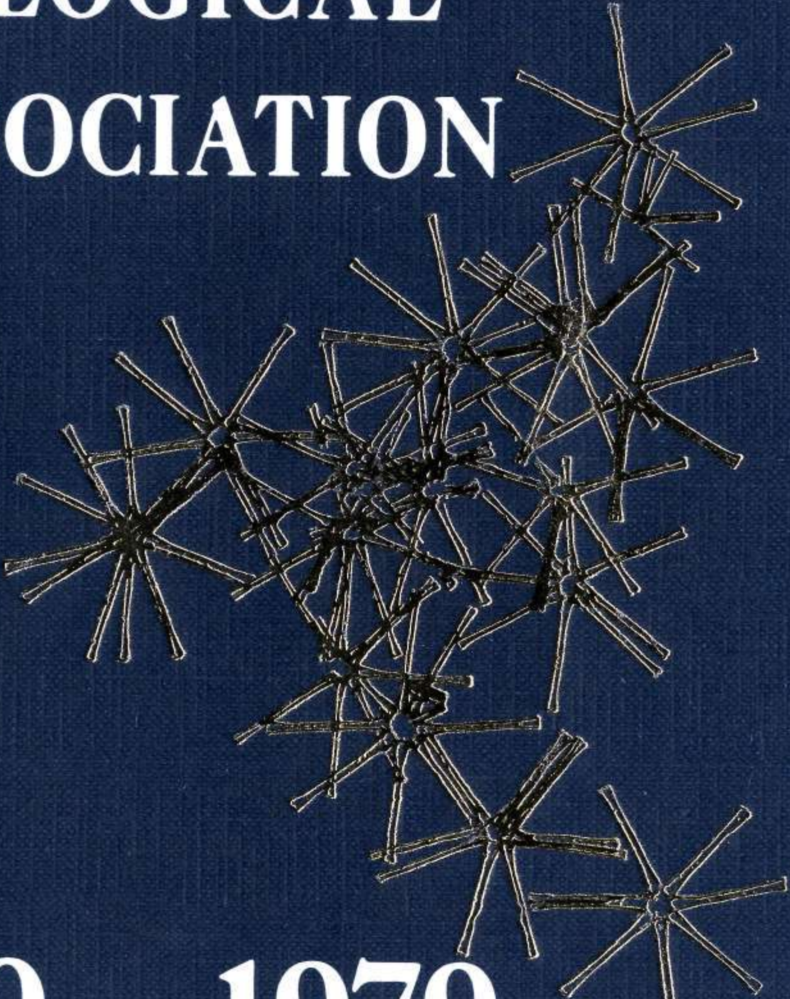
# FRESHWATER BIOLOGICAL ASSOCIATION



## 1929 – 1979

# FRESHWATER
# BIOLOGICAL
# ASSOCIATION

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## THE FIRST FIFTY YEARS

by G. E. FOGG

*Ambleside*
1979

# PREFACE

This booklet has been written primarily to celebrate the fiftieth anniversary of the founding of the Freshwater Biological Association – its Golden Jubilee. Professor Fogg is at present Chairman of the Association's Council and has been closely connected with the affairs of the FBA ever since he attended an Easter Course at Wray Castle in 1941. A student of Professors F. E. Fritsch and W. H. Pearsall, he has become a distinguished researcher in freshwater biology in his own right, and also an experienced author of scientific books. So we have been fortunate in being able to persuade Professor Fogg to undertake the writing of this text.

In so doing he has aimed to produce a readable account of those aspects of freshwater biology that have been among the main themes of the Association's research, as well as some aspects of its history and the philosophy guiding its foundation. Inevitably much has been left out, and especially many of the more recent developments in FBA research. Readers are advised to consult the contemporary *Annual Report* if they want fuller information on the current research programme. Nevertheless, it is hoped that this booklet will serve, not only as a jubilee review, but also as a general introduction to the Association and its work.

We are grateful to the many who have provided helpful comments on drafts of the manuscript and to those who have given permission for the reproduction of photographs they have taken. A list of the latter will be found on p. 40.

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# FRESHWATER BIOLOGY: ITS SCOPE AND USES

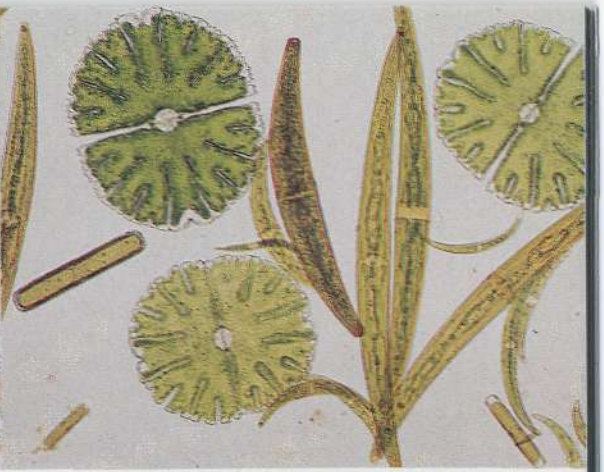
If the freshwater biologist has a popular image it is probably that of an amiable eccentric as exemplified by Mr Pickwick, who first appeared as the author of a paper entitled "Speculations on the Source of the Hampstead Ponds, with some Observations on the Theory of Tittlebats", or by Bertie Wooster's friend Gussie Fink-Nottle who kept newts in his bedroom in order to observe their mating habits. In reality, the freshwater biologist, although he may still get something of the small boy's enjoyment from dabbling in water and messing about with boats, is quite as professional and responsible a scientist as any other. The jam-jar and pond net still have their modest part to play but, to an increasing extent, refined chemical techniques, elaborate electronic devices, electron microscopes and computers are brought to bear on the problems presented by freshwater life. Freshwater biology includes the study of all aspects of all kinds of organisms – from bacteria, microscopic algae and protozoa to water weeds, planktonic and bottom-dwelling animals, fish and water fowl – found in fresh water both static and running (Plates 1 & 2). The demarcation with marine biology is indefinite; brackish waters and estuaries present their special problems and are perhaps best regarded separately for some purposes, but studies of sea and fresh waters have much in common. The term *limnology* is often used as if it were synonymous with freshwater biology but strictly it denotes the study of lakes – not rivers – from all aspects, geographical, physical and chemical as well as biological. In practice the freshwater biologist is obliged to take notice of the physical and chemical environment of all those organisms which are the primary object of his study, and much of the fundamental investigation of the physical aspects of fresh waters has been undertaken by biologists or at their instigation.

Freshwater studies have contributed much to general biological knowledge and some freshwater organisms such as the green alga *Chlorella* and animals like *Hydra* and *Daphnia* have played a notable part in the investigation of some of the major problems of biology. However, as an academic discipline, freshwater biology is particularly valuable because it forces attention to the interrelations of plants and animals and their environments, and calls for the integration of many different types of approach and investigation. To some extent a pond or lake is a self-contained unit and provides, both for teaching ecology at the elementary level and for advanced research, an accessible and manageable example of an ecosystem.

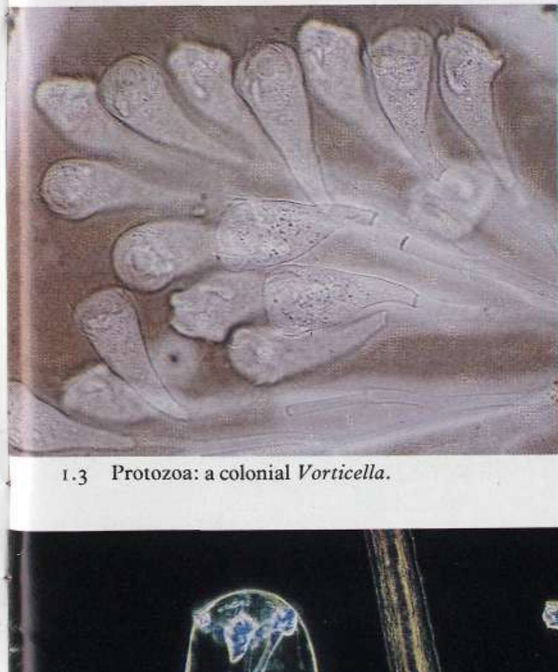
Freshwater biology is vital, both domestically and industrially, because our lives are dependent on reliable supplies of water free from harmful organisms and noxious or unpleasant materials. On the purely mechanical level, as blockers of filters, growths of algae in a reservoir are one of the principal worries of the water engineer. Beyond this, as demand for water increases, he must consider using new sources, creating reservoirs in estuaries and mixing waters from different catchment areas – all of which have biological implications. Thus, knowledge of the plants and animals of fresh water, and prediction and control of their occurrence, are essential for the water supply industry (Plate 3). Closely interrelated with water supply is disposal of waste. We rely on flowing water for the disposal of sewage and industrial waste but, except where it can be discharged into the sea in an unobjectionable manner, this water must be treated to avoid nuisance if not to render it fit for reuse (Plate 4). To do this properly again calls for knowledge of freshwater life. The problems of salmon and trout fisheries have long been the subjects of investigation by freshwater biologists and now there is increasing concern with fish-farming and the production of cheap high-grade protein (Plate 5). Coarse fishing – the sport with the largest number of actual participants in Britain – has received less attention, but there is no doubt that it could be improved with the help of freshwater science. Water itself is becoming more valued as an amenity. Visually, it is generally the focal point in landscape and, in addition to the age-old recreations of swimming and boating, there are now water skiing, SCUBA diving and other sports. All these call for reasonably clear and hygienically safe water and, therefore, biological management.

More and more, these various uses for water have to be combined and reconciled. It is becoming commonplace for a river to be fed largely from sewage works effluent, then to be used for recreation and perhaps cooling water for a power station, and then to provide the water supply for the next town downstream. Action by one of the interested parties will inevitably affect the others to a greater or lesser degree. In such situations, of even greater value than the specialist knowledge needed for the solution of individual problems is the freshwater biologist's ability to see things as the related parts of a whole ecosystem.

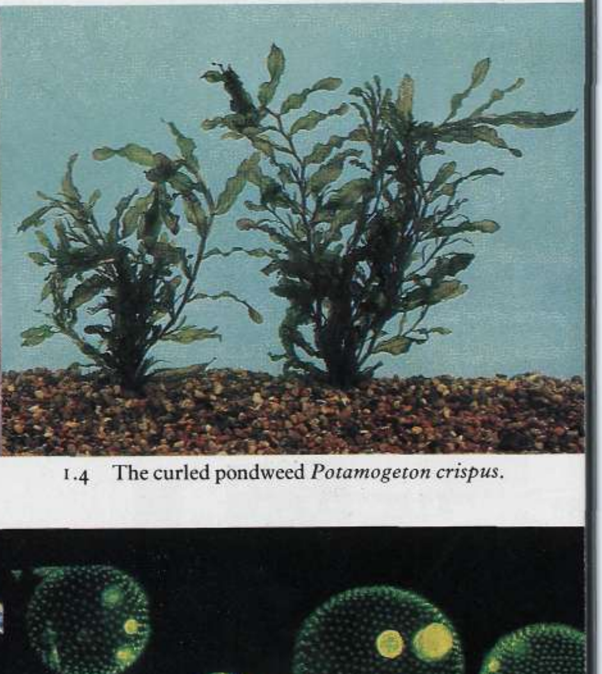
1.1 Algae: the diatom *Pinnularia* and the blue-green *Spirulina*.



1.2 Algae: the desmids *Micrasterias* and *Closterium*.

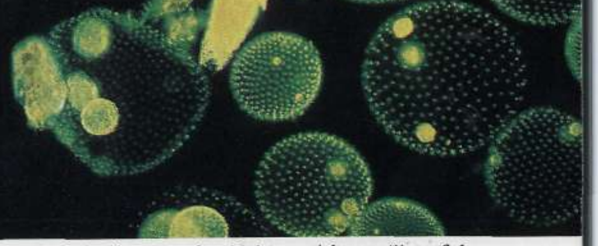


1.3 Protozoa: a colonial *Vorticella*.



1.4 The curled pondweed *Potamogeton crispus*.

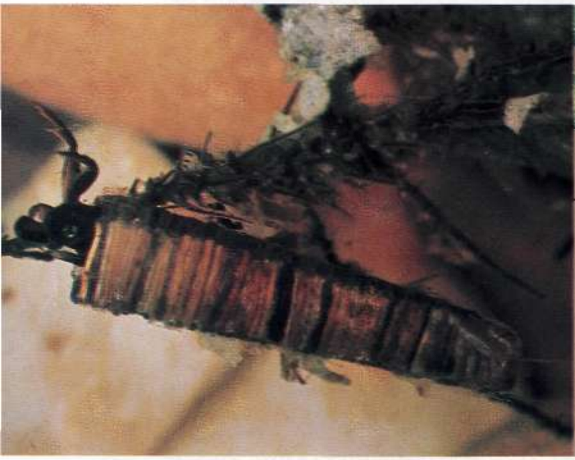
1.5 A planktonic rotifer, *Asplanchna priodonta* (male).



