THE DEVELOPMENT OF FRESHWATER SCIENCE IN BRITAIN, AND BRITISH CONTRIBUTIONS ABROAD, 1900–2000

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Introduction

The nineteenth century was a period in which the framework of science developed rapidly and internationally. At its close there were, in Britain, the background and many active ingredients of future freshwater science. Geology and natural history had prospered. Organic evolution was established on a Darwinian foundation. The form of river basins and lakes had been shown to be influenced by Pleistocene glaciations; the flow of a river could be related to terms of a water budget; the dissolved mineral content of surface waters was broadly characterized. Freshwater organisms – at least many of them – were named and classified. They attracted much interest in local societies of naturalists, whose largely amateur enthusiasm complemented the work of the fewer professionals in the field – such as L.C. Miall[329] at the Yorkshire College, later University of Leeds. Fishes, amphibians, birds and flowering plants had never been neglected by the wider public. The schoolboy caught and reared tadpoles, his father cast 'flies' for trout, his aunt pressed flowers of the water crowfoot and bogbean. There was the conspicuous spread in waterways of the introduced Canadian pondweed. However, naturalists became aware of a new microbial assembly – with often bizarre forms – when 'evenings at the microscope'[156] and books on microscopy[58] became not infrequent in their Victorian homes.

The boundary between 'natural history' and 'science' is clearly elusive, although the former tends to respect individual features *per se* rather than the theory of their wider interrelation. On this count our situation in 1900 was not expressive of unified freshwater science, even though the terms behind *limnology* and *hydrobiology* had already been coined – abroad. The following outline traces later British contributions, both to a deepened knowledge of specifics and to their interrelation as environmental and ecological science. It does not deal with the advancement of hydrological science, nor with indigenous research activities in the British Commonwealth. Also unrepresented is work in Britain by research students and others – such as sabbatical visitors – from abroad, although their contribution to freshwater science has been substantial.

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Mentions of individual works are necessarily brief and incomplete, but their character and many of the scientists involved are indicated in an extended sampling of the literature. Information on personal histories and human traits is to be found in several autobiographical accounts, as those from Hutchinson[225], Worthington[476], Rzóska[398], Hynes[231] and Jackson[233], as well as in obituaries (e.g. of Gurney[183], Pearsall[65], Beadle[328]) and biographical essays (e.g. on Fritsch[292], Gurney[342], the Wests[250], Jenkin[295]).

Pre-1915: pioneers

The Bathymetric Survey of the Scottish Lochs (1897–1909) was the brainchild of a distinguished man (Sir John Murray, formerly of the Challenger oceanographic expedition) that – besides bathymetry – brought into focus much of contemporary freshwater science. It naturally included environmental science as well as freshwater biology. In the first volume of its final publication[350] 'our knowledge regarding various limnological problems' was expertly and trenchantly surveyed by Wesenberg-Lund[454]. The book's overview was further backed by Chumley's detailed bibliography on lakes, and set the scene for developments elsewhere. In fact it did express – within the bounds of non-running waters – the ideal of integrated freshwater science. The Scottish lochs were also the basis for some classic work in lake physics, with observations and analysis of internal 'temperature oscillations' or seiches by Wedderburn[453] that were far ahead of their time.

Other developments arose from microscopists interested in assemblages of minute organisms. One, D.J. Scourfield, is mainly remembered for studies of individual species of flagellates and Cladocera that extended over half a century. He also brought together then unfamiliar subject-combinations, such as surface tension and behaviour of Entomostraca and the application of logarithmic plotting to planktonic population dynamics[401]. The last, though universally neglected, could have been of great significance. He was one of the first to advocate[402] the setting up in Britain of a freshwater biological station, contrasting the situation here with developments in Europe and North America.

Also based upon microscopy, and developing strongly after 1900, were studies on the identity of freshwater algae and small Crustacea, extending to the behaviour of their natural populations in ponds, lakes and rivers. Thus patterns of changing abundance with time ('periodicity') were traced for algae in English waters by West and West[458] and Fritsch with collaborators[126], and by Dakin and Latarche[85] for the plankton in Lough Neagh of northern Ireland. As these community studies were more qualitative than quantitative, and environmental measurements were often primitive, the aim of identifying the regulation of periodicity remained largely a future aspiration. The Wests also made an early approach to assessing wider patterns of geographical distribution. They used their extensive experience[456a] with phytoplankton and desmids (Fig. 1a) to distinguish a desmid plankton in lakes (later 'Caledonian lakes') on geologically older rocks of north-western Britain and northern Europe[457]. Like many other group-specialists they identified collections from distant parts of the world, and commented on contrasts of distribution – as with the algae of tropical African lakes[455]. These lakes included Tanganyika, whose remarkable endemic animals attracted attention and led to the hypothesis[334] – later disproved after several expeditions – that it was the relic of a Jurassic sea. For Britain notable contributions on the smaller Crustacea came from Gurney and Dakin, the former chiefly with taxonomy and faunistics, the latter with functional aspects like food supply. Others were concerned with groups of larger freshwater animals, such as molluscs, dragonflies and fishes[376]. Backed by evolutionary biology, there was interest in the general adaptations of animal life to fresh water as contrasted with the sea.

Development to ecological science: 1915–1935

In the post-war period of the 1920s there were new currents of thinking, and initiatives, in biological science. There was an undercurrent of dissatisfaction with the dominance of classical morphology allied to phylogeny, and advocacy of more attention to physiology, biochemistry and ecology. On one side a Regius Professor of Botany at Glasgow condemned 'botanical bolshevism'; on the other Elton's classic book *Animal Ecology* appeared in 1927. Criticism of Elton by Lowndes[286], in relation to a contribution on two freshwater copepods, partly reflected a scepticism of the new ecology.

An early (1928) achievement of exposition and integration in British freshwater biology was the book *Life in Inland Waters*[56]. Its author, Kathleen Carpenter, had a background in the study of Welsh streams and rivers[57], some with problems of metal pollution, and a special interest in the distribution and behaviour of flatworms (planarians, triclads). She avoided insularity of outlook by much reference to European, especially German, hydrobiology and had a delightfully enthusiastic style – as in her exposition of longitudinal succession in rivers. Other attractive general outlines, aimed at the amateur naturalist, were Ash's *Pond Life*[9] (that brought my father, and thence me, into the subject) and Furneaux' *Life in Ponds and Streams*[137]. Near this time there was the pioneer work of Percival and Whitehead on invertebrate-environment relationships at intensively studied sites on streams and rivers of Yorkshire[362].

Regionally extensive rather than site-intensive studies of animal distribution also sought to relate occurrence with environmental factors. Examples were the surveys by Gurney of Crustacea in the Norfolk Broads and the lakes and tarns of northwest England[170]. Another was the assembly of information by Boycott on the distribution of freshwater molluscs in Britain as a whole[36]. Both intensive and extensive approaches were used in two pioneer studies involving freshwater macrophytes and algae. One was undertaken by Butcher[47] and co-workers to assess conditions in several major English rivers, including the Lark[48], Tees and Wharfe. The other by Pearsall began from depth-distributional problems of aquatic macrophytes in the lake Esthwaite Water[352], and later extended to their distribution in most of the larger English lakes.

From the last followed by far the most influential of extended lake surveys[353]. Here Pearsall combined a wide range of environmental and biological information on the English Lakes to propose that they represented stages in development from 'primitive' to 'evolved' lake status. This was enormously productive as a stimulus and challenge to later work[301]. Yet it could be held as fundamentally flawed, in that later palaeolimnological studies by Mackereth[310] and Pennington and others[359] – based on the record in layered lake sediments – showed that individual lakes had separate pathways (though often with a more base-rich early phase) rather than attaining various stages on a single potential sequence.

