The developmental history of inland-water science

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Abstract

A general outline is given of the development and successive phases of the science of inland waters, variously encompassing ‘limnology’, ‘hydrobiology’ and ‘freshwater biology’. Three periods – pre-1930, 1930–1970 and 1970–present – are arbitrarily but conveniently distinguished. In the first, emphasis is given to the original contributions of pioneers; in the second, to the fuller development of fields of enquiry; and in the third to wider environmental-ecological linkages and outlooks. Example-situations and biographical involvements are illustrated by excerpts from the original literature.

Keywords: History; limnology; pioneers.

Introduction

In common with some other participants in freshwater science, I have felt a need to be aware of the history of its development. There are abundant records of the history of individual projects, but very few accounts – like that of Elster (1974) – of broader patterns over vistas of the past. With the latter approach it is desirable to be both balanced and connective, rather than provide a mere listing of individual components that are based on country, region or topic. I hope to engage the attention of those inclined to disregard historical aspects, or to view freshwater science as merely an aggregation of specialities.

The scope of this review is worldwide, but some bias has been unavoidable due to personal interests and contacts. It is divided into three chronological phases – each including some later references that concern earlier history – with differing treatments. In the earliest phase pioneers are recognised and much individual work is cited; in the second the focus is on developing subject-areas; in the third it shifts to broad influences and trends. I am conscious of the limitations of a formal history. Hence use is made of extended quotations (as ‘case examples’) from the contemporary literature, aiming to better convey circumstances and viewpoints of the time, and the human background. The choice is strongly influenced by my own experience. Applications of the science are not detailed. They have been linked with its basic content through the utilisation of water itself, of desirable resident organisms (especially fish), concern with issues of ‘water quality’ relevant to these utilisations and to visual amenity, use of watercourses as transport channels, and with contributions to human diseases from freshwater pathogens, parasites and their vectors.

Although the whole science is a cooperative development of findings and ideas, it also encompasses human disagreements. As Jackson (2000) comments: ‘At university, we undergraduates were told by Professor Omer-Cooper how, at Royal Entomological Society meetings in his youth, he had witnessed elderly and otherwise
respectable gentlemen, in silk hats and frock coats, shaking their fists and stamping their feet with rage.’

Such events were the basis for the elegant story of H.G. Wells (1927), The Moth.

**Early developments**

In the late 19th century the science of fresh – or better, inland – waters (Binnengewässer, eaux continentales) was developing in parallel with its marine counterpart. Within both fields there were two main approaches, the geographical–environmental and the biological. For inland waters they were influenced by the highly dissected nature of the habitats in diverse standing and running waters and much biological colonisation from some primarily terrestrial groups – especially insects and flowering plants. These features were much less evident in the marine setting. However, the two shared the topics of hydrography and hydrobiology, and the creation of first marine and later freshwater research stations. One contribution to this was an early enthusiasm for the study of plankton, whose devotees (e.g. Zacharias) could champion its status as a ‘model community’, later to be expressed in quantitative dynamics. The Hydrobiologische Anstalt Plön (northern Germany) was founded in 1892 and the journal Internationale Revue der gesamten Hydrobiologie und Hydrographie in 1908. These reflect a strong German influence in this early history. The combination of disciplines within freshwater science was expressed in the classic monograph on lac Léman (Lake of Geneva) by the Swiss Forel (1892–1904). His term limnologie (limnology, the science of lakes) was later extended non-etymologically to include running waters. The biological alternative, hydrobiology, did not logically exclude marine waters and – as with freshwater biology – the implied separation from associated physics and chemistry is limiting.