1.6 A green alga *Volvox*, with nauplius of the copepod *Cyclops*.

2.1 Crustacea: the planktonic cladoceran *Bosmina*.

2.2 Gastropoda: the ramshorn snail *Planorbarius corneus*.



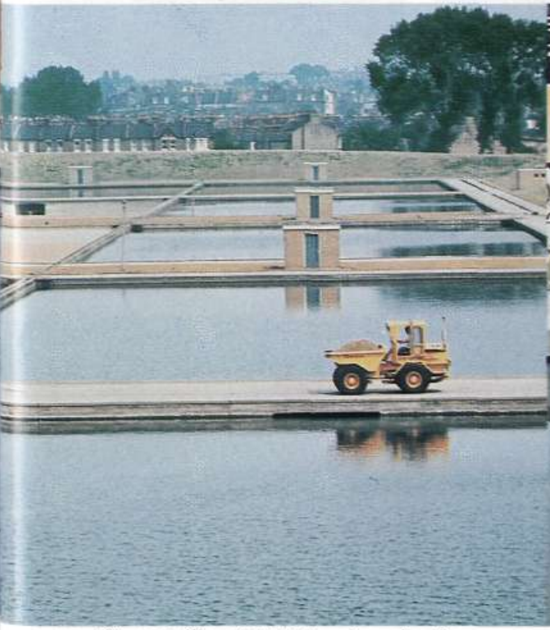
2.3 Insecta: the case-building caddis larva, *Brachycentrus*.

2.4 Insecta: the lacewing *Osmylus*.

2.5 The roach *Rutilus rutilus*.

2.6 Coots (*Fulica atra*) with young.

3.1 Thirlmere, which provides water for Manchester, "drawn down".



3.2 Coppermills water treatment works; slow sand filter.

3.3 Interior of a pumping station of the Thames Water Authority.

4.1 Windermere sewage works: trickling filters.

4.2 Basingstoke sewage works: activated sludge tanks.

4.3 Clay Mills sewage works.

# THE ORIGINS AND HISTORY OF THE FRESHWATER BIOLOGICAL ASSOCIATION

Although pond-life was popular with Victorian microscopists and there were some excellent pioneer studies of the physical limnology of Scottish lochs in Edwardian times, freshwater biology was slow to get under way as a distinct discipline in Britain. In Europe, freshwater laboratories had been established at Plön-im-Holstein, W. Germany, in 1892 and at Lunz-am-See, Austria, in 1906, and in the United States at Madison, Wisconsin, in 1896. The beginnings of organized freshwater biology in Britain may be seen in the work of W. H. Pearsall on the aquatic plants of the English Lakes, begun just before the First World War. With his father, a local schoolmaster, he eventually accomplished a comprehensive survey, including chemistry as well as biology, of all the larger lakes. The Royal Society gave support in its later stages, but the Pearsalls throughout their work rowed on the lakes, and transported themselves and their samples around the Lake District by bicycle. Characteristically ignoring the system of lake classification that was being elaborated on the continent, Pearsall arrived at the concept of the English Lakes as a continuous series representing different stages in an evolutionary sequence, a concept which has influenced much British freshwater biology since.

FIG. 1. F. E. Fritsch, W. H. Pearsall, J. T. Saunders.

With the Cambridge zoologist J. T. Saunders, Pearsall began to think about the establishment of a freshwater biological laboratory in Britain. The lack of this facility was underlined by Professor F. E. Fritsch, Professor of Botany at Queen Mary College, London in his

FIG. 2. Wray Castle, with Windermere in the background.

presidential address to Section K of the British Association for the Advancement of Science in 1927. The following year a committee was set up to consider remedying the deficiency. As a result the Freshwater Biological Association of the British Empire came into being in 1929. This was the time of the great slump and a bad time for a new venture; a purpose-built laboratory was out of the question, but help came from individuals, the Fishmongers' Company, universities, water supply undertakings and angling organizations, together with a small grant from the Development Commission, the government body then responsible for supporting fisheries research. This enabled the appointment in 1931 of two scientists and a laboratory assistant and the provision of some rooms in Wray Castle, a National Trust property on the western shore of Windermere. With Pearsall's work available as a background, the Lake District was the obvious place for the Laboratory and Wray Castle was very conveniently situated for work on two lakes of differing type, Esthwaite Water and the north basin of Windermere, as well as on several unpolluted becks. A nineteenth-century imitation castle, badly in need of repair and shared with the Youth Hostels Association, was not the best building in which to conduct scientific research, but it sufficed. Saunders had persuaded two Cambridge graduates, P. Ullyott and R. S. A. Beauchamp, to take on the scientific posts and they were joined by Miss Penelope Jenkin, supported by a research grant from Newnham College. The third of Saunders's appointments was of a local lad, G. J. Thompson, not quite 17 years of age, as laboratory assistant. Later on, as Laboratory Steward, Thompson was to play a major part in the Association's work, not least in establishing and maintaining understanding with its neighbours in the Lake District. Soon more appointments were possible and the Association took over the whole of the Castle. The Easter Class, which in its time produced more converts to freshwater biology than any other agency in Britain, was started in 1932. Accounts of this phase of the Association's development are nostalgic; it was still possible to do important science with home-made apparatus, the Lake District was not yet overburdened with tourists and the staff, who were all young, seemed to have devoted their leisure to the devising of elaborate practical jokes. In 1937, as a result of an inspection by the Development Commission the previous year, more government money was forthcoming and a full-time director, E. B. Worthington (another student of Saunders's), was appointed. Up till then, Pearsall, by now Reader in Botany in the University of Leeds, had acted as part-time director, travelling over at week-ends, still on his bicycle.

In 1939 the Association had a scientific staff of seven. Inevitably, most of these were called away for war service, but evacuees came from the British Museum (Natural History) and the Fisheries Laboratory at Lowestoft. The work of the Association continued, and at least one project begun to help the war effort, the trapping of perch from Windermere for canning, was turned to scientific advantage.

After the Second World War expansion began to be more rapid, and the award of the Einar Naumann Medal to the Association at the International Limnological Congress in Zürich in 1948 confirmed the international status that the laboratory was achieving. This recognition reflected credit both on the Association's scientists and on its scientific advisers. Three of these, Pearsall, Saunders and Fritsch, have already been mentioned. Others were Professor P. A. Buxton, an entomologist of unconventional and wide-ranging mind and Professor W. A. F. Balfour-Browne, the first Honorary Secretary. All these exercised their scientific guidance lightly and informally, but extremely effectively. Scientific foresight and wisdom were not, however, the only assets and the Association owed a great deal, as

FIG. 3. FBA Council at Wray Castle, 1947.
*l.* to *r.* E. B. Worthington, H. C. Gilson, E. Trewavas, J. T. Saunders, H. D. Slack, R. Beddington, ?, H. Godwin, H. Munro Fox, M. Graham, F. E. Fritsch, Lt-Col E. F. W. Mackenzie, P. A. Buxton, Sir Albert Atkey, F. T. K. Pentelow, R. C. S. Walters, Capt W. N. McClean, M. G. M. Pryor, W. H. Pearsall, J. E. G. Raymont, R. W. S. Thompson, Mrs T. G. Tutin.

it still does, to its lay officers. R. Beddington, President from 1932 to 1960, was not only a generous benefactor and link with the angling world but took a personal interest in the scientists and their work. Alderman Sir Albert Atkey, Treasurer from 1933 to 1947, contributed a special interest in water supplies as well as sound financial guidance.

H. C. Gilson, yet another pupil of Saunders, succeeded Worthington as Director in 1946, and by 1950 the staff totalled forty-one. Wray Castle was too small, inconvenient and inaccessible and in 1950 the Association, which by now had dropped "of the British Empire" from its title, moved its laboratory four miles down Windermere to the Ferry Hotel, which as The

Ferry House is still its headquarters (Plate 6). This was a far more convenient building with better road access than Wray Castle, equidistant from the two ends of the lake, and with Esthwaite Water and the fish hatchery at Wraymires within easy reach. The $4\frac{1}{2}$ acres of land in which it stood seemed ample at the time for any future developments. Besides laboratory, library, office and workshop accommodation there was room for visiting classes and living quarters for some sixteen staff or visiting workers. For a visiting scientist it was ideal to live on the spot and to be able to use laboratories and library at all times of day and night. Facilities were added and improved, perhaps the most noteworthy at this time being the acquisition of a new research launch, *Velia* (Plate 6), which was launched by Mrs Beddington in 1958, replacing the worn-out *Mysis*. In 1960 Mr Beddington retired as President and was succeeded by Sir Edward Chadwyck-Healey, who for many years had represented the Fishmongers' Company on Council. By 1965 the staff at the Ferry House numbered over sixty, of whom twenty-one were scientists.

From the earliest days it was agreed that the Association ought to extend its work to running waters and pay attention to the hard alkaline waters of southern England as well as the soft acid waters of the north. In 1939 a sub-station for the investigation of coarse fish, sponsored by the National Federation of Anglers, was established in Cambridgeshire, with P. H. T. Hartley in charge. The war interrupted this venture, but it was completed in 1948. The Association also collaborated with the University College of Southampton in the Avon Biological Research until the war ended this in 1940. When the Association had settled itself in The Ferry House, thoughts turned in this direction again and in 1957, after attempts to obtain a site on the Hampshire Avon had failed, a site at East Stoke, Dorset, on a chalk river, the Frome, was selected and planning of a new laboratory began. The River Laboratory was built in 1963 and formally opened by the Countess of Albemarle, Chairman of the Development Commission, in 1965. This, the first purpose-built laboratory the Association had occupied, was by the site of an old water mill which provided for experimental channels and carried fishing rights. In 1965 it had a scientific staff of seven, E. D. Le Cren being Officer-in-Charge. Work at the River Laboratory was from the start arranged largely on a team basis and centred on the energy flow in the river ecosystem. The first ten years were largely devoted to describing the structure of the system by estimates of the biomass and biological production of what were thought to be the main components of the system. In more recent years there has been a development of inter-disciplinary experimental approaches to elucidate the processes involved in river ecology and the factors determining the rates of production and the

FIG. 4. The Ferry House: the tank room.

abundance of various species. Some of this work has been orientated towards the needs of the water industry. This has given the work of the River Laboratory a rather different flavour from that of the Windermere Laboratory. There is more emphasis on team work and collaborative ventures, though at the same time individual initiative has not been suppressed.

The Science and Technology Act, 1965 transferred responsibility for the funding and guidance of fisheries research from the Development Commission to a body newly constituted under the Act, the Natural Environment Research Council (NERC). The Association then became a grant-aided institution of the NERC, receiving its funds via NERC from the Department of Education and Science. NERC soon proved as helpful as the Development Commissioners had been. Both The Ferry House and the River Laboratory were filling up rapidly and new buildings and facilities were needed. The River Laboratory had been planned with an extension in mind and this was added, together with a flowing-water aquarium or "fluvarium" (Plate 7), both being opened by Mr Peter Walker, Secretary of State for the Environment, in 1971. Other important acquisitions for the River Laboratory were about 1 km of fishing rights on the River Frome, and the Waterston experimental station. The latter had been a water-cress bed and gave space for experimental channels fed directly by spring water. Recently it has seen the development of a circulating channel, a facility with great potentialities which enables controlled simulation of different river conditions (Plate 7). Requirements at the Windermere laboratory were met by the construction of a new wing containing a spacious library and various laboratories including accommodation for an electron microscope. Planning for this building began in 1967 and after various set-backs it was occupied in 1973, when it was opened by Mrs Pearsall and named in memory of her husband, who had died in 1964. The building (Plate 8), which was designed by Mr J. C. Gill, blends admirably with The Ferry House and its surroundings in spite of its modern idiom, and was later given a Heritage Year Award by the Civic Trust. The optimism of this period of expansion was diminished by one tragic weekend in March 1972 when the Association lost, through heart-attacks, two men, F. J. H. Mackereth (chemist) and G. J. Thompson (laboratory steward), who in different ways had made outstanding contributions to its work.

Having seen the River Laboratory and the Pearsall Building through to completion, H. C. Gilson retired as Director in 1973, to be succeeded by E. D. Le Cren from the River Laboratory. The new Officer-in-Charge at the River Laboratory was Dr A. D. Berrie from the Department of Zoology of Reading University. During Mr Gilson's twenty-six years of office, membership of the Association had grown from 619 to 1700, staff from 29 to 117, and the annual budget from £15,000 to £384,000; some 800 scientific papers had been published.