One aspect of the sequential scheme was changes in assemblages of planktonic algae. Pearsall knew that these were liable to alter considerably on a seasonal basis, and set out to identify the factors responsible. For chemical ones there had been much progress with analytical methods – shared with marine science[10] – in the 1920s. Internationally, Pearsall's link between external silicon depletion and diatom abundance[354] was among the first to indicate chemical control of aquatic population dynamics. Its quantitative aspects were to be followed in detail by others[140, 148, 288, 294] later in the century. There was, however, another notable and partly quantitative study of planktonic dynamics (day-night and seasonal) during 1920–23 within the 'British Isles'. Two Englishmen, Southern and Gardiner, pursued this[412] from a small 'Limnological Laboratory' beside the Shannon outflow of Lough Derg in the emerging Irish Free State. This project was officially supported, keeping in view the scientific basis behind inland fisheries. Likewise, in England the need was felt for more basic knowledge of the changing condition of rivers, on which a small mobile team began chemical and biological surveys[48] in the late 1920s.

The Lough Derg venture demonstrated the advantages of a working laboratory close to the fresh water(s) being studied. This consideration had also led Eustace Gurney in 1903 to establish a small private laboratory, and accommodation for visitors, by Sutton Broad in Norfolk[172]. Here it facilitated important work on zooplanktonic and other Crustacea by his brother Robert, but was modest in size and brief in working duration. Much earlier there had been advocacy[402] for setting up a freshwater field station in Britain. This was one of the first achievements of the newly founded (1929) *Freshwater Biological Association of the British Empire* or simply the FBA (an analogue of the long-established *Marine Biological Association* or MBA), that was to be a principal source of freshwater research in Britain throughout the century. The biologists Pearsall, Fritsch and Saunders were among active ‘founding fathers’. The station and future FBA headquarters opened in a part-tenanted mock castle on the shores of Windermere in 1931. Lack of funds at this time of economic depression prevented a more orthodox new laboratory – embodied in an architect’s drawing[124] – from being realised.

The FBA laboratory and its small staff gave an impetus to several lines of early work. A Cambridge influence of experimental zoology led Beauchamp and Ullyott to continue a partly experimental study of flatworm tropisms and other behaviour in relation to ecological factors in streams[25]. Ullyott also cooperated with Pearsall – visiting from Leeds – in a pioneer application of the Bernheim selenium cell, with other photo-cells, to the measurement of underwater light penetration[357]. Later he used it for analysis of the light-dependent vertical migration of zooplankton[447]. Pearsall, with other co-workers, investigated the also light-dependent growth of algae exposed at various depths[281]. His interest in oxidation-reduction potentials of waterlogged soils later led to cooperative work with Mortimer on this factor in lake sediments[356]. Other visiting workers included two research students from Cambridge. Penelope Jenkin[295] took up some classical limnology, investigating the seasonal temperature stratification[244] and plant nutrients[246] in Windermere. Independently she had made, in 1927, a summer survey of stratification and chemical variables in Loch Awe, Scotland[241] with the first experimental measurements of algal photosynthesis in any British fresh water. At Windermere, Moon contributed work on problems of distribution and movement in the littoral zoobenthos[331]; the deeper zoobenthos was more briefly examined by Humphries[223]. By 1935, therefore, there was a new broad front of quantitative freshwater research. In 1932 there began an ‘Easter Class’ for students that was to influence several distinguished research careers.

The name of the new Association made reference to the British Empire, where there was a demand for freshwater research and management. This went far beyond the early faunistic surveys[5], and particularly concerned the fisheries and environmental characteristics of large African lakes. A two-man mission, Graham and Worthington, had made the first fisheries survey[159] of Lake Victoria in 1927–8, followed by one of lakes Albert and

Kioga by Worthington. In these Worthington added observations on the basic limnology and plankton, including the first study of day-night (diel) changes[473] in any tropical lake. From his academic base at Cambridge there also came G.E. Hutchinson, who organised pioneer limnological work on ‘pans’ in South Africa[226], and subsequently became the most distinguished limnologist of the century. Cambridge was the source of a large and wide-ranging expedition[474] to East African lakes in 1930–1. One of its participants was L.C. Beadle[21], whose interest in tropical fresh waters and swamps had been aroused during an expedition to South America in 1926–7 with G.S. Carter[60], and who, with Worthington, was to influence much work over the next 40 years on the lakes and rivers of Africa[23]. A young Cambridge student, Kate Ricardo, assisted with the laboratory assessment of the zooplankton collections[477], and subsequently worked in the field within surveys of fish stocks in lakes Bangweulu, Rukwa[386] and Nyasa (later Malawi)[31]. A still earlier Cambridge-based pioneer of limnology in Africa, working on Kenyan rift lakes during 1929, was Penelope Jenkin – already noted here for her later research at Windermere within the infant FBA. Her contributions on alkaline soda lakes like Nakuru[242] and the filter-feeding of flamingos there[245] introduced a new dimension of chemical and biological limnology. This was to be developed by others much later[434, 446].

Also influential was Jenkin’s marine work off Plymouth in 1933 and 1934 on underwater photosynthesis[243] that combined marine expertise from Atkins at Plymouth and Marshall and Orr at Millport, and which stimulated later work on this subject at Windermere[427]. Such work involved the disposition of inorganic carbon sources in fresh water and their relation to pH, a subject on which Saunders had made studies[399]. He also focused on pH as a factor determining the distribution of the ciliate *Spirostomum*, devised one of the first electrical temperature probes in limnology[400], and promoted work on an early wetland research project, at Wicken Fen[142]. He introduced, in 1925, the first course in freshwater biology at any British university.

The period encompassed various studies in Britain on the taxonomy, morphology, life-histories and general occurrence of freshwater organisms. Throughout there were those who, by the study of various groups, provided the vital taxonomic base that underpinned other future studies. Besides much work on individual species, or small groups of species, some of these studies culminated in monographs that aimed to cover all the then known British representatives of major groups. Outstanding examples include the Ray Society monographs on charophytes[169], water mites[411], dragonflies[287] and freshwater copepods[171]. The last, by Gurney, is still the most comprehensive guide to the British species of the animals concerned. Another important contribution was the revision by Fritsch[456] of an earlier work by G.S. West on British freshwater algae. Fritsch’s broad survey[125] of the ecology of freshwater algae developed the connection with classical environmental limnology. There were several further studies of their seasonal periodicity in ponds.

The mention above of marine expertise illustrates profitable transfer to freshwater science from other disciplines. Another instance is the adoption in lake hydrodynamics of the *Richardson Number* (Ri), developed by L.F. Richardson in studies of atmospheric physics.

The years 1935–1955: institutional support and the curious individual

In these years notable contributions came from institutions and universities, both in spheres subject to rapid expansion.

Within the FBA at Windermere the original workers dispersed and new ones appeared. Especially influential for the science were the arrivals of Allen in 1934, Macan and Mortimer in 1935, Hynes (as a research student) in 1938, Frost in 1939 (newly from a survey of the River Liffey in Ireland[127]), Pennington in 1940, Le Cren and Lowe in 1943, Lund in 1944 and Canter in 1945, Mackereth in 1946 and Smyly in 1947. The fields represented before 1950 included chemistry[307, 339] and physical limnology[294, 337], palaeolimnology[240, 358], bacteriology[435], algae[266, 288], fungi[51, 232], zooplankton[409], other invertebrates[227, 301] and fish biology[3, 13, 128, 273, 282]. Within them were contributions later acknowledged as classics. Windermere was now a principal centre of freshwater research on the international scene, in which it had close links with the *International Association of Limnology* (SIL).

The connection with research in tropical Africa was continued with individuals from the FBA (Beauchamp, Lowe) taking up the hydrography of large lakes[26] and fish biology[283]. In another region, the unique high-altitude lake of Titicaca – tropical yet cool – was investigated in 1937 by a further Cambridge expedition[152] led by Gilson. Some of its significant results were published much later[153]. All these pre-1940 activities from Cambridge are in contrast to a low profile of freshwater science thereafter, with the exception of some research that included the physiology of trout[44a], tropical crater lakes[164, 445] and the aquatic vegetation of rivers[189]. From London University there were, after 1950, numerous contributions to the biology of tropical waters. Thus Green and his associates made expeditions to freshwaters of Brazil, Cameroons[445], Sudan, East and Central Africa, and Indonesia[164].