Although many inland water bodies are small and shallow, there are also large water-masses in deeper lakes. These waters were found to be subject to an internal subdivision or differentiation under the influence of various factors. This entrained many other features, physical, chemical and biological, and was early considered a basic element of the science. One important characteristic, a deep temperature-density gradient, was (in 1897, augmented 1904) named the thermocline by Birge (Fig. 1), from studies on the American Lake Mendota. Later the term was also widely used in marine science. A web of still earlier and interrelated discoveries has been summarised in an essay on Birge – himself an outstanding pioneer – by Mortimer (1956):

‘In order to assess Birge’s debt to earlier discoveries we must go back to 1891 when Richter described thermoclines, under another name, in alpine lakes and attributed their formation to the alternate action of the warming sun by day and surface cooling at night. Several observers, including Thoreau (Deevey, 1942), described thermoclines during the nineteenth century, but Richter was the first to suggest how they formed. His ideas still have a limited application; but now there is no doubt, as Birge was the first to point out, that the wind is a main agent, with the sun, in thermocline formation. The year 1895 saw the publication of two influential works: Forel’s second volume, in which were set out the main features of the seasonal temperature cycle in temperate, tropical and arctic lakes; and Hoppe-Seyler’s paper on the depth distribution of the dissolved gases, oxygen, nitrogen, and carbon dioxide, in the Lake of Constance. He found that oxygen was being removed from solution below the thermocline and attributed this to living processes. Here, he suggested, was a possible means of studying these processes at work in lakes and seas. Three years later Delebecque (1898) presented summary oxygen profiles for four French lakes (one with little oxygen below the thermocline) and briefly discussed the stratification of carbon dioxide.

Nearer home, on water reservoirs in Massachusetts, Whipple and his collaborators, in a series of remarkable but little known papers, related the growth of phytoplankton to underwater light and to the seasonal alternation of circulation and stratification. As early as 1894 Whipple wrote that growth was ‘directly connected with the phenomenon of stratification’, and (in 1895, after a detailed temperature study with his newly invented electrical thermometer) that temperature affects microorganisms ‘chiefly in an indirect manner by bringing about physical changes … which influence their food supply’. Fitzgerald (1895) produced,
for the same reservoirs, the earliest detailed pictures of annual temperature cycles. In 1896 Whipple showed that the growth of the plankton diatom Asterionella, suspended in transparent bottles at various depths, depended on light intensity, and that the zone of photosynthesis extended deeper in the clearer reservoirs. Chemical analyses of the water, and of the diatoms, demonstrated (Whipple & Jackson, 1899) that it was scarcity of one or other of the essential chemical foods that stopped growth in the upper illuminated layers after the thermocline had cut them off from replenishment from below. In 1891 in the same reservoirs Drown had discovered summer stratification of oxygen; and this considerably antedated the European work. Whipple and Parker followed this up in 1902 with a study of seasonal changes in distribution of oxygen and carbon dioxide and its effect on phytoplankton.

Other early developments in the science were concerned with small and shallow water-bodies. Especially in Europe and Britain, ponds and pond-life attracted many naturalists in the late 19th century. A diverse and interesting biology emerged. Still earlier, the structure and behaviour of particular aquatic insects and their larvae or nymphs had been taken up, as by Swammerdam, Réaumur and De Geer (Miall, 1895). Microscopy brought other revelations, following the discoveries of Antoni van Leeuwenhoek (1632–1723), with organisms often bizarre and beautiful. The exploration of ponds with their remarkable microscopic life was eloquently expressed in a standard work on rotifers by Hudson & Gosse (1886). Although very different from modern descriptions, a passage accurately describes some of the attributes of the animals that are beautifully and copiously portrayed in this still useful monograph:

Fig. 1. E.A. Birge at work – on the lake, up the meteorological pole, and at his desk. From Mortimer, in Sellery, (1956).
'On the Somersetshire side of the Avon, and not far from Clifton, is a little combe, at the bottom of which lies an old fishpond. Its slopes are covered with plantations of beech and fir, so as to shield the pond on three sides, yet leave it open to the soft south-westerly breezes, and to the afternoon sun... But if, retaining sense and sight, we could shrink into living atoms and plunge under the water, of what a world of wonders should we then form part! We should find this fairy kingdom peopled with the strangest creatures – creatures that swim with their hair, that have ruby eyes blazing deep within their necks, with telescopic limbs that are now withdrawn wholly within their bodies and now stretched out to many times their own length. Here are some riding at anchor, moored by delicate threads spun out from their toes; and there are others flashing by in glass armour, bristling with sharp spikes or ornamented by bosses and flowing curves; while, fastened to a green stem, is an animal convolvulus that by some invisible power draws a never-ceasing stream of victims into its gaping cup, and tears them to death with hooked jaws deep down within its body.'