It has always been the view of the Association that it is better to investigate a limited number of waters thoroughly rather than to spread studies over a wide geographic range. Nevertheless, there are problems calling for attention that can best be solved at sites away from the main laboratories, or that require a broad "survey" approach where comparisons are made between a wide range of habitats. One such problem was that of the effects of building a regulating reservoir at Cow Green on trout, other fish and invertebrates, in the River Tees and its tributaries (Plate 9). Dr D. T. Crisp, who previously had worked at the River Laboratory, began an investigation of this in 1969 to obtain base-line data before construction began, using the Moor House laboratory of the Nature Conservancy as his headquarters. Later, this programme was expanded and the Cow Green Unit consisted of four members in 1977, when it became transmogrified into the Teesdale unit, based at Lartington treatment works of the

Northumbrian Water Authority and charged with the investigation of the ecological effects on fish of river regulation and the transfer of water from the Tyne to the Tees (Plate 9).

Another problem, that of highly eutrophic waters, has come to the fore in recent years as more and more organic waste and fertilizer from agricultural land find their way into fresh waters. The meres of north Shropshire are naturally eutrophic and in 1970 C. S. Reynolds, working from a small laboratory provided at the Preston Montford centre of the Field Studies Council, began a study of these waters which he carried on single-handed until, having achieved valuable results, he was called to the Windermere laboratory in 1975. This pattern of establishment of out-stations for the study of special problems has proved highly successful and may well be developed in the future.

In the period since 1970 there has been a growing feeling in governmental circles that science should be more orientated towards the solution of practical problems. At the same time the increasing demand for water has raised numerous management problems and accentuated the need for applied freshwater science. Inevitably the Association, which began as an organization for fundamental research, has been drawn into applied science, not least because many of the ideas which it produced from its "pure" research have become the basis for present day practice. The projects mentioned in the previous paragraph were initiated for practical reasons, and among others there was the work for the Morecambe Bay Barrage feasibility study carried on from the Windermere Laboratory between 1968 and 1971. The Rothschild Report, published in 1972, and the subsequent White Paper setting out the application of the "customer-contractor" principle to science, crystallized the situation. Some of the funds previously available to NERC, from the Science Vote administered by the Department of Education and Science, were to be transferred to executive departments so that these might commission research, of value to themselves, with the Research Councils, and through them with organizations such as the FBA. Initially it was a matter of seeing what existing research of the Association's was of interest to ministries, such as that for Agriculture, Fisheries and Food and the Department of the Environment, and making a book transfer of the necessary funding. Later, projects for commissioned research have evolved in dialogues between the Association's scientists and those in the ministries. Originally it was felt that it would be sufficient if about 20% of the Association's income were to come from commissioned research but, such is the practical value of freshwater biology, it had become almost 35% in 1978. This has inevitably meant a modification, but certainly not an abandonment, of the

Association's policy of allowing its staff, once they have established their capability, to pursue their own lines of research.

Other changes in the outlook, organization and work of the Association have followed from its success and growth. Increase in staff numbers has led to a continuous erosion of non-essential amenities. Living accommodation for staff has disappeared and in 1978 only a few small rooms in the annexe of The Ferry House remain for visiting research students. Accommodation for visiting classes from schools and colleges has had to be reduced. The Association's own Easter Class is no longer held, not so much for lack of space, but because it is felt that it has served its purpose and adequate training in freshwater biology is now available elsewhere. Instead, occasional specialist courses, as for example on freshwater microbiology or identification of aquatic invertebrates, have been given as needs have been recognized. Study of cost-effectiveness led to the conclusion, regretted by many, that the Association should no longer supply biological specimens for educational purposes.

The increase in staff numbers, which totalled 157 in 1978, and the increase in contract research and in the complexity of the Association's work have necessitated changes in organization; the days have passed when the Director or Chairman of Council could resolve a problem for a staff member over a casual cup of coffee in The Ferry House kitchen. When Dr. T. T. Macan retired in 1976, after having been with the Association since 1935 and its Deputy Director since 1946, it was decided that the Deputy-Directorship should be replaced by two Assistant-Directorships. Dr T. B. Bagenal, already on the staff of the Association, and Dr D. J. J. Kinsman, a graduate of Imperial College London who was previously Director of Graduate Studies in the Department of Geology and Geophysics at Princeton University, U.S.A., were appointed to these new posts. As a further step to maintain communications a house-journal was instituted in 1978.

In 1977 Sir Edward Chadwyck-Healey retired as President, having devotedly served the Association in this capacity for seventeen years. He was succeeded by Sir Edwin Arrowsmith. One of the first duties of the new President was to open the meeting room at the River Laboratory, the major part of the cost of which had been borne by the Nuffield Foundation. This was a much needed amenity providing space, hitherto completely lacking, for meetings, classes and general social purposes. With Stoke Mill Farm house and outbuildings, adjacent to the laboratory, purchased with NERC funds, the River Laboratory's immediate needs for accommodation have been ameliorated. Waters on which to carry out research were also extended in 1978 with the purchase of the West Holme fishing rights immediately downstream.

# THE PHILOSOPHY OF THE FRESHWATER BIOLOGICAL ASSOCIATION

The preceding pages have shown the outlook of the Association changing and evolving, but the basic philosophy is the same now as it was in 1929; that is, to achieve as complete an understanding as possible of the plants, animals and micro-organisms of fresh waters and of the ways in which they are related to their physical and chemical environment and each other. Sometimes the research to this end involves the carrying-through of a predetermined programme – as for example, in taxonomic studies on aquatic insects when the relating of larval forms to adults entails systematic rearing under controlled conditions. More often a complex situation is being dealt with and it is impossible to determine in advance what the key factor may be. A systematic working-through of a list of possibilities may pin-point the crucial factor but it will certainly be time-consuming and the right factor may not have been included in the list. Creative research is best carried out by individuals who are free to follow their own intuitions and possibly unorthodox ideas. Thus, from the start it has been the Association's policy to appoint, as key members of staff, persons who show the most promise of a capacity for independent research and then to allow them freedom to follow their own interests. In one distinguished case this resulted in a staff member, appointed as a zoologist, turning first to a study of lake chemistry in order to understand the factors controlling animal populations, then to hydrodynamics, in which field he has become a world authority, in order to understand the chemistry. In the long run this approach produces more practically useful knowledge than *ad hoc* investigations of immediate problems conducted according to schedules drawn up by committees. The body of knowledge of fresh water which has been built up in this way over 50 years by the Association is constantly drawn on to solve the everyday problems of water management. There could be no better evidence of this than that the Association's senior scientists, who have all followed their own unfettered ways in "pure" science, are now constantly in demand by government and industry as advisers on practical problems.

The control exerted by the Association's Council over the direction of research thus largely rests on the making of appointments and the provision of facilities. To ensure the best possible scientific advice on this, and to obtain informed opinion on all aspects of the use of water, membership of Council is drawn from a wide variety of organizations. Specialist members, covering all the relevant sciences from geology and chemistry to the various branches of biology, come from universities, government departments and research institutes, and in addition there are representatives of the water industry and fishing interests. All members of Council are encouraged to discuss research with individual members of staff, but the task of keeping abreast of the work going on is entrusted to the Scientific Advisory Committee, a body of about ten members drawn from and reporting to Council. This does its work mainly by informal dialogues between members and staff, and occasional seminars on particular topics. There is two-way traffic here; members of the Scientific Advisory Committee may be able to offer advice, but may also be educated in matters outside their own speciality at the same time. There is thus liaison with the water industry and customer departments via Council but there is also direct contact between the Association's staff and these outside interests in many ways. Time-analysis records show that at least the senior scientific staff spend a significant part of their time in activities not directly associated with their research. Such work, which includes editing, university teaching and service on working parties and committees, adds considerably to the Association's influence.

The customer-contractor principle has caused some modification in the Association's manner of operation. It is no longer possible for a senior member of staff to be completely free to pursue the research of his choice, but he must expect to spend some time on commissioned research within his field of competence. Inevitably this bears more heavily on some than others, but as far as possible the load is spread evenly and eased by provision of assistance. More often than not the commissioned research is on a topic he has initiated and would wish to work on anyway, and most scientists, in retrospect at least, welcome something which forces them to broaden their interests. Commissioned research accepted by the Association is mainly of the type described as "strategic", that is, research aimed at meeting forseeable or probable needs for knowledge, rather than at solving immediate practical problems. The latter type of investigation is more appropriately carried out by research associations or government or industrial laboratories. The decision to take on commissioned research is made by Council and its general progress is followed by the Scientific Advisory Committee, but the detailed running of a project is in the hands of the Association's staff concerned, in consultation with the customer's scientists.

# THE WORK OF THE ASSOCIATION – LAKES AND RIVERS AS ECOSYSTEMS

All sorts of living things in lakes, ponds, streams or rivers may be studied in many different ways but there is a single unifying concept which brings most aspects together. This is the concept of energy flow. The chemical elements from which living organisms are built are virtually indestructible; released by the excretion or death of one organism they are taken up by others, their chemical combination changed, released once more, and so on; always passing round in a cycle and never completely lost from the living world. The energy which all organisms need to drive their life-processes, on the other hand, enters and passes through the living world to be dissipated and lost irretrievably as heat. It arrives in the form of radiant energy from the sun, which green plants are able to convert into the chemical energy of organic compounds by the process of photosynthesis. This is called *primary production*. Animals, colourless plants such as fungi, and most bacteria are unable to do this and are dependent on the chemical energy which the green plants have stored. The production of animal material at the expense of plant material is called *secondary production*. Some animals, herbivores, depend directly on plants, others, carnivores, get their chemical energy at second hand (Plate 10). The flow of energy is not, however, a single stream from plant to herbivore to carnivore, but splits and joins up again in a complex way, so that it is better to speak of a *food web* rather than a food chain (Fig. 5). The flow of energy and the cycling of elements are loosely geared together so that, generally speaking, the availability of nutrient elements determines the magnitude of primary and secondary production.

Freshwater bodies are not completely self-contained and this introduces a complication into the study of energy flow in them. Lakes, ponds, rivers and streams all contain primary producers but in addition they receive chemical energy from outside in the form of organic detritus. The alder growing by a stream or lake drops its leaves into the water, and the inflow into a lake may bring, besides solid organic matter, dissolved organic matter from soil or sewage. The amount of this contribution from outside is relatively smaller the larger the water body. Thus for Windermere it is small, and the lake can be regarded as a self-contained system for many purposes, but for the River Frome detritus is a main source of energy. The river is inherently more difficult to study than the lake because it flows rapidly and often irregularly. It is not surprising, then, that freshwater

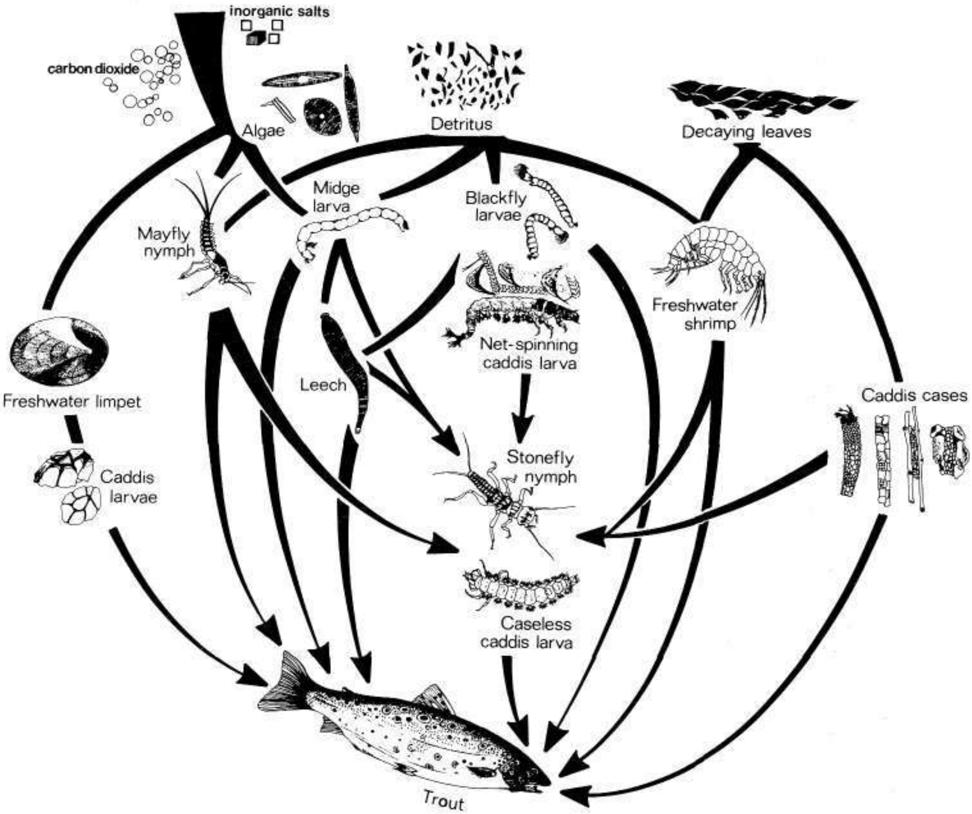


FIG. 5. Simplified picture of the foodweb in a stony stream. The basic sources of food are algae, detritus and fallen leaves. Some of the invertebrates and all the fish are carnivores.

biologists, including those in the Freshwater Biological Association, first turned most of their attention to lakes.

