosynthetic response with depth to changes in underwater light penetration, the latter often conditioned by the algal populations themselves. These and other features were further examined during the work of the Royal Society – IBP Team on L. George (e.g. Ganf 1974b).

## 6. Invertebrates

Many groups of African freshwater invertebrates are more diverse than those of Europe. In the main they are less well known, and a prime need has been (and still is) to gain a better understanding of their taxonomy. This can have immediate practical importance. Thus the vectors of several important human diseases such as malaria, schistosomiasis ('bilharzia'), onchocerciasis ('river blindness'), elephantiasis and dracunculiasis are freshwater invertebrates – mosquitos, snails, simulium flies and cyclopoid copepods.

Schistosomiasis, caused by blood flukes of the genus *Schistosoma*, is a debilitating and sometimes fatal disease that afflicts millions in Africa. The intermediate hosts of the flukes are certain freshwater snails whose ecology and interactions with their parasites it is clearly vital to understand if control measures are to be applied. A. D. Berrie spent several years studying these snails in Africa for the Medical Research Council before joining the FBA staff (Berrie 1970). Host/parasite relations are sometimes complex. For example two 'forms' of *S. haematobium*, with different geographical ranges, are transmitted by snails of the genus *Bulinus* (Fig. 4h) (Berrie 1973). Curiously, while members of the *Truncatus* group of *Bulinus* act as hosts in some regions they fail to do so in others. The occurrence of different strains of the parasite, each of which favours a certain species of snail, the ecophenotypic variability of the host snails (their form is altered by different environmental conditions) and the way in which they differ in form throughout their geographical range, compound the difficulties. Berrie (1968) observed inhibition of growth in a natural population of snails at high population density, a phenomenon only previously reported from aquaria and, with the collaboration of a chemist, he was able to isolate a substance from the water which affected the growth of snails under experimental conditions (Berrie & Visser 1963).

Studies on the life histories and infection rates of some of these snail

FIG. 4. Some African freshwater invertebrates studied by FBA staff and their significance.

a. *Caridina africana* – an atyid prawn. The very similar *C. nilotica* is now the staple food of young Nile Perch, *Lates niloticus*, recently established in L. Victoria with disastrous results.

b. *Lamproglena monodi* (female) – a common and widespread copepod parasitic on the gills of cichlid fishes (Lateral).

c. *Chonopeltis inermis* (female) (L. Malawi). A member of an exclusively African genus of branchiuran crustaceans. (Ventral). This species parasitizes clariid catfishes.

d. The newly hatched larva of *C. inermis*, a unique type of crustacean larva. (Ventral).

e. *Mutela bourguignati* (L. Victoria). A larva almost ready to hatch, still within the egg membrane. Up to this stage the eggs and the larvae which they eventually contain are still brooded within the ctenidia (gills) of this large bivalve mollusc.