The environmental science of small water-bodies was less developed than that of lakes, although an early discovery of day–night changes in gaseous concentrations induced by aquatic photosynthesis was recorded from Belgium by Morren & Morren (1841).

Flowing waters presented many other problems of environment and biology. Variable flow velocity and level were interrelated by discharge (e.g. in cubic metres per second), and the associated hydrological science – whose history is not detailed here – had its base in multiple water fluxes and budgets. Their practical importance for large rivers led to maintained long-term records (the oldest from the Nile: Talling, in press) that were lacking in most other branches of aquatic science. The water fluxes implied chemical fluxes of dissolved and particulate constituents. Their assessment led to inputs to the growing science of geochemistry, whose development was rudimentary before 1920 when Clarke compiled his Data of Geochemistry that included major inland waters. However, one early attempt to estimate the age of the world-ocean was based on the accumulation over geological time of salts contributed from freshwater run-off.

Interest in the life of rivers and streams was first centred upon fishes and the stratagems of fishing, but could involve food organisms as expressed in the classic guide of Isaak Walton (1653):

> 'You may guess what a work it were, in a discourse, but to run over those very many flies, worms and little living creatures, with which the sun and summer adorn and beautify the river banks, both for the recreation and contemplation of us (anglers); pleasures which, I think, myself enjoy more than any other man that is not of my profession'.

Such macroinvertebrate life in streams attracted many naturalists and subsequently group-specialists, with prominence given to various insects (e.g. Plecoptera, Ephemeroptera, Trichoptera, Chironomidae, Simuliidae), crustaceans and molluscs. There was also a beginning of systematic assessment of the differentiation of biological communities down the longitudinal course of rivers. An early example was the work of Lauterborn (e.g. 1916) on the Rhine (Lange, 1990), a later one within the 1928 book of Carpenter in Britain. Her enthusiasm is exemplified in her account of headwaters:

> 'At first sight we might be inclined to stigmatise the head-streams as biologically barren; only here and there a few close tufts of moss, encrusting liverworts, or slimy-coated Diatoms, grow close against the stones. No animals are visible, and we argue with justice that food is very scanty here, while the shallow water, continually streaming, independently acts as deterrent to the development of plankton and of nekton, and the absence of such fine bottom-detritus as collects about the roots of plants in quiet reaches discourages the settlement of a rich benthic fauna. But life is indomitably insurgent: no opportunity for its maintenance is ever neglected, and even in these unpromising situations we find each small advantage utilised to the full by living creatures. Lift a stone from the water's edge, and you will see some little animal scud hastily across to find a new retreat; carefully pluck a handful of the moss and shake it under water, and a whole company of small animals reveal themselves'.

By 1900 it was appreciated that free-flowing plankton, and possibly an adventitious ‘drift’, could exist in rivers. This raised questions about its possible longitudinal origin or lateral recruitment (e.g. Zacharias, 1898), issues that
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persisted throughout the following century. Longitudinal changes of chemical and biological features were also studied in relation to sources of pollution – as with an ‘oxygen sag’ and subsequent recovery downstream.

By 1915 it was recognised that cyclic change of species abundance with time (‘periodicity’) was widespread in the planktonic communities of lakes (e.g. West, 1909), ponds (e.g. Dieffenbach & Sachse, 1911; Fritsch & Rich, 1913) and at least some rivers (e.g. Fritsch, 1903). Its relationship to environmental factors was pursued, but hampered by limitations of population enumeration and chemical analysis. Pioneer work with algal cultures, as at Vienna by Richter (1909 – see Fig. 2), offered the prospect of an experimental approach to such problems.