In temperate regions a layer of warm water, perhaps ten metres or so in depth, becomes established at the surface of a lake in the summer. A layer within which temperature falls sharply, the *thermocline*, which separates this warm layer from the colder water beneath, is also a region of change in density and acts as an effective barrier to mixing of the warm and cold layers. It usually happens that only in the warm layer is light penetration sufficient for the photosynthesis and growth of the microscopic floating plants of the lake, the *phytoplankton*. Besides light, these plants require mineral nutrients such as nitrate and phosphate in order to grow. Thus the amount of plant growth in a lake is determined by the stock of nutrients contained in the warm layer at the time when this is sealed off from the bottom waters in the spring. Apart from having a limited supply to start with, the warm layer is continually depleted of nutrients as the dead bodies of organisms which have grown in it sink into the lower layer.

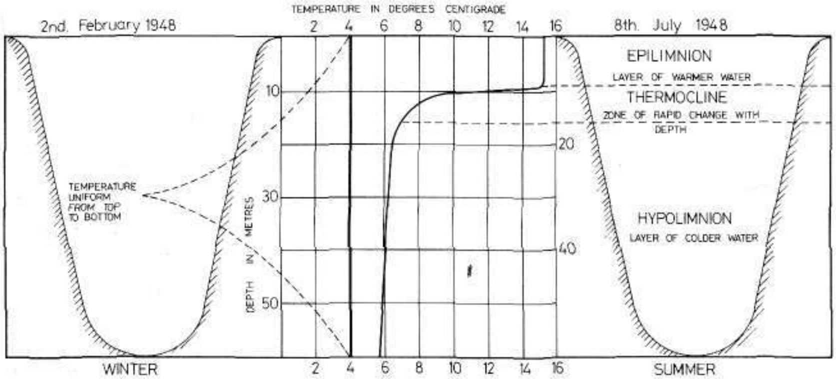


FIG. 6. The temperature of a lake (Windermere) at different depths, in winter (*l.*) and summer (*r.*).

Nearly 40 years ago, C. H. Mortimer carried out classic studies on Esthwaite Water which, being a shallow lake, has only a small volume of water below the thermocline. This means that the total amount of oxygen in the bottom layer is small and becomes used up as organic detritus decomposes, disappearing completely by about mid-July. In deeper lakes such as Wastwater and Windermere, the volumes below the thermocline are large, the amounts of organic matter decomposing are less, and oxygen never becomes exhausted during the summer. Using an ingenious piece of apparatus designed especially for this work by Mr B. M. Jenkin, Mortimer was able to obtain undisturbed samples of sediment, with overlying water, which could be investigated in the laboratory. So long as there was oxygen in the bottom water, the mud, although black and anaerobic at a depth of a centimetre or so, was brown and oxidized at the surface. As the oxygen became progressively used up in the lake the thickness of this layer diminished and it disappeared completely at the same time as the oxygen. Mortimer measured the thickness of the oxidized layer in the sediment of other lakes, and found it thickest in Ennerdale and progressively less thick in the other lakes as arranged in order of productivity (the "Pearsallian series"). In Esthwaite Water the disappearance of the oxidized layer is followed by an efflux of dissolved substances, among them ammonia, phosphate and ferrous iron, all important as potential plant nutrients. Mortimer was able to follow the physico-chemical events lying behind this efflux and in later work on water movements in lakes showed how the substances became rapidly distributed through the bottom waters by eddy diffusion. Thus during summer the bottom waters of Esthwaite become charged with nutrients and in autumn, when the surface waters cool and the lake becomes unstable enough for autumn gales to mix it from top to bottom, they become distributed through the whole lake. Mortimer had thus found an important distinction between lakes such as Esthwaite, and less productive ones such as the other large Lake District lakes, which maintain an oxidized surface layer on their sediments all the time and whose waters do not become recharged with nutrients in the same way.

The differing productivities of the English Lakes, ranging from the unproductive (or *oligotrophic*) Wastwater and Ennerdale Water at one extreme to the productive (or *eutrophic*) Esthwaite Water at the other, depend to a first approximation on the input to them of mineral nutrients. Wastwater and Ennerdale are surrounded by hard rocks and mainly uncultivated land, which yield little nutrient material in the drainage, whereas Esthwaite lies amid agricultural lands on softer rocks, and the water entering the lake is comparatively rich in nutrients (Plate 11). From the first, the Association has had a programme of monitoring the changes in concentrations of the more important nutrient elements in the Lakes and particularly in Windermere, Blelham Tarn and Esthwaite Water (and, incidentally, has been in the fore in improving techniques of water analysis).

The phytoplankton algae (Plate 12), the primary producers, show an annual cycle which can be related in part to the cycle of the nutrients on which they depend. Characteristically there is a burst of growth in spring when the waters have become charged with nutrients, and light and temperature are favourable. In mid-summer, seemingly corresponding with depletion of nutrients in the surface waters, there is a falling-off in the standing stock of phytoplankton, to be followed in the autumn with another burst of growth as nutrient-rich bottom water begins to be mixed into the upper layers. There are, however, many unexplained features in this cycle, not the least being that different species succeed each other in a pattern which, although varying in detail, shows the same general features from year to year. In setting out to investigate this in 1945, J. W. G. Lund decided that it was best to concentrate on a single species and selected the diatom *Asterionella formosa*, which is often dominant in the English Lakes. He then accumulated detailed records of changes in its numbers, and in factors possibly affecting its growth, in a small group of lakes over a long period. Eventually data covering a quarter of a century were available, but certain features were evident by 1949. In winter, nutrients are in ample supply and low temperatures and low light are not sufficiently limiting to prevent growth. However, the mixing of the lake which takes place in winter means that the population is distributed into the unlit depths and so, on the average, a cell gets insufficient light to multiply, and the greater rainfall means that cells are carried away in the outflow faster than they are produced. Once the lake begins to stratify and becomes more stable in the spring, a population of *Asterionella* can remain near the surface sufficiently long to get enough light to support multiplication. Thereafter, increase in the population follows a fairly regular course, with doubling every six days or so for about six weeks so that numbers increase from about 10 to almost 10 000 cells per ml. After this there comes an abrupt falling-off. Lund showed that in Windermere this always corresponds with the concentration of silicon in the water falling below a certain level. Other factors – light and concentrations of carbon dioxide, nitrate and phosphate – remain in sufficient supply for further growth so that other species, such as green algae, not requiring silicon are able to take over and succeed the *Asterionella*. Although they never seem to be the direct cause of the decline of *Asterionella* populations, epidemics of a fungal parasite, *Rhizophidium planktonicum*, often accelerate it. Dr Hilda M. Canter (Mrs J. W. G. Lund) pioneered the study of this and other fungal parasites of freshwater phytoplankton, and later extended her work to include protozoa which attack algae (Plate 12).

Another planktonic diatom, *Melosira italica* sub-species *subarctica*, having a quite different kind of periodicity from that of *Asterionella*, has also been investigated by Lund. This diatom, which is frequently

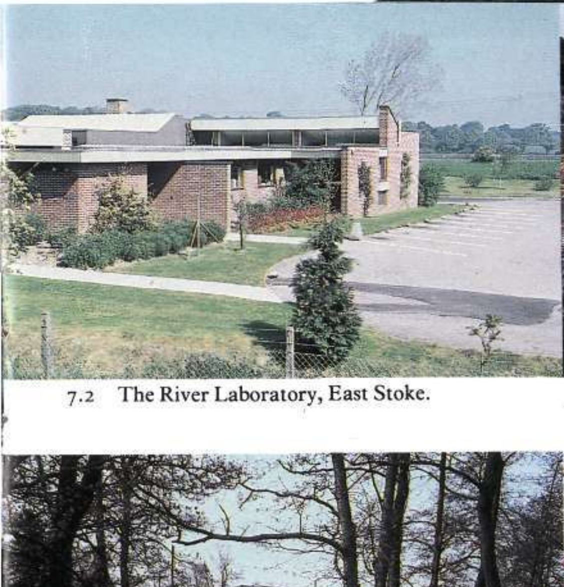
5.1 Pike fishing on the River Frome, Dorset.

5.2 and 5.3 Brown trout hatchery near Pickering, Yorkshire.

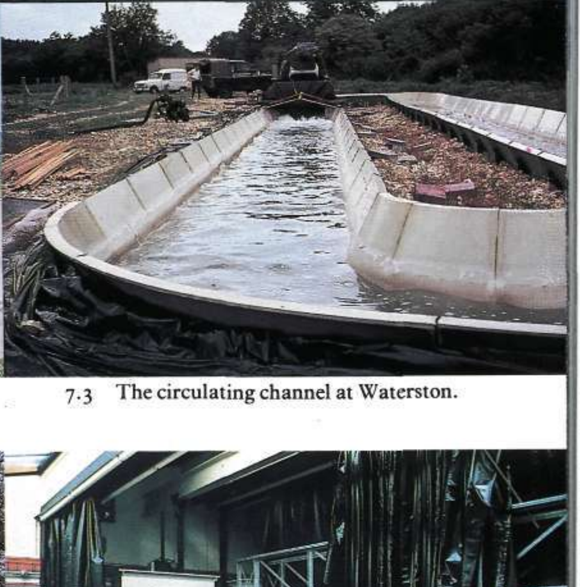
6.1 The Ferry House: looking across Windermere from Ferry Nab.

6.2 The launch 'Velia' at the jetty by The Ferry House. The fishponds are in the trees behind.

7.1 The River Frome, Dorset: *Ranunculus* in flower.



7.2 The River Laboratory, East Stoke.



7.3 The circulating channel at Waterston.

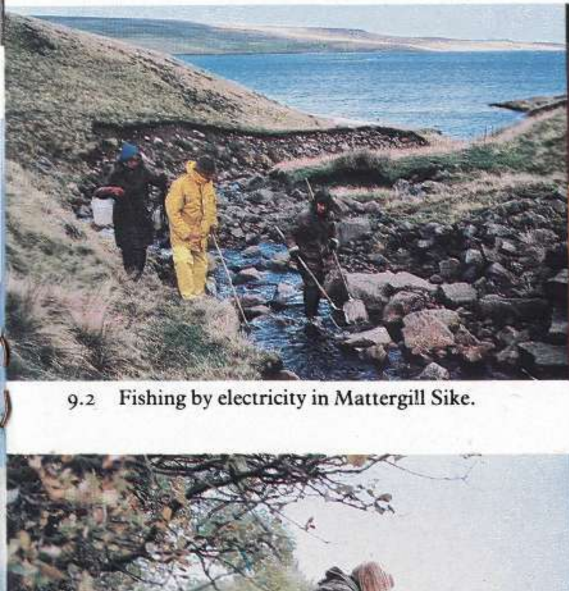
7.4 The fluvarium (downstream end).

7.5 The fluvarium (interior).

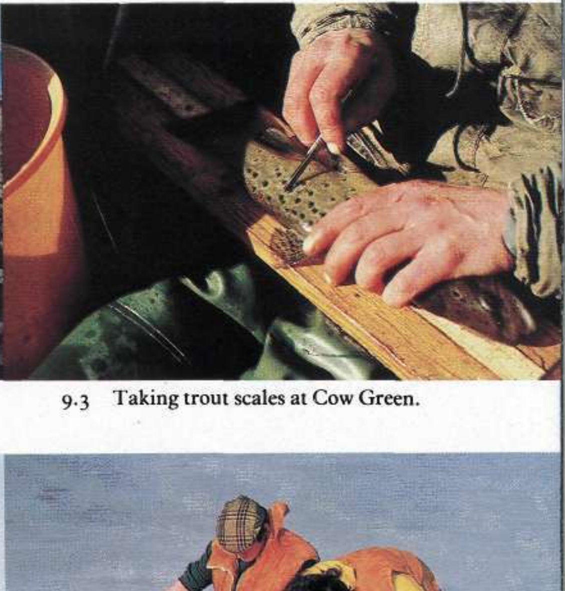
8.1 The Ferry House and the Pearsall Building, from the west.