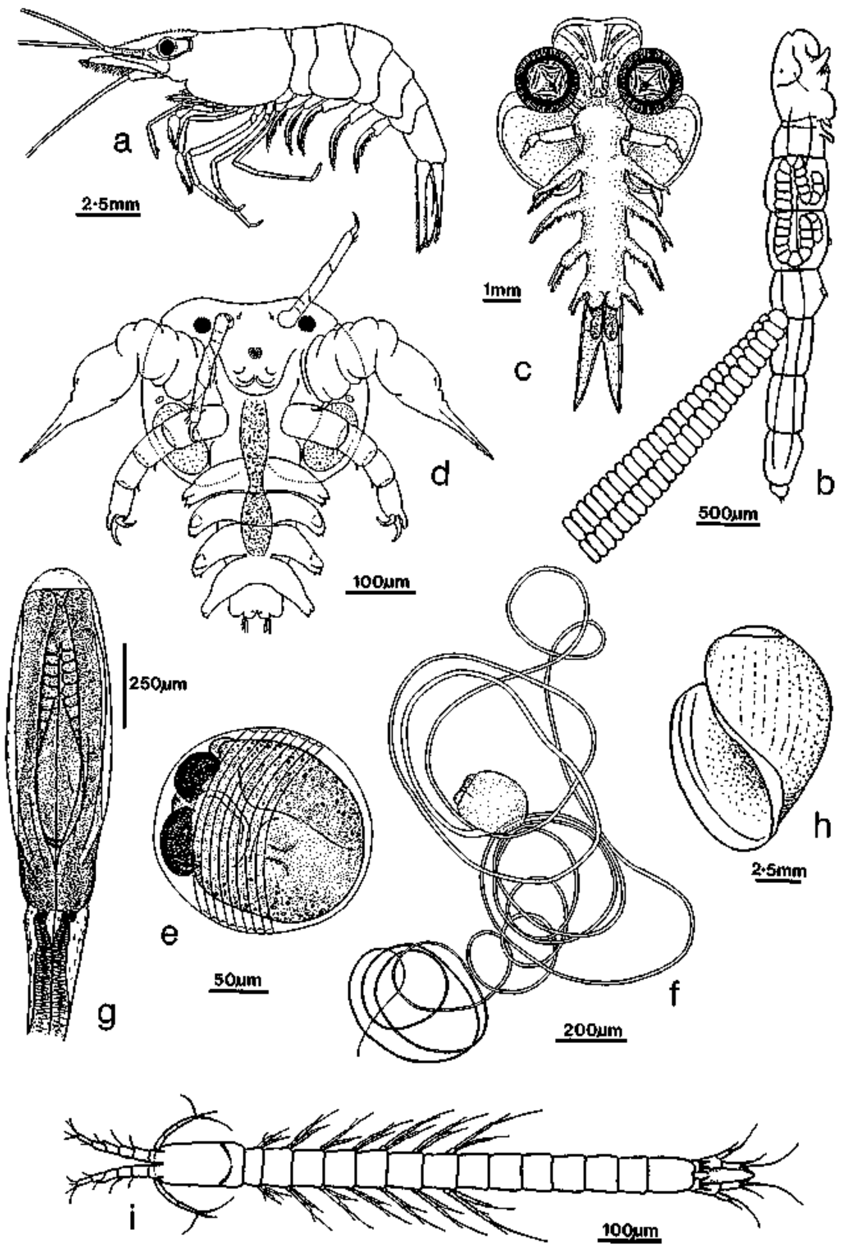
f. *M. bourguignati*. A larva liberated by the parent. The egg membrane has ruptured to free the immensely long tentacle with which the larva is provided.

g. *M. bourguignati*. A late stage of the parasitic phase of development. The larva settles on the cyprinid fish *Barbus altianalis radcliffi*, becomes a parasite, undergoes remarkable transformations, and ends this phase of its development as a minute bivalve located at the end of a stalk, from which it eventually breaks free. The stage seen here is one at which the foot, ctenidia and mantle of the adult-to-be are well differentiated but still enclosed in a larval pellicle. The long prolongations of the mantle extend into the host and, although ectodermal in origin, absorb nourishment.

h. A shell of the snail *Bulinus nasutus* (E. Africa). An important vector of *Schistosoma haematobium*, one of the causal agents of schistosomiasis ('bilharzia') in man.

i. *Parabathynella caparti* (L. Bangweulu). A blind, elongate representative of an archaic group of crustaceans (the Syncarida) that lives in the interstitial spaces among sand grains at the lake margin. (Dorsal).





vectors (Berrie 1964) are clearly of relevance to human welfare. Man is, however, not the only organism afflicted by parasites. Those infesting his domestic stock, or the fishes that he seeks to crop, are also important to him.

Crustacean parasites of freshwater fishes (Fig. 4b-d) are more diverse than in Europe. Again it is necessary to understand their taxonomy before biological studies can be undertaken. Some idea of how little was known of these organisms until recently can be given by noting that work initiated by Fryer led to the description of no fewer than 28 new species and the erection of new genera. Taxonomy had inevitably to take priority in this work, but some biological studies, e.g. on spermatophore formation in a branchurian (Fryer 1960c) and on life histories, were carried out. In addition, many observations on host preferences, levels of infestation and habitat selection were made (e.g. Fryer 1966). Of particular interest was the discovery of the larva of the endemic branchiuran genus *Chonopeltis* (Fryer 1956b). This proved to be a unique type of crustacean larva (Fig. 4d) whose subsequent development it was eventually possible to work out (Fryer 1961b). In one species at least this involves the use of an intermediate host. A review of our knowledge of the parasitic crustaceans of African freshwater fishes and a complete bibliography up to that time was given by Fryer (1968) but additional information, inevitably mostly of a systematic nature, has since been published (e.g. Fryer 1977b).