The war years of 1939–45 brought a temporary halt to much research activity, but at Windermere work on fish populations expanded. Fish stocks in the lake were manipulated by large-scale trapping of perch and netting of their predator, pike[475]. This work continued over later decades to generate a long-term record unique in its field[273, 274]. In and after 1945

further productive long-term records were maintained, especially on the changing abundance and composition of lake phytoplankton[288] and zooplankton[147, 410] and their physical and chemical environment[201, 288]. The chemical records were partly undertaken by biologists, beginning with Jenkin[246] and then Mortimer[336], but were later augmented and developed by Mackereth[307] and Heron[201] as professional chemists. The year 1947 saw a concerted effort to establish and interrelate physical, chemical and planktonic aspects of seasonality and stratification in Windermere[294]. Unexpected physical results led to work on internal waves by Mortimer using electrical recording[337], placing them in a world-wide context and extending to strongly developed examples in Loch Ness[338]. In several fields there were substantial contributions by research students from universities, as in work on bottom-living (benthic) algae (Godward[155], Round[391], Douglas[93]) and phytoplankton (Storey[419], Talling[427]). The investigations by Canter-Lund on fungi and Protozoa, that continued to the end of the century, showed – in conjunction with the algal records of Lund – that epidemics of their parasitism and grazing could severely and selectively reduce the abundance of algal species in the plankton[51]. Insights from the algal records into the controls of natural population dynamics were developed by Lund on a broad front. A key ingredient was the extensive use of experimental cultures, which were also much studied in Britain by Fogg, Droop and others[121], and had been initiated at Windermere by Pearsall[281], Storey[419] and Chu[64a]. Within the phytoplankton and other communities new species could spread from introductions, natural or man-made. Examples traced included species of larger Crustacea[332, 464]. Most of these topics appeared, with other British work, in the popular outline of freshwater biology by Macan and Worthington[306].

Later East African work was aided greatly when, in 1947, a fisheries research laboratory was set up at Jinja in Uganda. Its staff – that included Beauchamp, Fish, Greenwood, Lowe and McDonald – were to make major contributions to tropical freshwater science[113, 165, 284]. The scope was much wider than traditional fisheries science, and led to some local criticism of 'the sunburnt Wray Castle'. Not far away, at the university in Kampala, Beadle, Lind and others contributed work on swamps[24, 278] and Hartland-Rowe drew attention to lunar cycles of aquatic insect emergence[188]. These were subsequently investigated by Corbet[72]. Far downstream at Khartoum, the University College established in 1953 a *Hydrobiological Research Unit* that continued investigations of the White and Blue Niles[42, 373] (Fig. 1b). To the south, in 1951, a small but productive *Joint Fisheries Research Organisation*[233] was founded for work on fresh waters in some British territories of Central Africa.

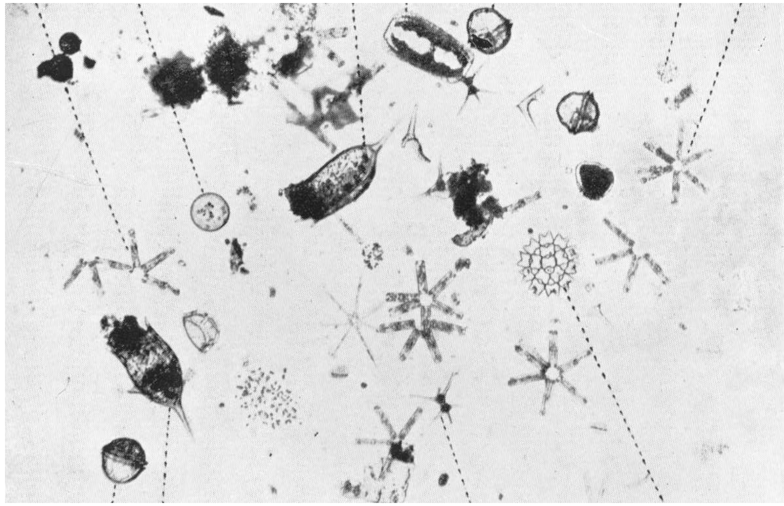
University biologists with freshwater interests were active elsewhere. About 1936 Reynoldson began studies at Leeds with Lloyd on the ecology of benthic invertebrates in sewage filter beds[279], later concentrating on triclads[384] in work from Bangor that was continued by Young[480] and Wright[478]. Hynes (from Liverpool) initiated other work on invertebrate ecology with mountain streams in Wales[229], from which grew a wide-ranging expertise for running waters[230] and problems of pollution[228]. His student, Brinkhurst, contributed on the biology of water-skaters[38] (gerrids) and oligochaetes that later broadened into a general survey of lake zoobenthos[39]. Also from Liverpool and north Wales there was work by Jack Jones and associates on aspects of salmonid biology[258]. At Reading Mann pursued the ecology of leeches[316]. At Newcastle there were, over a very long period, studies of the ionic and osmotic balance of aquatic insects and larger Crustacea by Beadle[22], Shaw[404], Stobbart[418] and Sutcliffe[421]. Here there were also studies, by Philipson and his associates, on the taxonomy[449] and ecophysiology[363] of caddis flies with their aquatic larvae.

In London, the University and the British Museum of Natural History had long contained individuals with interests in specific groups of freshwater organisms. They contributed to ecologically relevant matters (e.g. of Crustacea: Munro Fox[122]; fish: Trewavas[445] ; algae: Fritsch[125], Jane[235]; fungi: Ingold[232]). From their experience, expertise and motivation were passed on to new generations of aquatic biologists that included Badcock, Canter, Fogg and Lund, and later Clymo, Duncan, Evans, Fay, Gilchrist, Green, Greenwood, Stewart, Walsby and Willoughby.

After 1945 there was an accelerated expansion of older institutions and the creation of new ones, with a corresponding increase in the number of aquatic scientists. Close to London was the reservoir system operated by the *Metropolitan Water Board*, an organisation for water supply that encouraged research by its biologists. Although the issues were practical, they involved some fundamental aquatic science. To this Gardiner[140] and later Ridley[388] and Steel[415] made major contributions, including the feasibility of predicting troublesome planktonic growths[355]. Gardiner once made a plea[141] for relating fundamental and practical problems: 'It would undoubtedly be to our advantage if those in charge of what may be termed the more academic research laboratories could make a selection from such [practical] problems – many quite fundamental – which the applied

FIG. 1 *(Opposite)*. Varied approaches over the century to the investigation of freshwater plankton: (a) floristic and faunistic composition – net plankton from Lough Neagh[456a], 1900–01; (b) quantitative sampling over longitudinal river-sequences[42, 373] – the research launch *Malakal* on the Upper White Nile, 1953; (c) experimental manipulation in enclosed mesocosms – the Lund tubes[268] in Blelham Tarn, 1970.

(a)



(b)

(c)

biologist is expected to answer, as often as not on the telephone'. Steel later brought to bear some apparently abstract theory, involving the reduction of carbon gain and hence growth of phytoplankton by deepened vertical circulation, to practical gain for London reservoirs[415]. Gardiner himself cooperated with Pearsall in a fusion of 'academic' insights with waterworks practice[355].