8.2 The Pearsall Building, opened in 1973.

9.1 Seine-netting for trout at Cow Green reservoir, Upper Teesdale.



9.2 Fishing by electricity in Mattergill Sike.



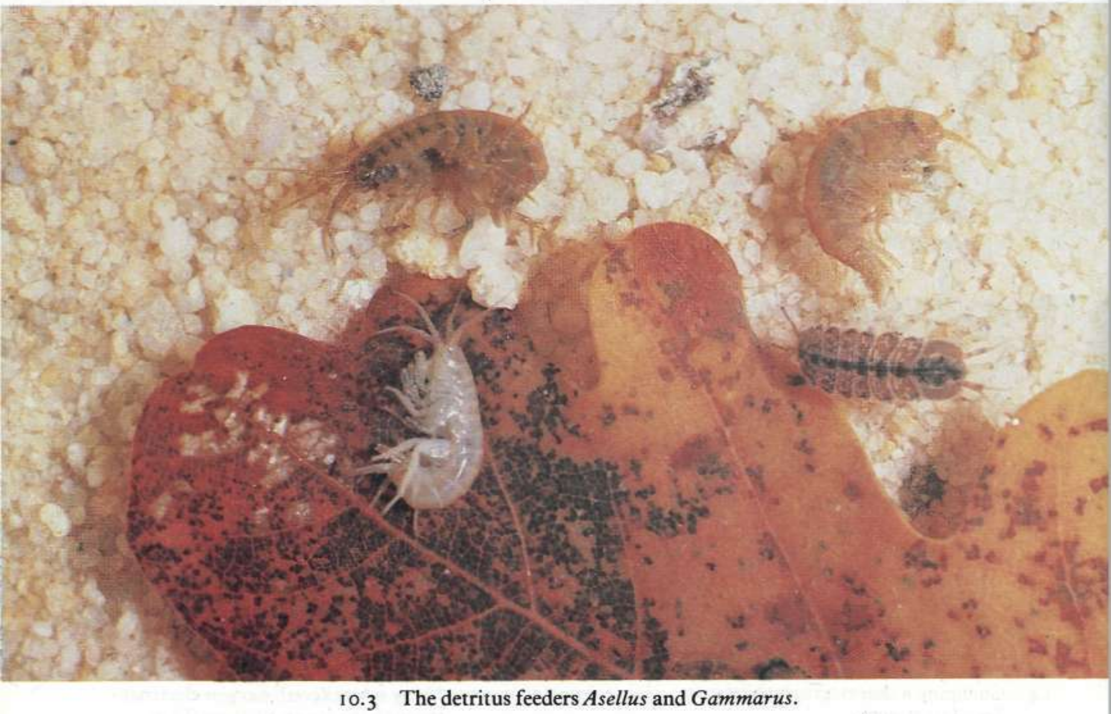
9.3 Taking trout scales at Cow Green.

9.4 Changing a thermograph chart on a Teesdale stream.

9.5 Using a Mackereth oxygen electrode through the ice on Blelham Tarn.

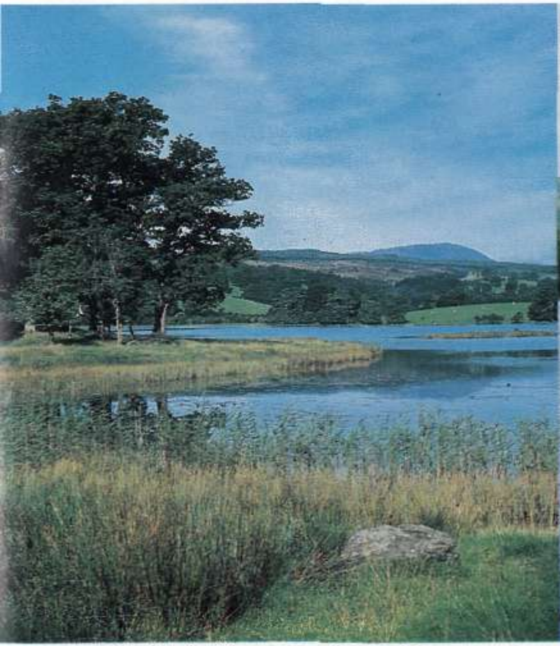
10.1 *Daphnia hyalina*: a herbivorous cladoceran.

10.2 *Dendrocoelum lacteum*: a carnivorous flatworm.



10.3 The detritus feeders *Asellus* and *Gammarus*.

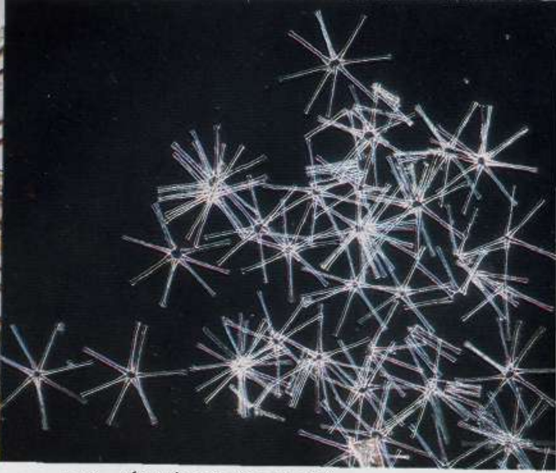
11.1 Ennerdale Water: an unproductive lake.



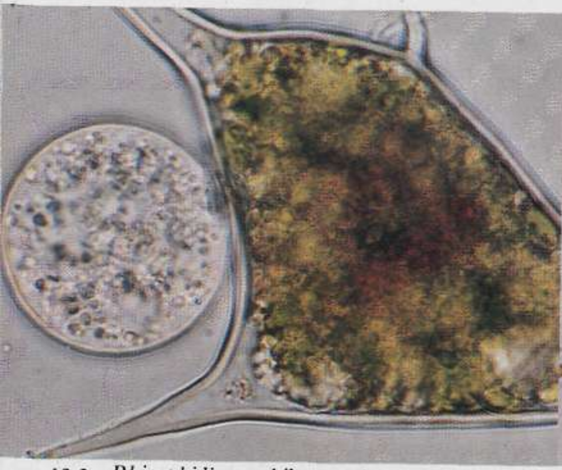
11.2 Esthwaite Water: a productive lake.

11.3 Sampling on Priest Pot, Esthwaite.

12.1 Diatoms and *Oscillatoria.*



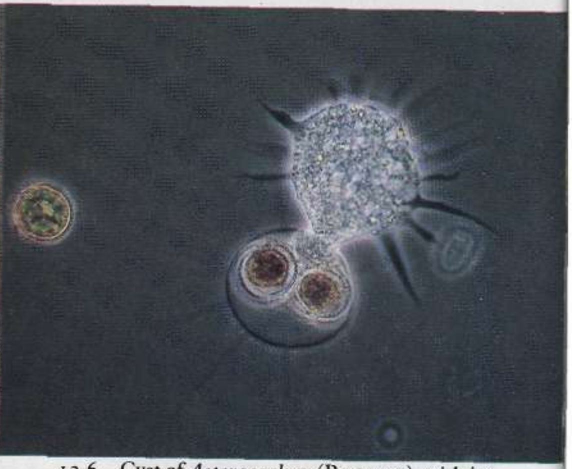
12.2 *Asterionella* (dead cells).



12.3 *Rhizophidium nobile*, parasite on resting spore of *Ceratium*.

12.4 Sporangium of a chytrid parasite on *Asterionella*.

12.5 *Cosmarium* parasitized by a chytrid, which bears another chytrid hyperparasite.



12.6 Cyst of *Asterocoelum* (Protozoa), with its amoeba emerging.

abundant in Blelham Tarn, has a thicker silica shell than *Asterionella* and consequently sinks 3 to 5 times faster, so that it is abundant in the plankton only during the period from autumn to late spring when the tarn is mixed vigorously by wind. If calm weather or ice allows the water column to become stable during the winter, *Melosira* disappears from the plankton as it does during the period of thermal stratification in summer. The cells are able to remain alive in the deposits on the bottom of the lake sufficiently long to ensure rapid re-establishment in the plankton once conditions become turbulent again.

To supplement these observations on lakes themselves, experiments with plankton algae in laboratory culture have been carried out. From this line of work has developed a precise means of determining the capacity of a given water to support phytoplankton growth. A chemical analysis can give some idea of the productivity of a water sample, but can be unreliable because of the complicated way in which factors interact to affect algal growth. It is much better to carry out a *bioassay* in which the growth response of one or more algae in the water sample under controlled conditions is determined. Such bioassays have been used to predict the amount of algal growth that might occur in the waters which would be accumulated if a barrage were constructed in Morecambe Bay, or in waters resulting from transfer between river systems.

An obvious approach to understanding the conditions which control algal growth in a lake is to carry out experiments with samples held under actual lake conditions. The great difficulty here is that as soon as one encloses a water sample in a bottle one has introduced a completely new and dominant factor – a solid surface. Among other things a solid surface encourages bacterial growth so that within a few hours one's sample bears little resemblance to what it was initially. Lund decided on the bold way out of this difficulty and has pioneered the use in experimental limnology of containers sufficiently large for the surface effects to be negligible. In 1970 he set up in Blelham Tarn two vertical tubes of butyl rubber, 45·5 m in diameter, floating at the top and bedded in the mud at the bottom (Plate 13). Each contains some 18 000 cubic metres of water and growth on the walls is negligible compared with that in the plankton. Over long periods the same species of plankton algae are found inside the tubes as occur outside and the same sort of seasonal cycle occurs. The populations are smaller inside the tubes however, evidently because access to nutrients entering the lake from outside is prevented. Observations and experiments on the water columns enclosed in these tubes are giving valuable insights into the nature of eutrophication and have given encouraging indications that once the excessive inflow of nutrients into a small lake ceases, its recovery to a more wholesome condition may be rapid. The effect of a fertilizer or other substance added to one tube may be determined by reference to a control tube without the addition. "Lund tubes", as they have come to be called, have proved to be a most valuable experimental facility and are now being used in several parts of the world (Fig. 8) both in fresh water and the sea, as well as for further experiments in Blelham Tarn.

Another line of approach to understanding phytoplankton production has been through examination of the relations of growth rates to photosynthetic rates and of these to the light and carbon dioxide concentrations available in lakes. Taking advantage of the fact that *Asterionella formosa* often occurs in nearly pure populations in Windermere, J. F. Talling has been able to relate its behaviour in laboratory experiments to its activity in the lake. His formulation of the relationship of photosynthesis to light intensity and depth in the lake has proved extremely useful and is used in many of the mathematical models of phytoplankton productivity which have been devised in recent years. The physical chemistry of the carbonate system in fresh water and the uptake of carbon dioxide by phytoplankton, which may be crucial factors in eutrophication, have also been studied by Talling.

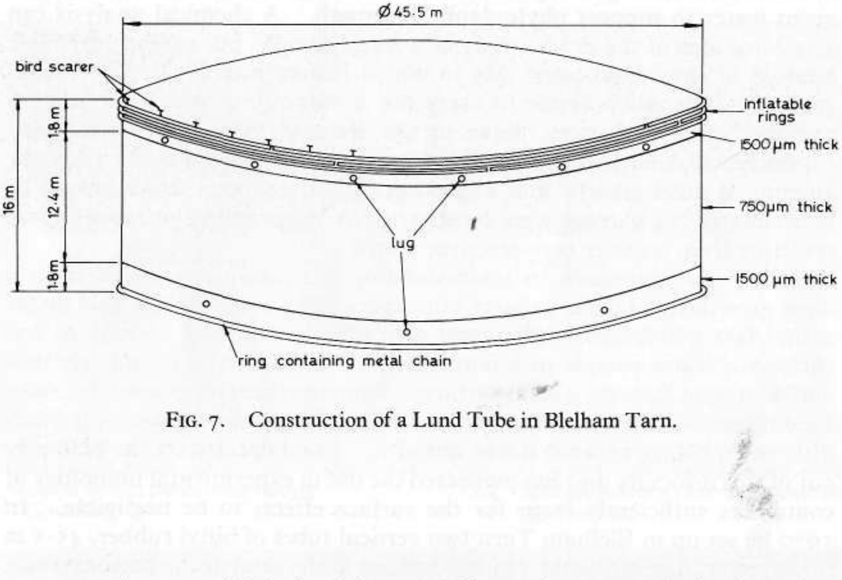


FIG. 7. Construction of a Lund Tube in Blelham Tarn.

FIG. 8. Lund Tubes in the 'Grote Rug' reservoir near Dordrecht, Netherlands.

Recent work has been exploring the phenomena described above in further detail, refining the scale in time and space of the biological and chemical events that take place in the lake and near the mud surface. For example, in recent years, the summer phytoplankton of Esthwaite Water (Plate 13) has been dominated by *Ceratium*, an alga which has the power, like animals, of swimming and so migrating up and down in depth. It may be able to use this behaviour to recharge itself with nutrients from the hypolimnion.