Perhaps the most exciting work involving parasitism in African freshwater organisms was the elucidation of the previously unknown life cycle of the bivalve mollusc *Mutela bourguignati* (Fryer 1961a). The minute free-living larvae (Fig. 4e, f) of this large bivalve have a remarkable tentacle, more than 70 times as long as the larva itself. This is shed when the larva becomes parasitic on a fish and here develops into another larva of a type utterly different from any previously known, whose development (see caption to Fig. 4g) and subsequent metamorphosis into a tiny free-living replica of its parent it was possible to work out. This study, in a roundabout way, had far-reaching consequences for molluscan taxonomy, and biogeography and our understanding of the evolution of large bivalves in the southern continents (Fryer 1970).

Free living crustaceans abound in African lakes, rivers and swamps. Again taxonomic difficulties have forced attention onto these aspects of their study and various new taxa, belonging to several groups, have been described (e.g. copepods: Fryer 1956a; syncarids: Fryer 1957b) (Fig. 4i). Information on the geographical distribution of the various species has also been provided for certain regions, such as L. Malawi (Fryer 1957a).

A now much-studied phenomenon is that of the diurnal migrations that are made by many animals of the plankton. Some of the earliest



observations of this behaviour in a tropical lake were made on Lake Victoria by Worthington in 1927 during his participation in a fishery survey (§2) (Worthington 1931). He later studied the same phenomenon in other East African lakes (Worthington & Ricardo 1936). Elsewhere in East Africa, the characteristics and quantitative distribution of the zooplankton of L. Turkana were finally assembled by Ferguson (in Hopson 1982) while working at the FBA.

Participants in the International Biological Programme (1966–72) at L. George, Uganda, have contributed to our knowledge of the distribution, biology, and productivity of both planktonic and benthic invertebrates – themselves important in the diet of certain fishes. Examples include the work of Burgis (1971, 1973, 1974) on crustaceans of the zooplankton, McGowan (1975) on 'midges', and Darlington (1977) on the benthic fauna, while invertebrates were considered in a wider context by Burgis et al. (1973) and Moriarty et al. (1973).

Among the crustaceans of Africa are certain small prawns of the family Atyidae. These are widely distributed and often abundant, but their role in nature is not yet fully understood. When in Uganda, Fryer (1960b) was able to study the functional morphology of two atyid species of the genus *Caridina* (Fig. 4a). At the time this seemed a rather academic exercise and, though it later provided useful comparative information during a study of other tropical atyids, it seemed of scant economic interest. Now, however, a large predatory fish, the Nile Perch, is rampaging in L. Victoria (§7) and it turns out that individuals up to about 40 cm in length feed almost exclusively on *Cardina*. Thus the information available on the habits of this prawn immediately becomes valuable. More recently J. A. B. Bass (unpublished) has studied some of the prawns that frequent the lower reaches of certain W. African rivers and streams.

Clearly such studies impinge on only a few of the many freshwater African invertebrates and reflect the interests of the small number of individuals concerned. For example, apart from the studies of McGowan and Darlington noted above, very little work on African insects has been published by those with FBA connections. Observations on some curious phenomena related to the periodicity of emergence of *Chironomus brevibucca*, the most important chironomid midge of L. Bangweulu, constitute one of the few exceptions (Fryer 1959b). Likewise work on the Protozoa is largely confined to a recent investigation of some of the ciliates that frequent two E. African soda lakes (Finlay et al. in press).