The early development of studies on plankton periodicity is outlined by Talling (2002):

‘Early observers of freshwater algae in general, and of phytoplankton in particular, soon became aware that the community abundance and composition varied considerably and often cyclically with time. Detailed assessments of such ‘periodicity’ attracted a number of eminent pioneer limnologists. Included were G.C. Whipple on reservoirs in New England (Whipple, 1894), F.E. Fritsch on the River Thames and ponds in England (Fritsch, 1903; Fritsch & Rich, 1913), C. Wesenberg-Lund in comparative studies of Danish lakes and two in Iceland (Ostenfeld & Wesenberg-Lund, 1906), and F. Ruttner on changes during 1908–1913 in the Lunzer Untersee in Austria (Ruttner 1929/1930). The Wests, father and son, were also active, with successive descriptions of periodicity which included the Yan Yean Reservoir near Melbourne (West, 1909: see Fig. 3a). Quantitative developments were often precluded by the use, even on time-‘graphs’ (Fig. 3a), of grades such as ‘common’ or ‘rare’. (It was with such grading of periodicity in Yorkshire ponds during the 1940s that I first entered the field of freshwater ecology). Also the spatial heterogeneity of populations – though investigated in vertical detail by Ruttner – was often unknown.

Causes of the observed changes in populations and communities have always been sought in part through correlations with changing environmental factors. The early repertoire of measured factors was very limited. In particular, prospects for effective nutrient analyses had to wait for the contributions of mainly marine workers such as W.R.G. Atkins who, incidentally, once applied his methods to the problems of algal periodicity in freshwater ponds (Atkins & Harris, 1924). Partly as a result of early deficiencies, and the ready availability of thermometers, emphasis was unduly given to direct temperature effects. This was opposed by Pearsall (1923) in relation to the behaviour of the diatom Melosira (now Aulacoseira) granulata. He pointed to records of this species as abundant in a diversity of subarctic, temperate and tropical lakes, from Thingvallavatn in Iceland to Lake Victoria in Africa, covering a wide range of temperatures. His argument can now be seen as eroded by incorrect taxonomic identification in many ‘examples’. But, as not infrequently on a general point viewed from a wide baseline, Pearsall was right despite some wrong reasons!.....’

By the late 1920s analytical methods were improving and work by Pearsall (1932) on the English lakes suggested a chemical control of seasonal diatom populations by the depletion of silicon – an essential nutrient – that they induced. This work was part of his foundation studies on the English Lakes that began with an interest in submerged vegetation (Clapham, 1971):

‘Even as a small boy Harold [Pearsall] accompanied his father on frequent week-end visits to the Lake District, and all the family holidays were spent there......It was holidays spent by Windermere and Esthwaite that led to the joint interest in aquatic plants. Father and son constructed a

![Fig. 2. Early experimentation with algal cultures: the window and Arbeitsstisch of O. Richter at Vienna. Photo. F. Ruttner. From Richter (1909).](image-url)
three-pronged and weighted dredger with which to bring up submerged plants. This was cast from the stern of the boat by one of the occupants, the other meanwhile rowing the boat over the area to be sampled. The work of hauling in the line, removing and identifying the catch and making notes was shared between them. On one of these occasions they found in Esthwaite a species new to the country, Elodea nuttallii (Planchon) St John (formerly called Hydrilla verticillata)... The Pearsalls were staying in a cottage by Esthwaite in the summer of 1914 and it soon became obvious that the aquatic and fen successions there “were so complete that a detailed survey would prove an admirable starting-point for the description of the plant communities of the other lakes and of the relationships underlying their distribution”. The survey was therefore begun in 1914 and continued during parts of the next two years, and it led eventually to the publication, in two parts, of that classic of British ecology

Fig. 3. Early representations of the seasonal periodicity of plankton: (a) as grades of abundance in the Yan Yean Reservoir near Melbourne, Australia (from West, 1909), (b) cube root transformation of abundance of Asterionella formosa versus time (Kugelkurven) from the Lunzer Untersee, Austria (from Ruttner 1929/1930), (c) logarithmic plotting – with future potential! – applied by Scourfield (1897) to plankton components recorded by Apstein from the Grosser Plöner See, N. Germany (+ some added enlargements). From Talling (2002).
The aquatic and marsh vegetation of Esthwaite Water’ (J. Ecol. 5 (1917), 180-202, and 6 (1918), 53-74). The more extensive comparative study of eleven lakes provided material for other important publications appearing in subsequent years.’