In Scotland the University of Glasgow set up a field station by Loch Lomond, with corresponding lake studies of which the earlier are described in a book by Slack[406]. There was later work on both zoobenthos[407] and plankton[324]. Another station, organised for research on the brown trout and its environment, was created in 1948 at Pitlochry[374]. This pioneered experimental studies in Britain of lake fertilization[211]. Access to numerous small water-bodies of varying retention time led to an interesting study of this as a limiting factor in relation to plankton development[43]. At a contrasting location, in metropolitan Whitehall, there was work on fish biology and especially toxicology in relation to problems of pollution[1] – a topic also under investigation by others[257]. From there, as well as from Pitlochry and Aberdeen in Scotland, the field problems of economically valuable salmon and sea trout were under study. River surveys, emphasizing invertebrates and fishes, were contributed by Frost in Ireland[127] and by Badcock[12] and J.R.E. Jones[256] in Wales. A newly created body that promoted knowledge and appreciation of nature by the young, the *Field Studies Council*, set up a nation-wide series of Field Centres with sites that came to include a Suffolk river (at Flatford Mill) and a calcareous upland lake (Malham Tarn in Yorkshire). The latter was the scene of many subsequent studies that included general biology[215], algal diversity and periodicity[290, 433], snail associations[48a], lime bioprecipitation[360] and chemical budgets[433]. Also in northern uplands, at Moor House in County Durham, the *Nature Conservancy* established a field station where attention was given to the chemical balance and biology of moorland streams[79].

These developments from organisational sponsors should not lead us to forget the continued contributions to knowledge from general naturalists. They continued to be supported by a network of local societies or associations, often with journals, like the *Norfolk and Norwich Natural History Society* and the *Yorkshire Naturalists' Union*[200, 387]. An outstanding naturalist-microscopist, Scourfield, continued to draw attention to the smallest forms of algae and Protozoa[403]. Much later their significance was demonstrated by others[289] in Britain and the smallest pursued – as *picoplankton* – with the use of fluorescence microscopy[180].

The years 1955–1975: expansion of groups, sites and national projects

In this period the expansion of universities and freshwater institutions continued in Britain and abroad. There was an infusion of new blood; some research projects were sustained and many new ones initiated. Those in the academic world depended mainly on individual interests. Within London, for example, there were new groups associated with Fogg and Green at Westfield College, with Dodge, Duncan and Evans at Royal Holloway College, and – after 1960 – with Rzóska at Sir John Cass College. All these were active in the training and inspiration of future freshwater biologists. Thus graduates from Cass with future careers in freshwater biology included Bailey-Watts, Dunn, Greenwood, Harmsworth, Lack, Litterick, McGowan and Reynolds. From Liverpool the earlier work on salmonids by Jack Jones led to a flourishing school of fish biology, influential as a source of applied expertise nationwide. In stream ecology there was at Exeter a group notable for work on interrelations of benthic invertebrates, their presence in drift and salmonid biology[219]. One of its research students, Elliott, continued to pursue these and other topics with quantitative rigour and on a long time-scale[101, 104] within the FBA at Windermere.

The widest range of freshwater science continued to be at Windermere. There field studies were begun or continued on time-changes in the physical and chemical environment and in species-populations and communities of phytoplankton[289], zooplankton[410], lake zoobenthos[348], pond and stream macro-invertebrates[303] and fishes[265]. Those on phytoplankton, and perch plus pike in Windermere, led to records that eventually exceeded 50 years (and are still active). Research on the role of fungi in the plankton[52] and elsewhere[465] was continued. There were new initiatives in physiological work on photosynthetic production by algae[428], ion uptake and respiration in Crustacea[422] and growth regulation in fishes[426]. Fryer began extended work on functional morphology with its ecological and evolutionary implications in groups of smaller and larger Crustacea[130]. Feeding behaviour was also represented within more general studies of fish biology[128]. The significance of predation by fish on invertebrates was demonstrated from a long-term study of a tarn[303]. There was a strong development of work on lake and tarn sediments that aimed to reconstruct ecological history over the post-glacial, initially centred on persistent microfossils[359] as pollen grains and diatoms[191], and later extended with more evidence from chemical constituents[78, 310]. At or near the sediment-water interface there were often abundant and active microbial communities of bacteria[70, 255] and ciliates[157, 452], whose study was pursued aided by the Jenkin surface sampler. Many other novel pieces of apparatus – temperature probe[341], oxygen probe[309], pneumatic sediment corer[308] –

were developed from a rare combination of individuals (Mortimer, Mackereth, Gilson) with mechanical expertise, inventive imagination and metal plus electrical workshops. The bottom sediment-water interface was shown to be the location of resting or diapause stages of diverse and otherwise planktonic organisms[135, 194, 409]. First studies were also made of the link between water movements in lakes and the horizontal and vertical distribution of zooplankters[69]. The consequences of artificially induced loss of temperature-density stratification were tested in Blelham Tarn. Finally, biological work to 1970 on the English Lakes as a whole was summarised by Macan[304].

These various endeavours involved the physics and chemistry of aquatic environments, considered as background to interpret the biology and as challenging subjects themselves. As essential background, much information was gathered from geographically based surveys of chemical concentrations; also from time-series influenced by external inputs and interaction with changing biological populations such as those of the plankton[339]. Included here was work on the seasonal stratification of lakes with the consumption and release of biogenic elements[197], and the causes behind longitudinal sequences in rivers[350a]. Contributions from the atmosphere[155a, 423] and drainage basins were usually involved, and budgets[148] attempted as an aid to a gross understanding. Finer quantitative understanding of basic mechanisms required more specialist rigour. Later examples appeared in the treatment of internal waves[340] and other water movements[408], interactions between oxidation-reduction and acid-base systems[88], the kinetics of reactions at mineral surfaces[220], and complex equilibria in the carbon dioxide–carbonate system[222].

Many freshwater biologists preferred to concentrate on individual groups or, as autecology, individual species. Thus examples of intensive autoecology were published on the dragonfly *Anax imperator*[71] by Corbet and the damselfly *Pyrrhosoma nymphula*[270] by Lawton. In work on these insects, and on various stoneflies, mayflies, caddis flies and chironomids with aquatic nymphs or larvae, the water to air emergence[271a] was a critical event. A ‘breeding out’ of adults was required in work on the taxonomy of these groups[302]. Other groups of animals under sustained study, outside the FBA, were Protozoa, rotifers[161], Cladocera[160], larger Crustacea and fishes; among autotrophs, various groups of algae[40, 120] and submerged macrophytes[190, 403a, 413]. Some groups seem always to have attracted much attention from amateur naturalists compared to that from professional biologists in Britain. Rotifers are an example. Noteworthy advances in our understanding of their biology resulted from the studies of Hollowday, Wright and Galliford[138]. There was an increase in physiological studies of individual species or groups; in these Crustacea[404], fishes[129], algae[116, 417] and aquatic macrophytes[413, 459] were strongly represented. Especially with fishes, *behaviour* (ethology) was a recognised factor[224] in animal ecology.

There was much interest in developing studies at new and rewarding freshwater sites. Within Northern Ireland Lough Neagh – in area the largest British lake – was chosen by the New University of Ulster and, for practical reasons linked to nutrient enrichment, by the governmental Department of Agriculture. In the late 1960s two well equipped field stations were set up by the lake at Traad Point and near Antrim, and a very productive sector of limnology in the UK began. Although centred on Lough Neagh[247, 471] it included extended surveys of other lakes in Northern Ireland, later to include the hydrographically complex Lough Erne[150]. Earlier, the *Water Pollution Research Laboratory* was established at Stevenage, where a group of biologists (Westlake, Edwards, Owens) investigated biological influence on chemical constituents such as oxygen dissolved in river water[100]. Independently, the special floristic and other features of planktonic[27, 424] and attached[319] algae in some English rivers were under study. The *Nature Conservancy*, although mainly concerned with terrestrial ecology and conservation, organised a survey of the most remote British fresh waters in Shetland[146], and later sustained more intensive work on Loch Leven from its branch at Edinburgh. From the University of East Anglia, Moss and others began to develop studies on the Norfolk Broads that drew attention to a multiplicity of man-made influences on their origin and subsequent development[344].