## 7. Fishes

The freshwater fish fauna of Africa is exceedingly rich. Such major rivers as the Zaire (= Congo) and Nile harbour many species but it is the lakes that are most famous in this respect by virtue of their remarkable endemic faunas, especially of the family Cichlidae. To the zoologist these lakes are laboratories for evolution where many of the problems relating to the origin of new species can be studied (§8). They are also a potentially rich source of human food. These facts are not incompatible. In order rationally to exploit such faunas one needs to know many things about the fishes.

It was with a view to providing the information necessary to enable these rich fish faunas to be exploited, while at the same time doing minimal damage to the stocks, that work on the fishes and fisheries of African lakes began, essentially in East and Central Africa, then under British colonial rule. The first major venture was a survey of L. Victoria undertaken by Michael Graham (1929) to whom Worthington served as a sort of apprentice. The latter was later to use the expertise so gained in several other African lakes (Worthington 1929). Some of his experiences he summarised in a book (Worthington & Worthington 1933).

Although early explorers had indicated the rich nature of the African fish fauna, its spectacular diversity was not realised when these early surveys took place, and much was unknown. For example, the fish that



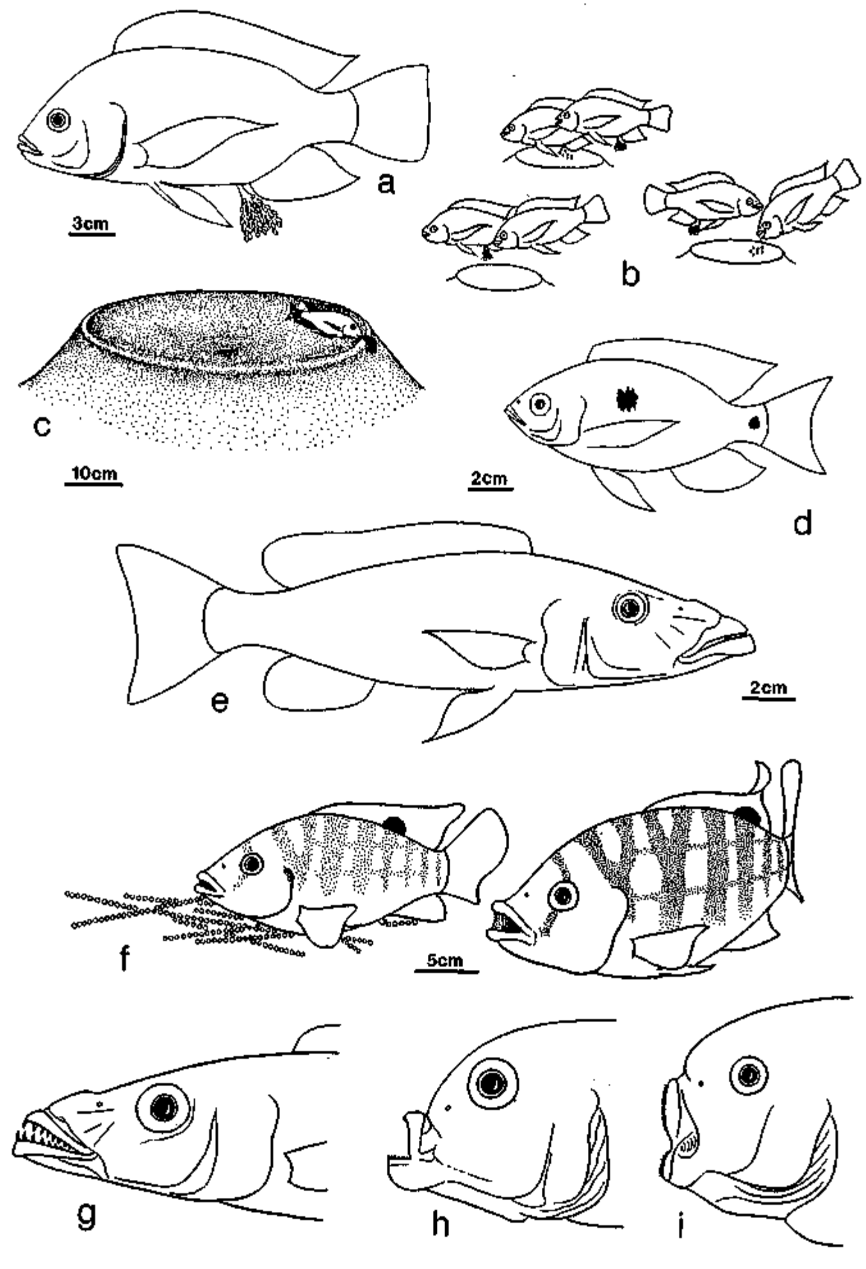



FIG. 5. African cichlid fishes displaying some of their attributes.