By this time there had been contacts with the remote and ancient lakes of Baikal (Siberia) and Tanganyika (Africa) that uncovered a rich zoological endemism. Early expeditions to Tanganyika, for example, collected distinctive thick-shelled molluscs reminiscent of marine forms (Moore, 1903). As early as 1875 the Polish political exile Benedict Dybowskii, banished to Siberia, had described a most remarkable species-flock of endemic shrimps (gammarids) in Baikal. This situation has been recalled by Rzőska (1942)
– a fellow Pole and at the time himself in wartime exile in Britain – and in a letter to me dated 7 May 1960:

‘Yes, Dybowski’s monograph is an important milestone in the history of hydrobiology which does not start with Thienemann, Ruttner and Hutchinson and not even with Forel. While looking at this – precious – volume reflections on the barbarism of present times creep into my mind. Dybowski was a political prisoner of the Tsarist regime arrested in 1864 for his participation in a Polish insurrection. Far from being victimised by Russian aristocratic and scientific circles he became soon after arrival to his place of exile a close member of the then Governor General of Siberia ‘entourage’ and was later chosen to the Russian Academy of Science (= ‘Akademiki’) with various titles! Can you imagine this happening now...???’

Nevertheless the expanding knowledge of freshwater environments and their biota was strongly centred on Europe-with-Britain and North America. It led several scholars to devise schemes of classification or ‘typology’ – a development reviewed by Elster (1958). Included were the Caledonian and Baltic lake types of Wesenberg-Lund and Teiling, the related oligotrophic-eutrophic seriation of Naumann and Thienemann (Rodhe, 1969) developed before the advent of reliable nutrient analysis, and the thermal types of Forel and (later) Yoshimura based on seasonal temperatures and heat accumulation. There were also systematic studies of the general geography and configurations of lakes, as by Halbfass (1922), and pioneer work on the environments and biota of very long rivers, including the Mississippi (Galtsoff, 1924) and Volga (Behning, 1928).

**Middle years (1930–1970)**

This period saw a strong development of fields already initiated, the addition of new ones, and the forging of a web of inter-relationships between them. The last was encouraged by the contemporary growth of general ecological theory and concepts. The numbers of freshwater scientists were expanding rapidly; their intercommunication had been improved by the formation (in 1922) of the International Association of Limnology (Rodhe, 1975) with well-attended Congresses in many countries. The international spirit was strong in freshwater as well as marine science. Local groups of diverse composition led to some small but outstanding centres of originality, as during the 1930s at Madison (USA), Langenargen (Germany), Hillerød (Denmark), Kossino (Russia) and Windermere (UK). Early experience at the last is recounted by Hynes (2001):

‘When I had been there in the spring there had been several resident scientists, including K.R. Allen, Clifford Mortimer, T.T. Macan, Charles Taylor and Rosie Rosenberg, many of whose names later became well known to limnologists the world over .... The building was old, leaky, draughty, cold and inconvenient, and it was so damp that one’s shoes went green under one’s bed, but I look back on my time there as being one of the happiest of my life. I was doing what I always wanted to do. I was learning a great deal about a field that fascinated me, and I had guidance and friendship from a wonderful group of eccentric people.... It was a very stimulating place, and remote and very beautiful with it. It was delightful to wake up in that pure mountain air and go out collecting in clean aquatic environments, and I soon realised that I was very blessed to be there, even though it rained nearly every day.’