The Freshwater Biological Association achieved, in 1963, its long-held objective of a ‘Southern Station’, as the River Laboratory by the Frome in Dorset[272]. There a group of biologists and chemists was built up, with new prominence given to work on plant nutrients[62], organic detritus[16], aquatic macrophytes[90], benthic invertebrates[269] and fishes[318] of rivers and streams. Their desired interrelation in ‘ecosystem’ studies was centred on the chalk stream[460] and later on an experimental stream analogue[320]. Elsewhere single FBA-supported individuals (Reynolds, Crisp) began sustained studies of the Shropshire Meres[378] and the impounded reservoir-river system in upper Teesdale[80]. The former brought modern limnological approaches to bear on small water-bodies that were relatively nutrient-rich and liable to spectacular water-blooms. The latter enabled study of a sequence of development in the plankton[11], benthos[7] and fish[83] of a newly created upland reservoir, and effects on water characteristics and the invertebrate[6] and fish[82] populations of the river downstream. There the local and slightly altered temperature regime and the hydrodynamics of the gravel bed[53] were factors likely to influence the growth and early life history of salmonids[81]. One participant, Carling, later extended his work on river-bed dynamics to generalised issues involving many other rivers[55].

Contributions from the FBA[136] and others continued on African rivers and lakes, reservoirs and fishponds[296a]. In field work from Khartoum on the upper Nile, Hammerton[177] followed Rzóska, Brook, Prowse and Talling, Gay and Berry. During 1960–61 the Tallings worked on Lake Victoria and other East African lakes[434] from Jinja in Uganda, where other British freshwater biologists were active[74, 106, 143, 175]. In 1964 there was additional cooperation involving two British university biologists (Prosser and Wood) in Ethiopia who had already turned to a study of some crater lakes[371] in that country, which they continued subsequently[20, 469, 470] with work on temperature, salinity correlates, chemical and phytoplankton stratification, and seasonality[469]. The environments and biota of other tropical crater lakes, that are often regular and attractive units, were investigated by Green and his associates[164, 445]. Vastly larger African lakes attracted British-sponsored investigations of fisheries[233, 285] that yielded other results of wide scientific interest; they included Malawi[234], Tanganyika[75], Albert[106a, 212] and Chad[216]. The first two, with their rich endemic faunas, had long been attractive sites at which to study the ecology and evolution of the remarkable flocks of cichlid fishes and other organisms that have arisen there. British investigators[134, 165, 283, 444] were involved from the outset. There was work on new and large man-made lakes on the Zambezi (Kariba[181, 182], Cahora Bassa[87]), Nile (Nasser-Nubia[395]), Niger (Kainji[34]) and Volta (Lake Volta[249]), and on Lake Chilwa[346], with progressive change in environments and aquatic biology[326]. Work was also undertaken on the ecology of aquatic vectors of major tropical diseases such as malaria (mosquitos[276]), schistosomiasis (snails[29]) and onchocerciasis (*Simulium*[264, 463]) – studies that drew upon expertise in the London and Liverpool Schools of Tropical Medicine.

During the decade 1964–74 British biologists helped to develop an international project centred on biological productivity, the *International Biological Programme* or IBP. (Their promptness led some foreigners to label it the International *British* Programme). In freshwater biology this involved much extended work at the sites of Loch Leven in Scotland and the River Thames at Reading, with relationships over a range of trophic levels that involved plankton[33, 267], benthos[64] and fish[317, 437]. British freshwater biologists also contributed[45, 448] at an intensively studied site on the equator, the highly productive Lake George in Uganda. The results[166] were later assimilated within an attempted global synthesis[275] in which many latitudes were represented – an aim foreshadowed in 1910 by Wesenberg-Lund[454]. A central theme was the quantification of rates of organic production in fresh waters. For primary (photosynthetic) production this followed a world-wide surge after 1955 of measurements on phytoplankton; for secondary production[14] there was attention to feeding and assimilation rates[95], energetics[317] and the ratio of production rate to biomass (*P/B*)[275]. New comparisons were also possible within the UK, as between the ecological behaviour of benthic chironomids investigated in London reservoirs[349] and in the larger shallow lakes of Loch Leven[64] and Lough Neagh[61].

About the same time British governmental bodies began research programmes in freshwater biology in the Antarctic based on Signy Island[202] and later – around fishery development – at the closed-basin African lake of Turkana in Kenya[217]. Both contributed fundamental information on the ecological regimes of these environmentally extreme and little known waters. At Malacca in Malaya a *Fish Culture Research Institute* was set up, largely from the initiative and enthusiasm of C.F. Hickling[205]. Besides advancing tropical fish culture, it contributed interesting work on plankton biology[97]. In the same region, Johnson made studies on the smaller invertebrates[252] and Prowse on the freshwater algae[372].

Within the UK, there were consequences in basic freshwater research from the practical problems of water pollution and water supply. Thus the *Water Research Association* (successor to the Water Pollution Research Laboratory) was primarily concerned with these problems and their amelioration, but also supported some basic work as on plankton (daphniid) dynamics at Farnmoor Reservoir[253] near Oxford. Its *Technical Publications* on methods[451] complemented the longer established *Scientific Publications*[302] (including subsequent revisions) of the Freshwater Biological Association. These latter publications, among other 'servicing' activities, provided an inexpensive means to identify species in many groups of freshwater invertebrates, otherwise illustrated by several more popular books[67]. Other FBA publications dealt with methods – chemical, instrumental, microbiological and statistical. There was widespread involvement of both Government bodies and the research community with the increasing nutrient enrichment (eutrophication) of many waters. This often centred on phosphorus as a suspected limiting nutrient. It also involved rising concentrations of nitrate in rivers and aquifers that were a source of drinking water, and directed attention to agricultural practices and the microbial physiology of organic decomposition, nitrogen fixation[218, 416], nitrification and denitrification that governed the nitrogen balance of inland waters[174]. Nutrient enrichment led to other undesirable consequences, such as conspicuous water-blooms[389] that could contain potent toxins[68], or a novel abundance of the filamentous alga *Cladophora* ('blanket weed') in lakes and rivers[461]. On another front, there was rising attention in governmental research laboratories throughout the UK to the biology of populations of migratory trout and salmon[2].

The years 1975–2000: changing support and groupings

This period brought much 'structural change', but there were also lines of continuity with the past. In both universities and institutions many freshwater scientists of experience continued their work. Some used regional knowledge to make broad summaries of aquatic characteristics and biota. These are exemplified by books on the English Lakes[132, 430], the River Wye[99], the reservoir Rutland Water[184], the larger Scottish lochs[313], Scottish fresh waters generally[315], Lough Neagh[471] and the Norfolk Broads[344]; also a review of the Shropshire-Cheshire meres[378]. British-based biologists also contributed to accounts of the River Nile[395], Lake Chilwa[262] in Malawi, inland waters of West Africa[249], the River Niger[168], African Great Lakes[285] and the Euphrates-Tigris system[397]. Geographically integrative works dealt with the inland waters of tropical Africa[23] and the tropics generally[351, 432], in which description was blended or replaced with general issues. Distinctive characteristics of rivers were taken up in several books[49, 55, 396, 462].

Also in this period *Freshwater Biology*, a new and long-awaited journal that was launched in 1971, developed strongly. The character of its contributions over time reflected changes in factual knowledge, interests, and views on length, scope and presentation. Pressure upon space mounted; by 2000 most submissions akin to lengthy classic papers of a few decades earlier would not be accepted.

Nevertheless, passage of time increased possibilities for the assembly of long-term series, duration typically 20 to 50 years, in freshwater characteristics and biota. Examples from the FBA involved fish populations of perch, pike and charr in Windermere[77, 265, 273] and of brown trout in nearby streams[101], sequences of phytoplankton[298] and zooplankton[145, 147] abundance in several of the English Lakes plus Loch Leven[15], and the changing chemical composition of Cumbrian waters[423]. Others made similarly long-term studies on Lough Neagh[151] and streams, including the Broadstone Stream[472] and the Bere Stream[62] in southern England. Nutrient enrichment and its consequences (eutrophication) continued to be a major concern[364]. In several lakes a 'clear-water phase' in early summer, influenced by grazing of zooplankton, could be recognised. Especially for temperature stratification and zooplankton, and probably for fish biology, it was shown that one important factor regulating differences from year to year was the northerly or southerly disposition of the North Atlantic Drift or 'Gulf Stream'[147]. The finding from Cumbria was later confirmed and extended by others in Central Europe[420]. Some long-term changes found in the English Lakes could be compared with those deduced as palaeolimnology from the sedimentary record[192]. Certain long-term trends were capable of reversal by human manipulation of inputs, as with

lake acidification[19, 441] and phosphorus enrichment[364]. A special form of input, that of caesium and ruthenium isotopes from the accident at the Chernobyl nuclear power-plant in 1986, was recorded with subsequent distribution in water, sediment and biota[210]. Viewed over decades, the variable levels of nitrate in Windermere were shown to be strongly influenced by the character of consuming phytoplankton liable to sink out and the correlated extent of deep deoxygenation[196]. Thus both internal and external factors operated within an overall nutrient budget.