a. A male *Oreochromis variabilis* (L. Victoria) displaying its genital tassel that probably mimics a cluster of eggs. Females, which carry fertilized eggs in their mouths, attempt to seize the tassel after collecting shed eggs and thus bring their mouth close to the male genital aperture. Fertilization is thereby ensured.

b. Part of an arena (display ground) of *O. variabilis*. Here groups of males each make a simple sandscrape nest. Females ready to spawn visit them, and courtship, egg-laying and fertilization occur. Association of the sexes is transient. Females take away the eggs and brood them and the ensuing young elsewhere.

c. A male of *'Cyrtocara' heterodon* (L. Malawi) making its nest, which serves as the centre of its territory. This is another arena frequenter. Its nest is much larger than that of the larger *Oreochromis variabilis.*

d. *'Cyrtocara' pleurostigmoides* (L. Malawi), an example of an open-water, plankton-eating, shoaling species. It has silvery sides to reflect light and render it almost invisible to predators, but as it needs to keep in close contact with its shoal-mates it bears spots, inconspicuous to predators but readily visible to its compatriots swimming alongside.

e. *Rhamphochromis longiceps* (L. Malawi) – a piscivore that shows many beautiful adaptations to its way of life.

f. *Tilapia zillii* (widespread) spawning. This species is a substratum spawner. The female lays rows of sticky eggs, each of which is fertilized by the male. This species shows firm pair-bonding. Both sexes guard the eggs, then the young after they have hatched.

g-i. Adaptations to different diets of three species from L. Malawi. g–*Rhamphochromis macrophthalmus*, a piscivore, h–*Genyochromis mento*, which has the curious habit of scraping scales from other fishes, and i–*Petrotilapia tridentiger*, which scrapes loosely attached algae from rocks with an array of fine spatulate teeth.

destroyed by bad management – was not even described when the 1927 survey took place. This fish, the celebrated Ngege, *Oreochromis esculentus* – better known as *Tilapia esculenta* – belongs to a group of large cichlids, conveniently described as tilapiine cichlids, that are, or in some cases were, of great economic importance in many African lakes. The Ngege itself, and the related Mbiru, *Oreochromis variabilis* (Fig. 5a, b) of the same lake, were a prime concern of the laboratory established at Jinja in Uganda with Beauchamp as director. These fishes were studied by Lowe-McConnell (1956a) and Fryer (1961c) though they were not the only workers to study them, the outstanding work on the Ngege being done by Garrod (1963), now a member of the FBA Council.

Lowe (1952) had already undertaken a study of the tilapiines of L. Malawi, building on the work of Bertram, Borley & Trewavas, and added much to our knowledge of these fishes in other African lakes, from Turkana in northern Kenya to L. Jipe in Tanzania (Lowe 1955, Lowe-McConnell 1958). This work involved studies of breeding behaviour (Lowe-McConnell 1956a) as well as those aimed directly at understanding the fisheries for these species. This interest she has maintained, culminating in two books on tropical fish communities.

As a short-term project involving FBA support, Winifred Frost paid a visit to Kenya, there to make a pioneering study on the biology of eels in the rivers (Frost 1955).

As a result of his years spent on L. Malawi, where he studied the ecology of littoral cichlids (Fryer 1959a) – inevitably having to describe new species – and subsequently on Bangweulu and Victoria, Fryer developed a deep interest in the cichlid fishes of African lakes. This led eventually to a book by him and a colleague (Fryer & Iles 1972) that attempted to summarize knowledge of the biology and evolution of these fishes up to that time. The L. George IBP team, also, contributed to our understanding of fish communities and production in that lake: publications by those involved (Dunn, Greenwood, Gwahaba, Moriarty) are listed by Burgis (1978). More recently M. T. Furse, currently at the River Laboratory, participated in a study of the fishes and fisheries of L. Chilwa, Malawi, a water-body subject to periodic drying out (Furse et al. 1979).