Outlines of these and other regional developments over time are known to me for North America (Frey, 1963), Germany (Elster, 1974), Poland (Rzóska, 1943), Russia (Lastochkin, 1945), Britain (Talling, 2004), Mexico (Alcocer-Durand & Escobar-Briones, 1991), Brazil (Tundisi et al., 1995), Antarctica (Fogg, 1992), southern Africa (Allanson, 2003), and tropical Africa (Talling, 2006). Research institutes, with private or state affiliation, developed in many countries, as described by Dussart (1966). Although the account of Elster (1974) gives special attention to events in Germany and Europe, it is also a thoughtful history of general developments in limnology to its date.

Because of the intricate overlaps in contributions from individuals and geographical regions, the following outline centres upon some broad approaches to the subject. Amplification can be found in the regional histories cited above, as well as in summary reviews of major fields commissioned for the 50th anniversary of the International
Association for Limnology and published within Issue 20 of its Communications (Mitteilungen) in 1974.

**Water movement** (hydrodynamics) is clearly fundamental to almost all other relationships involving inland waters. There is dominance of gravitational flow in running waters and atmosphere-water influence (wind stress, heat transfer) in ‘standing’ waters. The former led to the measurement and analysis of water flows and much of the science of hydrology. The last encouraged an involvement of meteorologists (e.g. Bryson, 1964) and to attempts to interpret the dynamics of vertical stratification in a water-mass. The chemical and biological consequences of such stratification were studied extensively by limnologists throughout the world, helped by attention to depth-sampling methods and with results that may be described as classical ‘Ruttnerian limnology’ after the distinguished Austrian pioneer (e.g. Ruttner, 1940). The seasonal timescale was the main centre of attention. However, short sampling intervals and – after 1950 – electrical recording (Mortimer, 1952) led to the better interpretation of dynamic change and recognition of the widespread occurrence of periodic waves or seiches on internal temperature/density interfaces. The small-scale spatial pattern of ‘Langmuir lines’ also attracted study, including its biological significance for mobile zooplankters (e.g. George & Edwards, 1973).

The study of chemical circulation, with biological influence (biogeochemistry), engaged more effort than its physical counterpart. A major stimulus, as in marine science, was the development of more rapid and reliable analytical methods. Most information concerned the distribution of concentrations in time and space. In running waters spatial interpretation centred upon external inputs, diffuse and localised; in ‘standing’ waters vertical gradients were interrelated with temperature/density stratification (e.g. Einsele & Vetter, 1938), interacting with the penetration of solar radiation (Sauberer & Ruttner, 1941) plus sedimentation and exchanges across the sediment-water and atmosphere-water boundaries. In both systems there was much time-variation from seasonality in the catchment and from uptake and release by aquatic biomass – on which experimental studies now ensued (e.g. Mackereth, 1953). A beginning was made with integrated flux-time estimates and their use for chemical budgets (mass balances) and input-output relationships (e.g. that of Mortimer, 1939 on lake nitrogen balance; and later Vollenweider, 1969a). There was an approach to the overall ‘metabolism’ of a lake, exemplified by the work of Einsele & Vetter (1938), Mortimer (1941–42) and Hutchinson (1941). It was foreshadowed in the essay of Birge (1907), *The respiration of an inland lake*.

Although much detail followed from chemical diversity, a few supposed master-variables – that directly or indirectly determine other variables – received particular attention. Among them there were, successively, emphases on salinity with electrical conductivity as a convenient surrogate; acid-base status with pH and titration alkalinity (acid neutralising capacity) as indices; oxidation-reduction with the redox scale of measurable electrode potential (e.g. Pearsall & Mortimer, 1939); and loading by the macro-nutrient elements N and P associated with biological consequences of enrichment or eutrophication (Hasler, 1947; Rohlich, 1969). The assessment of N and P availability was rendered difficult by the multiple chemical sources and pathways involved, with some initial underestimation – especially for P – of the dynamic situation (Rigler, 1973). By the 1950s there were the beginnings of use of radioisotopes to follow chemical transfer in natural systems (Hutchinson & Bowen, 1950) and sub-systems (Hayes, 1955).