There was increasing palaeolimnological work by British scientists at other sites in the UK and also abroad – much by Battarbee and his associates[18, 19], mainly based at University College London. Long-term changes so investigated included the acidification induced by 'acid rain'[19, 321], eutrophication[28], and salinity-associated shifts linked to climate change[115]. Issues of acidification in Britain and Scandinavia were further studied by other techniques within a major international project[321] of the 1980s. Other work on freshwater science in Britain also took account of potential consequences of climate change[145]. Normal year-to-year variability of climate favoured one study of the physics of ice-cover[322], and another of accentuated daily cycles of stratification involving warm near-surface water during the exceptionally hot summer of 1976[431].

Individual groups of freshwater organisms continued to have their adherents. In taxonomy and ecology, for example, there were relatively numerous biologists especially interested in and publishing on cyanophytes[59], diatoms[393], desmids[41], Protozoa[270a], rotifers[325, 367], Crustacea[133], caddis flies[449], chironomids[8, 61, 366], dragonflies[73] and fishes[314], and rather fewer on aquatic macrophytes[189], ostracods[167], water-mites[154], oligochaetes[385] and leeches[105]. The huge number of species of freshwater algae, and taxonomic changes, have always posed difficulties for their correct identification. To assist this, the *Fritsch Collection of Algal Illustrations*[291] (originally Fritsch's personal aid) was adopted by Lund, transferred to Windermere, and there maintained and expanded. There was also maintenance of a national *Culture Collection of Algae and Protozoa*[91] that had previously developed at Cambridge after 1945 and supported work on the general characteristics of these organisms[66, 204]. Work by others on a British freshwater algal Flora[251] was almost complete by the end of the century. The great diversity and intrinsic beauty of the organisms was brought out in the uniquely illustrated book by Canter-Lund and Lund[52]. Other books of British origin reviewed the characteristics of particular groups, such as desmids[41], charophytes[333], diatoms[393] and cyanophytes[59], and their ecology[392], as well as more general implications[379] of 'the phytoplanktonic ways of life'[117]. Expression of the latter in diverse forms of algal seasonal cycle had been illustrated by studies on several English lakes, a pond near Bristol[178], the Shropshire–Cheshire Meres[378], Loch

Leven[15], Lough Neagh[151] and two interconnected lakes in Snowdonia[179]. New techniques enabled some studies of genetic differentiation between populations within and between species, such as planktonic daphniids[377] and salmonid fishes[109]. Bacterial isolates were similarly examined genetically[365], in part prompted by national concern with hazards in the release of genetically engineered micro-organisms ('GEMS').

A noteworthy development that covered a wide range of organisms, both terrestrial and freshwater, was the continued accumulation, and analysis, of an increasing number of accurate locality records and of their plotting on maps. These activities were sometimes sponsored by official bodies or societies that harnessed the enthusiasm of large numbers of recorders. Especially with regular updating, the results often revealed a dynamic situation as organisms reacted to such influences as climatic change, especially global warming. For aquatic animals this was particularly applicable to insects with winged adults[103]. For example, dragonflies were well-studied in this respect and showed a northern spread of several species. Geographical gradients of community composition and species distribution were examined quantitatively by Green for some planktonic organisms on a much larger scale, including the temperate to tropical transition[162] and its altitudinal modification[163].

Problems of organic production and distribution in fresh waters were studied in relation to the physiology of individual species of bacteria[254], algae[237], fungi[50] and Protozoa[110], often maintained in culture. One example was the use of algal assays for judging the relative availability and limiting roles of different nutrients in lakes, applied to phytoplankton[293] and – later – also rock-attached algae[299]. Work continued on the physiology of larger aquatic plants in relation to problems of depth-zonation and photosynthesis[297] in lakes and rivers and – abroad – in tropical papyrus swamp[259]. They were shown to take part, with plankton and snails, in transfer of the heavy metal lead within a mine-polluted English lake[107]. There was also work on the potential or actual limitation of aquatic photosynthesis by the sources of inorganic carbon, for which there could be large differences between species[300, 428]. Ecological relevance was demonstrated for the control of algal growth rates by light and temperature[123, 149], cycles of phased cell division in flagellates[199], uptake of nutrient ions[237, 375], the near-surface inhibition of photosynthesis by strong light and UV radiation[187], N-fixation by some cyanophytes[139], and the adjustable buoyancy conferred by gas vacuoles to planktonic cyanophytes[450]. This and other physiology was also applied to predicting behaviour in natural populations by modelling[380], for which an additional evaluation of loss processes[248, 382] was often required. There was, it seems, less work on the application of physiology to the ecology of freshwater animals. Examples here are the endocrinal and other regulation of fish

growth, critical tolerance limits of fish[17], physiology of anaerobic ciliates[110] and other Protozoa[16c], and ion balance[368], digestion[63] and use of assimilates[37, 467] in Crustacea. Further investigated in relation to the biology of fishes was parasitism, external by Crustacea[131, 263] and internal by cestodes[425], that could involve complex life histories and was troublesome in the now expanding commercial practice of fish culture in cages. Other pathogens were responsible for crashes in some populations, such as perch in Windermere[330] during 1976 and the native white-clawed crayfish at many British locations[414]. Also, bordering on physiology, there was work on animal behaviour in relation to physical factors of the environment that included the hydrodynamics of stream flow[54, 98] and surface tension at the water-air interface[173].

Non-living, dispersed organic matter was studied in three additional roles. One involved fundamental chemistry and the widespread influence of humic-cation complexes[405, 440] – including that in the forest lakes of Finland. The other involved the relative importance of various sources of carbon, differentiated isotopically, for organic production in lakes. Planktonic production in Loch Ness, for example, followed over several years from Lancaster University, was found to be strongly influenced by carbon of terrestrial plant origin[261]. The same source was earlier appreciated for the production of invertebrates in running waters[30].

Within the FBA there were intensive studies on several types of productive water with some unique facilities. Large confined mesocosms ('Lund tubes': Fig. 1c) in Blelham Tarn were used for experimental work[296] on the consequences of isolation from inflow and sediments, and the interactions of vertical circulation[383], nutrient loading, phytoplankton production, microbial distribution[254] and zooplankton grazing[436]. In Esthwaite Water an improved understanding of 'lake metabolism' (the subject of a classic study there during 1939–40 by Mortimer[336]) was sought that integrated physics, chemistry and plankton biology[197]. This work extended from the 1970s to the 1980s, with later concentration on the mobilisation and interactions of iron and of manganese[89], diel changes[431], and the dynamics of an abundant dinoflagellate[194, 198]. The vertical migration of this and other flagellates was followed experimentally in laboratory columns[195]; also, outside the FBA, in shallow absorptive lake waters of Finland[260].

For both Esthwaite Water and Windermere there was work on the nature and origin of uneven horizontal distribution in the plankton[198]. Also in both, the distribution and vertical movement of trace elements were followed[176], in part from Lancaster University. Esthwaite Water showed the generation of bicarbonate-alkalinity in productive and anoxic waters[197]. The chemistry was further pursued by Davison[88], with application in gravel pits near Kings Lynn, and the process tested on a large scale by experimental fertilisation of the acidic upland water of Seathwaite Tarn[144]. Further south, in Dorset, other experimental facilities in the form of artificial stream channels were used for analysis of physical–chemical–biological interactions in running water. These included chemical exchanges between particulate and ionic constituents[220] and interactions involving benthic algae, nutrients and grazing invertebrates[320].