The study of aquatic micro-organisms other than algae has been generally neglected, but there is no doubt that they play a vital part in fresh water in the decomposition processes which ensure cycling of nutrients, and it is likely that they are also of importance as food for many animals. Bacteria in Lake District waters have been studied by C. B. Taylor, V. G. Collins and J. G. Jones (Plate 13) and fungi by L. G. Willoughby. Techniques have been worked out and a general picture of the distribution of these micro-organisms has been built up. Stratification and deoxygenation in a lake have a major influence on the populations, and there is a relation to the algal population and the concentration of nitrate and phosphate. A study of the nitrogen cycle in Grasmere, in relation to the recent installation of a sewage treatment plant for the village, has been carried out.

The *zooplankton* shows a general relationship to the phytoplankton in that there is a peak in numbers following that of phytoplankton in the spring in any given lake, and in the whole series of lakes the abundance of zooplankton is greater the greater the phytoplankton productivity. On the whole the variation between lakes is in abundance rather than species. The crustaceans *Daphnia hyalina, Bosmina coregoni* var. *obtusirostris, Leptodora kindti* and *Bythotrephes* occur in most lakes and *Diaptomus gracilis* is present in all of them (Plate 14). Interpretation of the fluctuations in zooplankton numbers requires a knowledge of the life cycle of the organisms, and for a number of those in the English Lakes this has been provided by W. J. P. Smyly. Most planktonic crustaceans have a resting stage, which is sometimes the egg, but in *Mesocyclops leuckarti* it is the final copepodid instar which spends the winter dormant in the bottom sediments. The factors controlling dormancy are not yet fully understood but it may be ended by a rise in temperature. The increase in numbers in the plankton depends on the balance between recruitment rate and mortality. The growth of individuals is affected by the amount and kind of food, and egg production by food, age and body size. For *Cyclops abyssorum* in Buttermere, an unproductive lake, it has been found that clutch size is limited by the food supply. The clutch sizes of Buttermere females can be doubled by feeding them artificially. The stock of a particular zooplankton species is not, however, very closely related to clutch size; it seems to depend much more on survival of young after hatching. Competition with other species for food, as well as predation, is a cause of mortality. Lund tubes are providing a means of investigating competition and predation under field conditions.

Samples of plankton have been taken and preserved routinely almost since the beginning of the Association's activities. This provides a means of checking back on the composition of the plankton at any time and the value of the material is particularly well shown by the work of an American visitor, W. T. Edmondson. Working through 400 samples collected over a two-year period, he was able to examine the relationship between egg production by planktonic rotifers (Plate 1), and the abundance of various phytoplankton species. His results suggest that these rotifers are selective in their feeding, *Keratella cochlearis* and *Kellicottia longispina* preferring a small flagellate, *Chrysochromulina*, whereas a third species, *Polyarthra* *vulgaris*, preferred another flagellate *Cryptomonas*, even although other forms of a similar size were more abundant at the time. In general our knowledge of the food organisms for zooplankton is fragmentary.

The mechanisms of feeding of crustaceans are varied and often elaborate and highly specialized. These mechanisms have been the special study of G. Fryer. Apart from species from the zooplankton of the English Lakes he has studied others such as the atyids, tropical freshwater prawns of considerable commercial importance. Those studied are detritus feeders and have various elaborate modifications of their mouthparts for collecting, sorting and masticating their food. The knowledge of their life histories gathered by Fryer points to the importance of conservation of their habitat if they are to continue to be an important food source in the West Indies, and suggests the possibility of artificial culture in temperate climates.

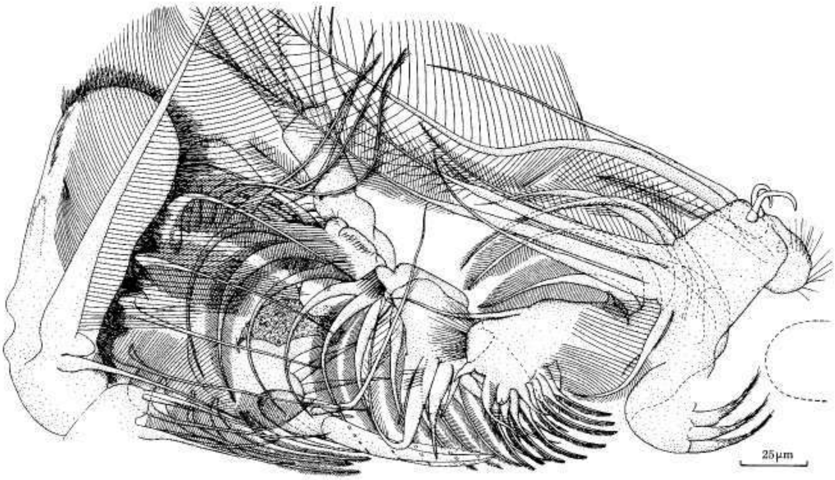


FIG. 9. Cladoceran feeding mechanism: the filter chamber and associated structures of *Ilyocryptus sordidus*.

Even in a large lake such as Windermere the life in the shallow littoral is a substantial fraction of the total. The character of littoral communities in any one lake is determined largely by degree of exposure, and we find reed swamp and water-lilies in the mud of sheltered bays whereas the more stony substrata of exposed shores have only submerged plants such as the pteridophyte *Isoetes* and the stoneworts *Chara* and *Nitella* (Plate 14). The proportions of these types of littoral communities vary between lakes. At one extreme Esthwaite has a preponderance of pond weeds such as *Potamogeton* spp. (Plate 1), *Elodea canadensis* and *Naias flexilis* among its submerged vegetation, whereas at the other Wastwater is characterized by *Isoetes* and stoneworts. The extensive investigations of T. T. Macan have show that bottom-living invertebrates, too, are distributed in accord with the Pearsallian series, with steady progression from a fauna in which Ephemeroptera and Plecoptera predominate to one in which these groups are scarcely represented, and the commonest animals are planarians, crustaceans, snails and leeches (Plate 15). Much of Macan's work has had to be taxonomic, since with large groups of insects existing taxonomy did not include the nymphs and larvae which are the forms encountered by the freshwater ecologist. There are also great difficulties in quantitative sampling but a standardized collecting procedure carried out for a fixed time has yielded useful results. It is clear that the biomass of the bottom fauna diminishes with the productivity of the lake. Thus nearly 6000 invertebrates belonging to various phyla were collected in 100 minutes from a stony substratum in Esthwaite as compared with less than 200 in a comparable collection from Wastwater. Variety is different as well as amount; whereas only two species of water-snail are found in Wastwater there are eight in Esthwaite.

Within any one lake such as Windermere the amount and variety of the fauna are related to the nature of the substratum. Macan found that among the water-bugs (Plate 15), *Micronecta poweri* occurred only where the percentage of organic matter in the deposit was low. *Sigara scotti*, on the other hand, was found only where this percentage was as high as 50. Enrichment is another factor affecting the fauna. That part of Windermere which receives sewage effluents is, like the most productive lake, Esthwaite, characterized by an abundance of flatworms and the water hoglouse (*Asellus*) (Plate 10) and a paucity of mayflies and stoneflies. Another approach to understanding the distribution of invertebrates is via their physiology. D. W. Sutcliffe is investigating the osmoregulation of Crustacea and insects in relation to the chemistry and acidity of streams.

The fish of the English Lakes (Plate 16) are mostly carnivorous and subsist on the zooplankton and bottom-living invertebrates which have been discussed above. Again, the distribution of species is related to the Pearsallian series. Trout dominate the less productive lakes, and perch and pike are absent from Wastwater. In the more productive lakes trout persist but coarse fish such as perch, pike, rudd and roach become more abundant. Eels are probably present in all lakes, but the char, *Salvelinus*, which is closely related to the trout, is absent from some of the productive ones – Derwentwater, Bassenthwaite, Ullswater and Esthwaite. The presence and abundance of a particular species in a lake depend upon a complex of factors including temperature, oxygen concentrations, the availability of spawning grounds and, perhaps most importantly, conditions and food supply for the youngest stages. Reliable information about the operation of these factors is difficult to acquire but, thanks to the painstaking observations of K. R. Allen, E. B. Worthington, W. E. Frost, E. D. Le Cren, C. Kipling, J. C. McCormack, T. B. Bagenal and others, we now have a good knowledge of the natural history of most of the Lake District fish. There are still gaps in our information about the Windermere char; little is known about the fry, for example. Frost found that there are two distinct breeding populations, one spawning in shallow water in the autumn, the other in deep water in the spring, and they can be distinguished by the number of gill-rakers on the lower part of the first gill arch and by small differences in the scales.

A major study of the population dynamics of perch and pike in Windermere originated from the trapping programme started in 1941. By 1947 when fishing ceased, 50 tons of perch had been removed from the north basin and between 1941 and 1964, 70 tons from the south basin. In both basins monitoring of the population continued after fishing had stopped and has shown the effects of the fishing to have been long lasting. The fishery for pike was started in 1944, again with the idea of promoting trout production, with an initial catch of about 3 tons and has continued up to the time of writing with an annual catch of 1 ton. The ages of samples of both perch and pike have been determined from opercular bones and from this they can be placed in year classes. Analysis of the data by Le Cren and Kipling has shown that pike year-class strengths are correlated with temperature conditions during the first few months of life but perch year-class strengths are less dependent on temperature conditions. Several factors may reduce the success of a perch year-class. A strong year-class is unlikely to occur when perch biomass in the lake is already high, when predation by pike or mergansers is high, or when ice-cover the previous winter was high. A combination of favourable circumstances is rather rare. Recent analysis by J. F. Craig of natural changes in the perch population between 1966 and 1976 has shown that the total weight or biomass over this period was similar to what it had been in 1940 before the trapping experiment began. However, this weight of fish was made up of a much smaller number of faster-growing and thus heavier individuals. In 1976 a new factor unexpectedly came into operation. A disease attacked the perch and killed 98% of the adults. The primary cause of this disease is still unknown, but it is probably the same disease which has attacked perch populations elsewhere in England in recent years. The effects of this catastrophic mortality cannot yet be assessed, but monitoring in 1978 suggested that the perch population may already be beginning to recover.

Accurate knowledge of the relationship between feeding and growth, which is necessary for the interpretation of field data, as well as for efficiency in fish farming, has been obtained for brown trout by J. M. Elliott. Energy budgets for fish fed on the freshwater shrimp, *Gammarus pulex*, were determined at various temperatures. Appetite increased with rise in temperature to a steady value between 13 and 18 °C, the amount eaten increasing with weight of fish. The number of meals per day increased from one at about 4 °C to three at about 18 °C and the rate of gastric evacuation also increased with temperature. For most

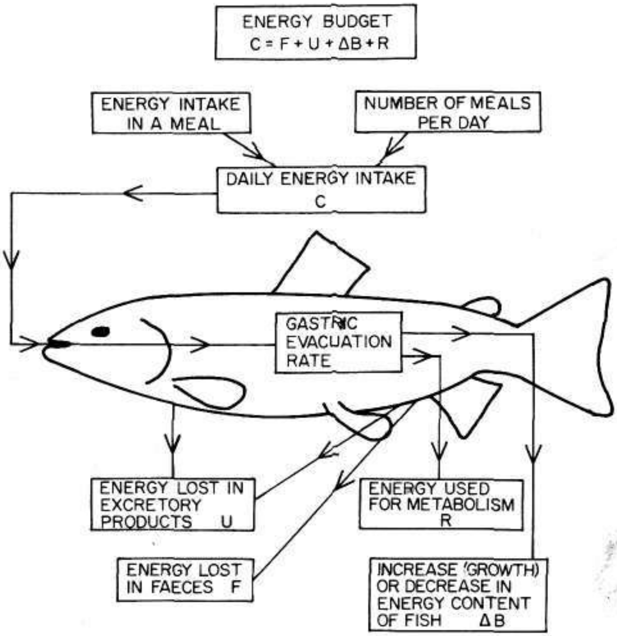


FIG. 10. The relationship between the major components of the energy budget of a trout.

combinations of temperature and ration size, from 70 to 75% of the food energy taken in was available for metabolism and growth, the rest being lost in faeces and excretion products. The relationships of these various quantities to temperature, body weight and time have been combined into a mathematical model which can be used to predict the growth of both wild and hatchery-reared trout feeding on a variety of food organisms.