As well as leading to recommendations relating to the fisheries, studies on African fishes by those with FBA connections have involved such topics as taxonomy, breeding and other habits (Fig. 5a-c, f), functional morphology (Fig. 5e, g-i) and ecology, and have led to the putting forward of ideas relevant to evolution. Nor has the flow of information always been in one direction. While it might be supposed that methods employed in a modern European laboratory would be more likely to find applications in the depths of Africa than would African methods in Britain, this has not always been so. Gill netting, so important as a means of catching many fishes in African lakes, was not at that time used in English lakes until introduced by Worthington who was familiar with the method in Africa. Likewise the Perch trap, celebrated as the means whereby millions of Windermere Perch have been caught both for scientific and culinary purposes, is the lineal descendant of an African fish trap.



## 8. Evolution and Conservation

As sites where matters having a bearing on evolution can be studied, the Great Lakes of Africa have few rivals. This became apparent as the diversity of their faunas was gradually revealed, in part by the Cambridge Expedition of 1930–31 of which Worthington was a member and who (Worthington 1937, 1940) was among the first with field experience to make suggestions concerning the evolutionary processes being enacted there.

Many African lacustrine organisms throw light on evolutionary phenomena. The unexploited potential of inadequately studied groups, such as the snails, to do so presents a great challenge, but it is the cichlid fishes that, not surprisingly, have proved the most attractive to date. Especially in the clear waters of lakes Malawi and Tanganyika many of these can be watched under water. On rocky shores the spectacle rivals that of a coral reef. Here one can observe the diverse feeding habits of numerous species and relate what one sees to their complex jaw morphology and specialized dentitions (e.g. Fryer 1959a). Territorial behaviour can be observed more precisely than in most birds, for males often have small territories, in sandy shore species sometimes centred on an elaborate nest. Here one can compare the behaviour of closely related species that often live in intimate association with each other, an exercise facilitated by the fact that the males of such species pairs or complexes often differ strikingly in colour at times of reproduction – a device that helps to prevent inter-specific matings. Mating behaviour, in many cases involving elaborate courtship, can be watched. All the Great Lakes cichlids exhibit parental care. In most cases the female collects the eggs in her mouth and broods them until they hatch, and sometimes well beyond hatching. In others eggs are laid on a suitable substratum and there guarded by both parents.

All these and many other habits and attributes (reviewed by Fryer & Iles 1972), especially when studied from a comparative point of view, provide abundant material for the ethologist. All are grist to the mill of the student of evolution, and these fishes have thrown much light on such key processes in evolution as speciation and the nature of isolating mechanisms.

Past and present members of the FBA have been much concerned with evolutionary matters (references in Fryer & Iles 1972, Fryer 1977a) and continue to maintain an interest. For example there has been involvement in the discussion on the fossil mollusc sequence of L. Turkana and its significance (Fryer, Greenwood & Peake 1983, 1986).

Information utilized in discussions of an evolutionary nature is relevant to those who seek to exploit these fishes as a source of human food as it sometimes has a bearing on how they respond to fishing pressure. Unfortunately technological developments tend to advance more rapidly than scientific understanding, and if means whereby fishes can be caught more easily are available they are often used without due regard to the long-term consequences. An example is the use of trawlers on L. Victoria. Likewise, when gill nets are used, as they are extensively in African lakes, there is a temptation to use small mesh sizes, that give an immediate large return, rather than restrict fishing to nets of larger mesh that, while they will not give an immediate, but short-lived, bonanza, will ensure a steady yield over an indefinite period. The unfortunate consequences of malpractices are well seen in the history of the *Oreochromis esculenta* and *O. variabilis* fisheries in L. Victoria (Fryer 1973, 1984).