Traditionally, much research on the ecology of running waters was mainly concerned with benthic macro-invertebrates and fishes. In later work faunistic issues[311, 335] were increasingly replaced by community-functional ones from long-term observations, as in the work of Elliott[101] at Windermere and and Hildrew, Townsend and their associates from streams in southern England. The latter group explored many aspects of community structure, including the influences of the physical and chemical environment[442], predation in a patchy environment[208, 209] and long-term persistence[443, 472]. There was, however, an extensive harnessing of faunistic information to the biological assessment of water quality. This is exemplified by the Severn-Trent and the later RIVPACS models[479]. Other systems were developed and used elsewhere, but the long-established *Saprobiensystem* of Central Europe made little headway in Britain. In parallel there were studies involving the nature and implications of chemical characteristics in running waters. Biologically, there was particular interest in acid-base status, nitrogen and phosphorus. Chemical distributions had links with the hydrology of regional river systems, including gross altitudinal and downstream transfers[221, 236] that could be influenced by microbial activity[158] in benthic 'microfilms'[280]. The distribution and activities of attached and dispersed bacteria and Protozoa in chalk streams also received attention[16a, 16b]. Work was carried out on the quantitative ecology of algae and macrophytes in rivers, benthic[214, 319] and planktonic[381], that involved some revision of earlier concepts of river plankton; also on the river-lake systems of the Norfolk Broads[345], from which Moss and others developed an hypothesis of *alternative stable states* dependent upon nutrient loading and with either aquatic macrophytes or (later) phytoplankton predominant. There was here associated evidence of strong 'top-down' as well as 'bottom-up' controls in the food web[271]. In these and other river systems the macrophytic vegetation received much attention, regarding floristics, abundance and habitat preferences[189].

Several examples above relate to complex systems in which an overall outcome is determined by the quantitative interplay of component relationships. Such systems were increasingly reconstructed or *modelled*, and where possible the theoretical outcome compared with observed reality. Three areas illustrate extensive use of modelling in freshwater science. At a purely chemical level there has been predictive modelling of chemical kinetics and distributions, as in systems prone to acidification[439].

Carbon assimilation (photosynthesis) in vertical columns of phytoplankton has been integrated to yield overall production rates[427] or derived growth rates, the latter also derivable from component growth kinetics[380]. Assimilation and growth in animals have likewise been related under conditions appropriate to those in natural populations; there have been notable applications to fishes[104]. Points of interest included the relative sensitivity of system response to primary variables and the differing responses generated between biological species. Application to population changes required the additional incorporation of loss rates[248, 382].

The study of ponds as environments has been sparse compared with that for lakes. Their inhabitants are often extremely diverse. Vertical gradients in the water can be steep with day-night and seasonal temperature stratification, deep anoxia with special microbial communities and ecologically influential ciliates. These features were demonstrated in especially intense work on one large pond, Priest Pot[112], in Cumbria. There the diversity and depth-zonation of communities was studied, from bacteria and ciliates to macrophytes. From this and earlier work, belief in the 'element of chance'[238] in pond communities was largely discounted (and evidence for ubiquitous dispersal strengthened) for many smaller (<1 mm) organisms[111], though not the larger ones[369]. Also investigated were temporary ponds, with problems for biological colonisation and persistence[390], and – at higher altitude – the special features of tarns[193] and lochans that had stimulated earlier investigations[213, 277]. Ponds have always been much appreciated features of lowland British landscapes. A majority of ponds there were lost from agricultural operations during the century; conservation and recording were promoted by the organisation *Pond Action*[32], later the *Ponds Conservation Trust*.

There was continuation from traditions of British work overseas, especially in tropical regions and in Antarctica. One speciality was tropical crater lakes[164]; another, African shallow lakes[429] for which information was assembled with European cooperation[46]. There were also comparative surveys of species diversity, distribution and seasonal dynamics for tropical phytoplankton and zooplankton[432]. A challenge was presented by the increasing number of large tropical 'man-made lakes' with investigations of sequences of environmental change[326], community development[23], changes in fish populations[34] and fisheries; also of pesticide action against aquatic vectors of disease[347] and the undesirable persistence of pesticides like DDT in water and food chains[323]. Another challenge came from the consequences for fisheries of the changing hydrology of large tropical rivers and their floodplains[14a, 453a]; also the frequent seasonal impermanence and the pollution of many tropical streams, represented in long-term studies of stream biology by Dudgeon at Hong Kong[94]. Attention was attracted to a highly condensed form of seasonal impermanence, but with dense colonisation by some Crustacea or insect larvae, in rainpools. This sequence was studied earlier at Khartoum[394] and later in Malawi[327] and Kenya[206]. National and international surveys for fisheries and conservation of the big lakes Malawi, Tanganyika and Victoria brought together much new information that included general limnology[4, 76, 285]. From the University of London, work on tropical zooplankton in Sudan, Sri Lanka and Brazil was promoted or advised by Green and Duncan[96]. Work on the ecology of African aquatic vegetation was surveyed and integrated by Denny and his collaborators[92]. There was also an intensive multidisciplinary survey of a Tanzanian reservoir[91a]. Harper and his associates made long-term study of biological changes in Lake Naivasha of Kenya, many due to introductions of temperate species to this elevated and relatively cool equatorial lake[186]. Also for Africa there were long-continued studies based at the British Museum on snails of medical importance[44] and on fish taxonomy, diversity and evolution[165]. In Antarctica, researches on freshwater environments and biology continued to be made by staff of the British Antarctic Survey[193, 203, 345, 370]. These led to the wider surveys by Fogg of polar ecology[119] and its history[118]. After 1995 there was an increasing involvement with the study and management of freshwater bodies in China[361].

The present period was one of great 'structural change' in the support of research. This owed less to the old division between fundamental (or 'strategic') and applied science than to the emphasis on control by the funders. There were roots in the customer-contractor principle of the Rothschild Report of 1971 and advocacy in the 1970s of 'mission-oriented' rather than 'subject-oriented' research. By the 1980s the objectives of publicly funded research were widely and officially tagged as 'wealth creation' and 'improvement in the quality of life'. The latter could elastically cover aesthetic as well as practical benefits. In concrete terms it supported a major increase in conservation research, that saw the old role of the *Nature Conservancy* partly passed through the *Nature Conservancy Council* and then divided between the separated *English Nature*, *Scottish Natural Heritage* and the *Countryside Council for Wales*. Included were the twin objectives of conserving valued habitats and retaining biological diversity under threat. In fresh waters the latter led to work on rare species, including fishes such as schelly and vendace[312, 468], with threatened local distributions. A monitoring and management role[185], with special reference to pollution, was given in 1989 to the *National Rivers Authority* that became, in 1996 and with wider scope, the *Environment Agency* that functioned alongside the *Scottish Environmental Protection Agency*.

The principal administration of national funding for freshwater research rather than management remained with a government-related body, the *Natural Environment Research Council* (NERC). However, an increasing

proportion of funds was required to be sought from other sources, which tended to emphasize circumscribed projects with local application and divert time and energy from science itself. The NERC supported much university research in freshwater science, and in 1989 took over direct rather than indirect control of most freshwater staff and research previously of the Freshwater Biological Association to constitute the *Institute of Freshwater Ecology* (later incorporated in the *Centre for Ecology and Hydrology*). Nevertheless the FBA persisted with a small staff but large (c. 1800) international membership, a variety of supporting activities, and a sizeable annual contribution to published research.

These 'structural' and policy changes, rather than national economic factors, determined an overall decline in the numbers of established freshwater scientists and ongoing basic research[207]. This applied to both universities and institutes. The Freshwater Laboratory at Lough Neagh was closed by its parent university in 2000; staff numbers of the Freshwater Biological Association fell from 139 in 1980 to 88 in 1989. *Ad hoc* research projects, and their often short-term staffing, increased. A few were conceived on a large national scale, sponsored by a Research Council, with many cooperating bodies. An example in the 1990s was the Land Ocean Interaction Study (LOIS) that centred on contributions from eastern rivers to the North Sea[236].