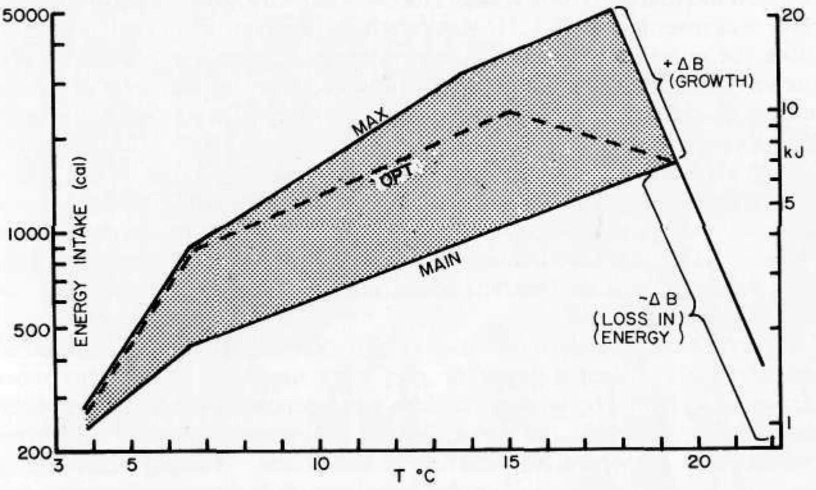


FIG. 11. The relationship between the maximum, optimum and maintenance energy intake for a trout.

Another fish that has been studied in detail is the river lamprey, *Lampetra fluviatilis*, a representative of a primitive group of vertebrates, which as a parasite on other fish is of interest from both the academic and economic viewpoints. A. D. Pickering has studied the physiological changes which occur during the complex life cycle of this unique animal.

On the geological time scale, lakes are ephemeral features of the landscape and subject to continual change. Those in the English Lake District date from the last glaciation about 14 000 years ago. However, as bottom deposits accumulate, so they incorporate the more durable remains of plankton, pollen and dust from the air, arrow heads, coca-cola bottle tops, and chemical evidence of prevailing conditions – all in chronological order, provided that slumping does not occur. The history of a lake thus lies recorded in its deposits, if only we can read it. Pearsall and Mortimer perceived the importance of this and initiated work on sediments. The first problem is to obtain cores, with a minimum disturbance of their layering, from deposits which may be six metres or so in thickness in the deepest part of a lake. The first corer to be used by the Association consisted of drain-pipes, and cores were successfully obtained. The second was designed by B. M. Jenkin; this cut a half-cylinder of mud without compression or smearing but since it had to be operated from a pontoon moored with four anchors its use was restricted. A more portable corer was invented by F. J. H. Mackereth. This consists of two concentric tubes the outer of which has at its lower end a large metal cylinder, the anchor chamber. The apparatus is lowered from a boat and when the anchor chamber touches bottom it is pumped free of water so that it sinks into the mud to provide a firm base for further operations. The inner tube is then forced down into the deposit by compressed air and, when it has been driven in up to the hilt, the air is diverted to fill the anchor chamber. This then becomes buoyant and the apparatus returns to the surface. The Mackereth corer has operated extremely well and has been used widely in the Lake District, Scotland and elsewhere, in upland tarns as well as larger lakes.

A core from Windermere has at the bottom, at about six metres, laminated clay, then a layer of grey silty mud and above this more laminated clay. The laminated clays were deposited during times when there were glaciers in the Lake District mountains, and the silty layer represents a temporary amelioration of conditions. On top of these clay deposits is some four and a half metres of brown mud which has accumulated in the post-glacial period. At the top is 20-30 centimetres of black ooze. Horizons in the core may be dated either by pollen analysis, in which the distribution of different kinds of pollen extracted from it is matched up with that from dated cores from other sites, or by radiocarbon dating. Just before his untimely death, F. J. H. Mackereth developed a technique for measuring the magnetic properties of cores, which provides a detailed and accurate record of the behaviour of the earth's magnetic field over the last 15 000 years, and thus a means of dating. Examination of diatom frustules and other remains of organisms, and analysis of both inorganic and organic composition, may give a good idea of the productivity of the lake and its catchment area and the chemical conditions prevailing when the deposit was laid down. The picture that has emerged from the studies of the palaeolimnological team led by Dr Winifred Pennington (Mrs T. G. Tutin) is that the lake waters were richest in nutrients just after the ice had retreated and that, until man's activities in recent years reversed it, the trend was one of increasing impoverishment as mineral ions were leached from the catchment. So Esthwaite has been

FIG. 12. Wide-diameter Mackereth mini-corer being operated from its pontoon.

productive from the beginning and Pearsall's series does not actually represent an evolutionary sequence as he thought. The brown mud has been laid down in the period following the recolonization of the land by plants, and changes in its composition can be related to forest clearances from about 3000 B.C. (Neolithic times) and from Roman times onwards. The surface ooze has been formed in the last 150 years as a result of the adoption of water closets and the consequent increased discharge of sewage into the lakes. These palaeolimnological studies are not only of great interest in the wider context of the history of climate and vegetation in the British Isles but provide a basis for prediction of future changes in the lakes.

Various studies on Lake District streams have been carried out since the Association was founded, but the main effort on running waters began comparatively recently with the establishment of the River Laboratory. As in lakes, algae and macrophytes (mainly aquatic vascular plants) are active as primary producers but a river also receives a considerable input of dead organic matter from the catchment. The regular analyses of the chalk streams around the River Laboratory (Plate 5) which have been carried out by H. Casey since 1964 have shown that there is nearly always in the waters an excess of nutrients over the requirements of the plants. Small chalk-streams do not carry a natural phytoplankton and most algae live attached to stones and weeds. This makes their amount difficult to estimate but A. F. H. Marker has devised a method for algae growing on stones which depends on the extraction of pigments in methanol. This has shown that, as in lakes, there is a peak of algal growth in spring and variable growth during the summer and autumn. The maximum biomass of algae is probably between 10 and 20 g dry weight per square metre as compared with 100 to 500 g of water crowfoot. Measurements of algal photosynthesis suggest that annual production is over fifteen times greater than the maximum biomass. The algae are prevented from accumulating by washing off and grazing by herbivorous invertebrates. Photosynthesis is limited by light and temperature in winter but biomass is probably controlled by variations in discharge and changing patterns of weed beds.

The growth and production of river macrophytes has been studied by D. F. Westlake and his associates (Plate 7). With these plants, in contrast to the algae, more of the production accumulates as biomass. In watercress beds this is a good thing; elsewhere it can be a nuisance and water authorities spend a great deal of effort in keeping down weed growth in streams. The results obtained at the River Laboratory suggest various means such as the judicious planting of shade trees along the bank, which might greatly reduce the need to cut weeds.

The nature and quantity of organic detritus in streams are, as one would expect, extremely variable. Estimates of its quantity on an hourly or daily basis, made with the aid of regular water samples, drift nets or screens, show variations of one-hundredfold in the same stream. I. Farr has shown that, even in the unusually stable flow conditions of a chalk-stream, floods play a large part in this variation, the peak movement of particulate organic detritus having a particular timing in relation to the changes in water flow. At times this detritus may consist mainly of material produced outside the stream, alder leaves for example, at other times it may be largely the remains of water-weeds. Microbial activity probably plays a part in modifying detritus before it is eaten by animals. Studies by J. H. Baker on the bacteria have shown that, except during winter spates, when the species found are largely derived from soil, a river has its own characteristic microbial flora. The average bacterial concentrations at any one site along a river increase with its discharge.

The invertebrates which convert these various materials into food for fish have been studied from the taxonomic point of view by L. C. V. Pinder, T. Gledhill and others. An ability to identify the species of invertebrates present is an essential prerequisite to the longer-term aim of elucidating their ecology. The taxonomy of the non-biting midges belonging to the family Chironomidae has been particularly confusing, but an illustrated key to the adult males of the British species has been published by Pinder. Work on keys to help distinguish the larvae of chironomids is now in progress, in collaboration with experts in other countries. The population density of these larvae has been found to reach 17 000 per square metre on bottom sediments and 100 000 per square metre on water crowfoot in the Tadnoll Brook in early summer. The factors influencing the dynamics of these populations are still obscure but the quantity and quality of food and the availability of suitable habitats are clearly important. Chironomids are among the most ubiquitous of freshwater invertebrates and are a major source of food for trout and salmon parr as well as other fish.

FIG. 13. The larva of a species of *Chironomus*.

A team led by M. Ladle has been working on the ecology of those stream invertebrates especially associated with organic detritus. Life tables have been constructed for the freshwater shrimp, *Gammarus pulex* (Plate 10), which is a detritus feeder reaching population densities of 10 000 per square metre. The physiology of the freshwater species of *Gammarus* in relation to their osmoregulation has been studied at Windermere by D. W. Sutcliffe. He is also collaborating with L. G. Willoughby in an investigation of the role of fungi in processing the detrital food of *Gammarus pulex*. Another group being studied at the River Laboratory is the family of biting-gnats called the Simuliidae. Their larvae are abundant in chalk-streams, where they attach themselves to weeds and feed by filtering out particles from the water. Different species inhabit different types of river and one, *Metacnephia amphora*, has been discovered to specialize in living in those small temporary chalk-streams known as winterbournes.

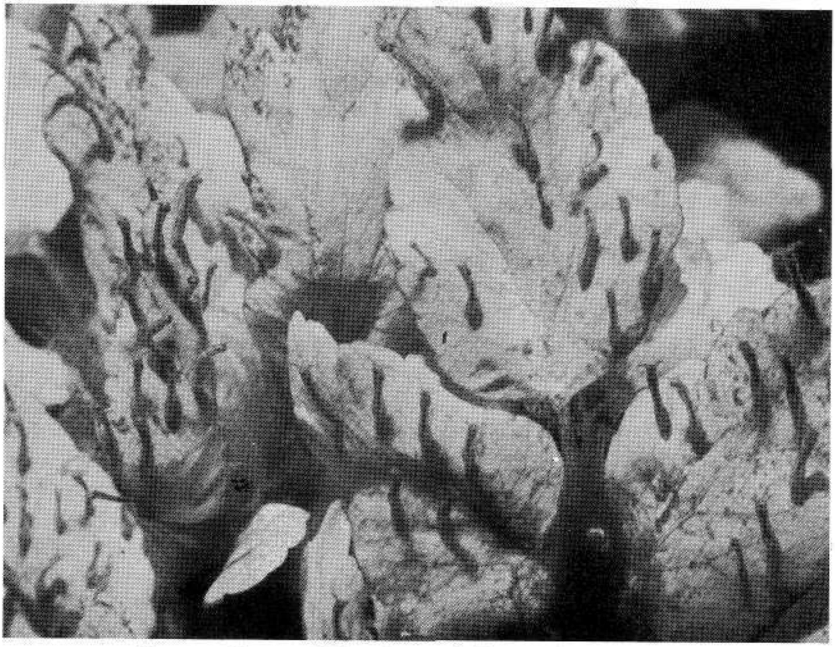


FIG. 14. Larvae of *Simulium* on the leaves of aquatic plants.

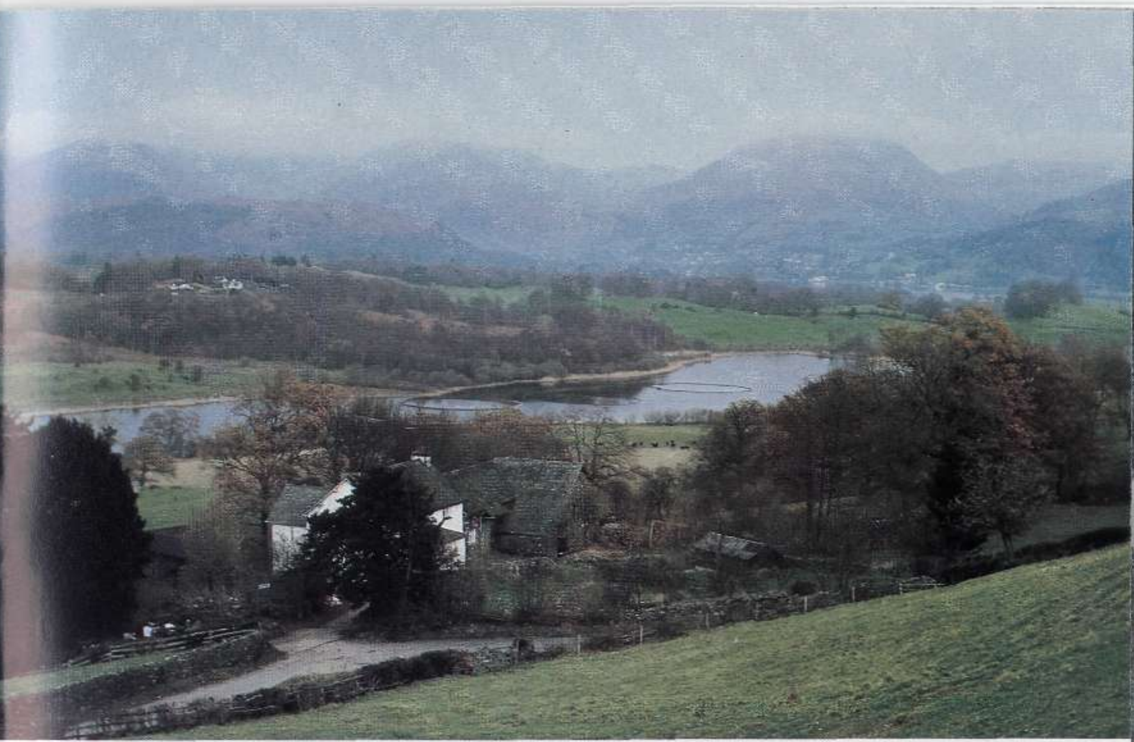
The presence of different macro-invertebrates is widely used in the water industry as a method of surveying and monitoring the water quality in rivers. J. F. Wright and his colleagues at the River Laboratory, with help from water authority biologists, are now surveying some forty representative rivers all over the country with the aim of identifying more clearly their communities of macro-invertebrates. Work is in progress at Windermere to develop better methods of sampling benthic invertebrates in deeper rivers. These two commissioned projects, together with that on the River Lambourn and other chalk and limestone streams, are extending the earlier detailed findings of Macan, Elliott and others, and relating the distribution and abundance of the invertebrates of flowing waters to environmental factors such as discharge, gradient, catchment geology and pollution.