The fisheries are also threatened in other ways. The introduction of a large predator, the Nile Perch *Lates niloticus*, into L. Victoria is the prime example. A simple biological principle tells us that such a predator can never be as productive of flesh useful to man as can the herbivores on which it feeds. Yet in spite of the uncertainties involved – debated since the time of Graham (1929) – and of specific warnings (Fryer 1960a) the introduction of this fish was advocated by some biologists and is now a fait accompli. The results have been disastrous. In areas like the Nyanza (Winam) Gulf, where the Nile Perch is well established, many of the haplochromine cichlids have not merely declined in abundance but have virtually disappeared, and the great *Oreochromis* (Tilapia) fisheries are a thing of the past. The Nile Perch continues to spread and wherever it appears the endemic haplochromine cichlids are drastically reduced in numbers. Many of them are in grave danger of extinction. Even proponents of the idea now admit that, when the fishery settles down, one can expect yields 80% less than could have been provided by the herbivores! At present small Nile Perch are feeding largely on the prawn *Caridina* (§6): large individuals on their own offspring!

The FBA continues to take an interest in this appalling situation and has been instrumental in bringing it to public notice by an article in *Nature* (Barel et al. 1985).

Hydro-electric developments can also have repercussions on fisheries. For example the Owen Falls Dam on the outflow of L. Victoria now impedes the former upstream migration of the large *Barbus altianalis*, and serious problems involving human welfare have been created on the Nile, Zambezi and Tana rivers.



Past and present members of the FBA have been actively engaged on studies of both organisms and environments in African lakes, and at various times have drawn attention not only to problems of fishery management, but also to the threat of pollution, noting that tropical lakes with vast volumes of deoxygenated water, such as Malawi, Tanganyika and Kivu, are particularly susceptible to damage by oxygen-demanding pollution. Because renewal times are extremely long, nature could not easily rectify a catastrophe (Fryer 1972). Pollution would not merely damage or destroy fisheries but could have serious consequences for the largest reservoirs of fresh water in Africa. In this connection concern must be felt over recent proposals to drill for oil in the vicinity of the Great Rift lakes, especially Tanganyika, an exercise that, notwithstanding its possible economic value to the countries concerned, is fraught with danger to the lakes themselves. The FBA is aware of these threats. While in no position to dictate policy to independent sovereign states, and with no desire to do so, it is at least able, and willing, to make available such expertise as it possesses to assist in the making of rational decisions that will conserve these lakes and their remarkable faunas and floras to the benefit of science and human welfare into the foreseeable future.

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# BIOLOGICAL AND CLIMATIC INFLUENCES ON THE DACE *LEUCISCUS LEUCISCUS* IN A SOUTHERN CHALK-STREAM

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## Introduction

The dace, *Leuciscus leuciscus* (L.), is a member of the Cyprinidae or carp family. It is widely-distributed in England, Wales and mainland Europe, and typically it inhabits clear, fast-flowing rivers and streams that provide clean gravel areas for spawning. It is the most important cyprinid, in terms of population biomass, in the chalk-streams of southern England. In the upper reaches of these waters it is often culled (usually by electrofishing) to reduce its supposed, but unproven, competition for food and space with the brown trout, *Salmo trutta* L. Such a management regime is less prevalent in fisheries for salmon, *S. salar* L., further downstream. Here the dace contributes, often substantially, to the coarse fishing practised during the salmon close season.

Many aspects of the ecology of the dace have been examined at the River Laboratory, principally in the River Frome, Dorset but also in the neighbouring rivers to the east, the Stour and Avon (Mann 1967, 1971, 1974, 1979, 1982; Mann & Mills 1985; Mills 1980, 1981a, b, 1982; Mills & Mann 1985; Mills et al. 1985; Scott in press). The dace thrives in all three catchments and a 709 g specimen was reputedly caught in the Frome in 1902 (Lonsdale & Parker 1930). This must have been an impressive fish, for the largest two caught in our studies were 261 g (Frome) and 321 g (Avon). The current British rod-caught record is 680 g for a specimen from the River Ivel, Bedfordshire.

A characteristic of chalk-streams is their relatively stable flow regime, unlike more upland rivers where sudden spates are often encountered. Similarly the temperature regimes of chalk-streams do not show such