Another trend to large-scale projects, but stemming from external political change, involved participation by several European countries with funding from the European Community. Examples ranged from the electronic monitoring of lake environments to distribution and behaviour within and between species of fishes. These were quite different in character from the projects in developing, often tropical, countries that had long been supported by international agencies such as FAO (Food and Agriculture Organization of the United Nations), WHO (World Health Organization) and UNEP (United Nations Environment Programme), or nationally by the UK. A proposal for conformity within the European Community over broad issues of environmental quality in fresh waters – the 'Water Framework Directive' of 1997 – will involve much work in the UK. European links were already strong within the *International Association of Limnology*. During conflicts in the 1940s and 1950s some European hydrobiologists – including Pringsheim from Germany, Rzóska from Poland and Fay from Hungary – had been displaced and contributed various research initiatives[108, 395] in the British sphere. A reverse participation by British scientists in some European projects took place in later years. Some émigrées, including Hutchinson, Hynes, Mann and Mortimer, were scientifically productive and influential in North America. Overseas cooperation had been greatly furthered – especially with Eastern Europe – during the years of the International Biological Programme, and from 1999 were promoted by periodic *Symposia of European Freshwater Science*. Links with Russia were considerable, and included participation by British limnologists at the *Baikal International Centre for Ecological Research*[35, 114].

Within the UK, the exchange of information on freshwater topics was aided by the *British Ecological Society* and the formation of regional *Freshwater Groups*. Among other activities the FBA also organised scientific meetings and, by setting up honorary Fellowships after 1990, continued its support to others and contributions to published knowledge.

Retrospect

The foregoing is a brief outline of a changing scene, in which the net extension of knowledge is manifest. This has ultimately rested upon a network of individual initiatives and insights, favoured or disfavoured by structural-organisational changes and the wider requirements of society. For freshwater science, these requirements have mainly concerned practical matters of water supply plus flood control, water pollution, fisheries and aquatic vector-borne diseases, to which higher education and conservation may be added. There is varied individual assessment of the respective – and not incompatible – roles of curiosity in nature and economic gain.

Britain has an even longer tradition of marine science, that shares many fundamentals with freshwater science. With a few exceptions, which include the ecophysiology of phytoplankton, the potential for productive interaction has not often been achieved. There was but limited attention to intermediate brackish waters[16d]. There has been no combined journal comparable to the North American *Limnology and Oceanography*; the two sectors are kept separate by the main funding Research Council. A few British oceanographers have used lakes as convenient test-beds. Examples in the past century are studies of vertical migration by zooplankton in Windermere[84], of stratification dynamics and modelling from Lake Bala (Llyn Tegid)[86], and of internal surges in Loch Ness[438]. Some scientists have combined experience in both sectors, from Sir John Murray onwards. Hopefully the connections will be reinforced in the present century.

Divergences have affected the perception of the subject. These are seen in general texts[239, 305, 343, 466] published over the century. It can be viewed as a unitary whole (limnology in the extended modern sense, not just of lakes but of all inland waters) or – more widespread in Britain – an aggregation of scientific specialities. It is not a primary science like physics and chemistry, but neither does it fairly fall within Rutherford's somewhat mischievous category of 'stamp collecting'. It can be held to offer especially favourable conditions for penetration in depth within ecological

science. To my mind the foundations are twofold, in structural-compositional aspects and dynamic flux-stock relationships[432]. There are blurred boundaries with relatively 'soft science', as in the diverse issues raised by conservation. These issues were doubtless prominent for Worthington in his book of personal reminiscences[476] when he referred to the 'ecological century' – including freshwater ecology over most of it. In 'hard' science, however, the loom and competition of other disciplines like molecular biology have been a reality.

Within the subject, as knowledge increased and practitioners became more numerous, more specialization was inevitable – in spite of increasing interaction between disciplines. As the food-chain is ascended, there has tended to be less interest in the basics of environmental physics and chemistry. And, reversing these domains, the converse was also true. There was some separation – fortunately incomplete – between work on the plankton and benthos. There has been a traditional divergence between research on standing and running waters, and – less acknowledged but very real – between large and small examples of either. I once heard a pioneer of African rift lake limnology refer to the content of meetings of the *International Association of Limnology* as 'pond-life'. (Another attitude, that research on tropical and polar fresh waters was essentially descriptive, is no longer defensible). Large rivers were little treated in the influential book of Hynes[230] on running waters. Divergent views have also been held on the value of relatively passive 'monitoring' over the long-term – an activity unlikely to appeal to the experimentalist but with some prospect of significant scientific reward[102]. Be this as it may, long-maintained observations have been a characteristic feature of much British freshwater research. Most scientists would object to the idea of any nationalistic science, but national traditions are not negligible. In 1900 our subject was dominated by German contributions, in 2000 by those from North America.

Between these two dates the character of freshwater science has developed radically and, of course, not only from the British contributions. In the future the pace of change is likely to accelerate.

Methods have undergone enormous extension, mainly from advances in other sciences with their technological spin-offs. One can instance chemical analytical methods, analogue and digital recording of data with computer manipulation, and a range of new sensors. Light microscopy has changed relatively little, but after 1950 electron microscopy opened new possibilities – as with the diagnostic cellular structures of diatoms and chrysophytes. Approaches have tended to become more quantitative, with attention to statistical resolution and confidence; models are often used to transfer relationships to complex systems; deductions from correlations have been more often augmented by those from experiment, in which mesocosms and microcosms have seen use.

Ecosystem circulation has been explored for chemical elements (biogeochemistry) and energy, with quantification of fluxes, system budgets, and interrelations in food webs. The significance of organic detritus was often evident. One source of information has been the distribution of isotopes such as ^{13}C. The basic constraints are set by mass balance and energy balance, the maximal efficiencies of individual transfers, and the abundance and diversity of constituent organisms. Another circulation determines water balance, a primary determinant of freshwater habitats, that has had its influence illustrated for degrees of permanence, retention time, discharge and salinity, all linked with biological consequences.

Ecophysiology has progressed with advances in basic physiology and biochemistry, perhaps most notably for metabolically versatile autotrophs (cf. N-fixation, alternative C-sources, nutrient-ion uptake and light-photosynthesis relationships).

Population dynamics came to form a core area in ecology. Application to freshwater populations has demonstrated advantages of sampling in a spatially discrete aqueous medium, validity for small autotrophic organisms as well as animals, and the development of varied population fluctuations in organisms ranging from flagellates to fishes – with associated diversity in the magnitude of intrinsic rates of increase and in loss processes. There has been debate over the relative importance of 'bottom-up' and 'top-down' regulation within the food-web, with implications for community structure.

Production ecology developed strongly after 1950. This gave recognition to the value of assessing absolute magnitudes of organic production in units (e.g. of carbon or energy flux per unit area) that aided wider comparisons of organic production in aquatic habitats and their components. It has drawn upon information from population dynamics and, especially for autotrophs, from ecosystem circulation and ecophysiology.

Evolutionary consequences, already an attractive area to many in 1900, have been taken up in relation to the functional morphology, adaptive radiation and ecological 'strategies' of aquatic organisms and the concentration of endemics in ancient lakes. The central consequence, biological diversity, has required large-scale and small-scale endeavours in systematics and taxonomy. The development of new methods of DNA and RNA analysis have furthered identification of genetic novelty and its survival and dispersal in freshwater populations.

Overall, there has been greater willingness to consider specifics and descriptive 'case-examples' in relation to general principles. Opinions

differ on the balance between intensive-reductionist and system-holistic approaches, and on the anthropocentric attitude ('man is the measure of all things'). Such differences of attitude are unlikely to be extinguished.

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These are given only as *examples*. Naturally they postdate the actual time that the work was done.

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