Just as the "Lund Tubes" have been a valuable experimental invention to advance understanding of phytoplankton ecology, so work on relationships between chemistry, algae, detritus and invertebrates at the River Laboratory has recently centred round an experimental stream. This has been constructed on the site of a disused watercress bed at Waterston. Built of glass-reinforced resin, this stream is designed to simulate the headwaters of a natural chalk-spring-fed brook. It is 80 m in length, oval in shape and has an Archimedes screw pump to circulate the water continuously. The water can be topped up or replaced at varying rates from a nearby borehole. The first experiments have involved building up a natural ecosystem from basic components, starting with plain water in the dark, then adding light, a natural gravel bottom and invertebrates. The results obtained so far have proved extremely stimulating and revealing, though, as is often the case in such research, they have raised more problems than they have solved and revealed some very basic gaps in knowledge. This experimental approach is now being expanded by the construction of two more replicate streams.

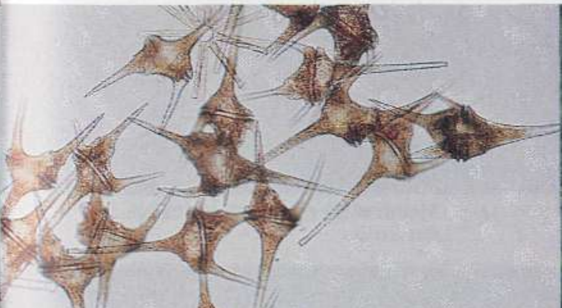
Fish studied at the River Laboratory have included trout, salmon, roach, dace, chub, minnow, bullhead, pike and eel (Plate 16). At first the populations of small chalk headwaters and two rather different rivers – the Frome (Plate 7) and the Stour – were studied, and R. H. K. Mann and his colleagues obtained basic information on numbers, age, growth and diet. For the small headwaters, data on population numbers, mortality and production were obtained. Among other things, these data revealed that that small, insignificant fish *Cottus gobio* (variously called the bullhead, miller's thumb or sculpin) was very abundant and had one of the highest rates of production yet measured for a natural fish population. Later, further details of the food and population ecology of the bullhead were obtained by two research students, R. Abel and P. Fox, working at the River Laboratory. Fox was able to demonstrate striking population-density effects on the fecundity of the bullhead in simple experiments he carried out at Waterston.

The data on coarse fish in the rivers Frome and Stour demonstrated that, as in Windermere, coarse fish showed marked year-to-year variation in the success of their breeding. C. Mills is now studying this phenomenon in more detail in rearing experiments with dace fry in the fluvarium and cages in the mill stream at East Stoke.

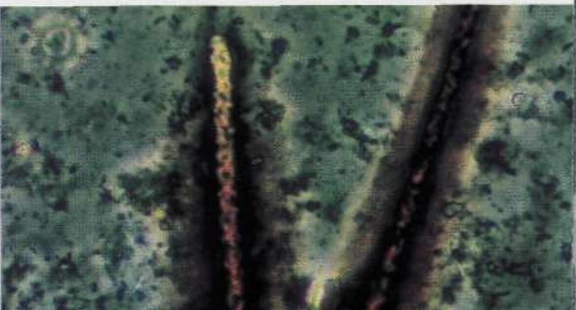
The River Laboratory has also undertaken projects on the ecological effects of water-management techniques. One of these was on the Gussage winterbourne – a winterbourne being a chalk-stream having a dry phase of variable duration. There was need to supplement flows in the nearby River Allen by abstracting ground-water from a borehole. As a technical experiment the water engineers decided to convey the water in the Gussage rather than in a pipe. In order to avoid percolation-loss in transit the bed of the Gussage was lined with waterproof materials. M. Furse carried out biological surveys of lined and unlined sections subject to various maintenance practices. These showed that experimentally extending the duration of flow had distinct effects on the flora and fauna. Prevention of grazing also altered the bank-side vegetation, but no changes directly resulted from lining the stream bed.



13.1 Blelham Tarn, with three Lund tubes.



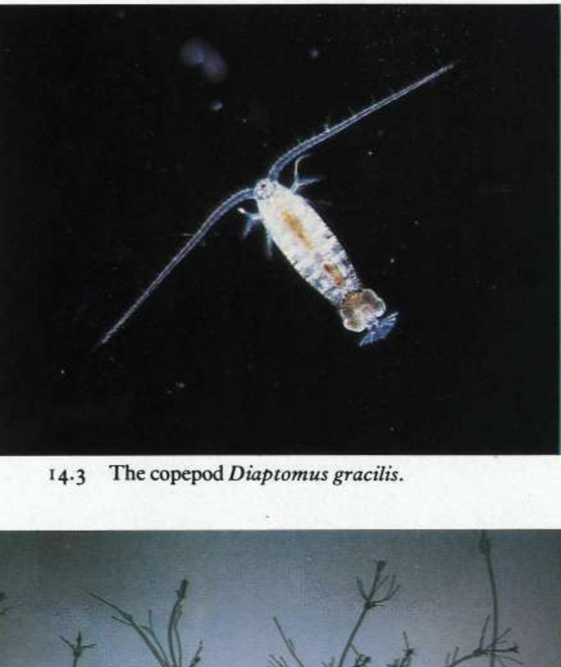
13.2 Phytoplankton from Esthwaite: *Ceratium* and *Anabaena*.



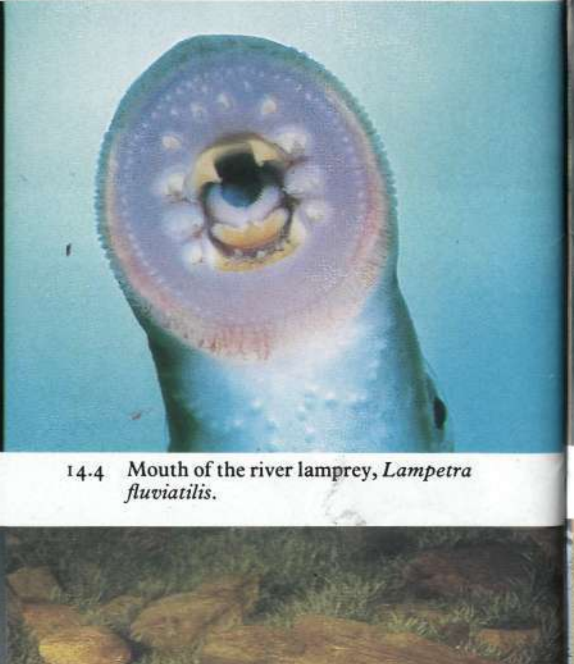
13.3 Bacteria: *Leptothrix*.

14.1 Zooplankton: the cladocerans *Daphnia hyalina* and *Bosmina*.

14.2 The copepod *Cyclops vicinus*.



14.3 The copepod *Diaptomus gracilis*.



14.4 Mouth of the river lamprey, *Lampetra fluviatilis*.

14.5 Stonewort: *Nitella flexilis*.

14.6 *Littorella* on the bottom of an unproductive lake.

15.1 The river snail *Viviparus viviparus*.

15.2 The medicinal leech *Hirudo medicinalis*.

15.3 Nymph of the mayfly *Ephemera*.

15.4 *Ephemera*: sub-imago.

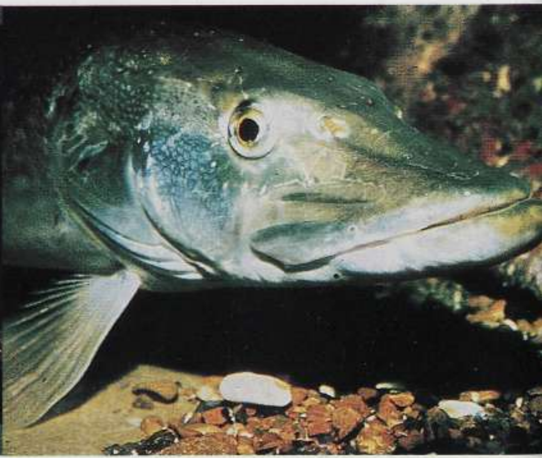
15.5 Stonefly nymph: *Dinocras cephalotes*.

15.6 Water-bug: *Corixa punctata*.

16.1 Perch: *Perca fluviatilis.*

16.2 Char: *Salvelinus alpinus.*

16.3 Eel: *Anguilla anguilla.*



16.4 Pike: *Esox lucius.*

16.5 Bullhead or miller's thumb: *Cottus gobio.*

16.6 Dace: *Leuciscus leuciscus.*

# RELATIONSHIPS WITH OTHER ORGANIZATIONS AND INTERNATIONAL CONNECTIONS

As a multi-disciplinary science, freshwater biology impinges on many other activities and interests and it is of the greatest importance for the Freshwater Biological Association that full exchange of information and ideas with others should be maintained and promoted. Some ways of ensuring this, as for example having a wide spectrum of interests represented on Council, have already been mentioned; connections with sister institutes supported by the Natural Environment Research Council and with the Water Research Centre are particularly valuable. This in turn leads to scientists belonging to universities and other research institutes becoming personally involved in the Association's research. There are many examples of the two-way exchange which results. The palaeolimnological research group has long had a connection with the University of Leicester and some of its members still enjoy the University's hospitality; microbiologists from the Department of Biological Sciences, University of Dundee, have used the Lund tubes in Blelham Tarn to study the nitrogen cycle in lake waters; the research team of the University of Reading carrying out projects on the rivers Lambourn and Kennet continued to be under the direction of Dr Berrie after his appointment to the River Laboratory. A formal arrangement exists with the University of Lancaster whereby members of the Association participate in teaching and enjoy the use of the University's computer and other facilities.

A series of informal meetings has been arranged every other year with the fishery and other technical officers of River Boards and like organizations. Officers of the Water Authorities as well as post-graduate students from universities attend the occasional short specialist courses that are offered from time to time. These meetings and courses have led to valuable contacts between FBA scientists and those concerned with the day-to-day practical management of rivers and reservoirs. Practical applications of research findings have also been promoted by the Association's series of *Scientific Publications*. These inexpensive practical guides to the identification of freshwater animals or methods for freshwater research and survey are widely used, and some of them have run to two, three or even four editions.

At the international level, one of the most welcome means of maintaining contact is via the visitors from abroad who visit the Association's two laboratories to obtain advice, consult the library (which is now one of the best in the world in its field) or to carry out research. Indeed, quite a

FIG. 15. Part of the library in the Pearsall Building.

significant part of the total research output from the laboratories has resulted from work done by visiting researchers. Lately Council has introduced the practice of having among its members a limnologist from continental Europe. Members of the Association's staff frequently go abroad to attend scientific conferences or to carry out some particular study. Among the international conferences which are attended, those of the International Association for Limnology are first in importance. Dr Macan was Secretary General of the International Association from 1953 to 1968 and the FBA was its host for the 1953 meeting. A major international venture in which the Freshwater Biological Association has been involved was the International Biological Programme, a co-ordinated effort by biologists of all nations to assess the world's biological resources. The Bere Stream studied by the staff of the River Laboratory was one of the few rivers contributing data to the range of sites studied by the "Productivity of Freshwaters" Section. Further, the Association, and in particular Dr J. F. Talling, had a large part in training and guiding the Royal Society African Freshwater Biological Team, which consisted of some seven members and worked on Lake George in Uganda from 1967 to 1972. The resulting study, which covered hydrochemistry, primary production, zooplankton, zoobenthos, fish populations and fish digestive physiology, is perhaps the most comprehensive ever to have been carried out on a tropical lake. Knowledge of African waters has been further extended by the work of many members of staff, including Worthington, Beauchamp, Talling and Fryer (though not all of this was carried out while they were on the staff.)

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