**Biological activities** continued to depend upon, and therefore encourage, a foundation in sound taxonomy. Major monographs appeared on individual groups; also regional handbooks for identification over wider ranges of aquatic organisms, some – like that of Ward & Whipple (1918) – linked with ecological material. Such linkage also appeared in works on ‘general biology’. A fine example is the last major work of Wesenberg-Lund (1943), on aquatic insects. Also now beginning was the elucidation of structural mechanics behind feeding and locomotion, and of growth in relation to food intake and assimilation.

Taxonomic influence also appeared in the group-based partitioning of community composition, as in ‘plankton quotients’ (Nygaard, 1949), and the presence–absence–relative representation of species and systematic groups in relation to ranges of environmental variables. These ranges were sometimes miscalled ‘gradients’, but
otherwise true gradients could be involved with respect to dimensions of space and time. Indicator organisms were sometimes used in ‘systems’ of environmental response, as in the European Halobienspectra (relating to salinity) and Saprobinsystem (relating to decomposition). Lake typology – an environmental analogue of biological systematics – once aroused much discussion (Elster, 1958), although it was avoided by others (e.g. Pearsall). There were also studies concerned with longitudinal changes in rivers and their attempted generalisation (Illies, 1961), with depth differences in lakes, and with seasonal changes. The last included extension (e.g. by Lund, 1949, 1964) of the earlier studies of plankton periodicity, aided by success in the culture of some common planktonic species (Chu, 1942), and work on interactions – as by grazing, parasitism, external metabolites – within plankton communities.

There was improvement in the measurement and interpretation of environmental factors (e.g. nutrient concentrations), and deductions from abundance-factor correlations interpreted against information from chemical budgets, physiology and experimental systems. The last, as mesocosms (e.g. Hasler, 1963; Lund & Reynolds, 1982) and entire lakes (Schindler, 1990), as well as microcosms (cultures), began to be more widely developed and used. For many organisms the time-changes involved increments of individual size and succession of stages in the life history. Issues of abundance versus time moved from qualitative to more quantitative interpretation, as expressed in the growing discipline of population dynamics (Hutchinson, 1978). In the present aquatic situations, intrinsic rates of increase covered a wide range that could be represented in food webs, such as those linking micro-algae and fish. Useless measures of abundance based on numerical sums in size-heterogeneous aggregates gave way to those founded on more homogeneous units such as organic dry weight, cell volume, cell carbon and chlorophyll a – as deduced either from microscopy or direct chemical analysis.

Some disciplines (e.g. population dynamics) were also consolidating as general topics as well as components of freshwater science. Production ecology centred upon rates of organic production per unit area and unit time. Challenges lay in the realistic measurement of production rates for individual species and especially trophic levels (Rigler, 1975), and the mechanisms of their regulation (Vollenweider, 1969b; Edmondson & Vinberg, 1971; Vinberg, 1971; Downing & Rigler, 1984). These dimensions, and with organic dry weight, carbon or energy content as measures of biomass, allowed comparisons between different communities and organisms in a ‘common currency’. Use could be made of gain quantities in population dynamics and of environmental reactions (e.g. nutrient or deep-water oxygen depletion, day–night or upstream–downstream changes of oxygen content (Vinberg & Yarovitziina, 1939; Odum, 1957)) as indices of production; also of energetic-efficiency ratios (Lindeman, 1942) in a trophic series (food-chain) that included the primary input of solar energy and its photosynthetic conversion measured from oxygen and carbon dioxide exchange (e.g. Manning & Juday, 1941; Vinberg, 1960; Talling, 1982). Thus there was the aim – a great stimulus to many of us – to use energy transfer as a characteristic in biological as well as in physical systems. However, there were many problems in bridging the interfaces linking primary with more terminal (e.g. fish) production, so there was some resort to empirical and statistical summaries (e.g. Melack, 1976).

After 1956 the introduction of the radioisotope 14C increased sensitivity and stimulated a phase of extensive measurements of primary planktonic production. Such physiological measurements contrasted with the more obvious approach based on direct increments of biomass, which was usually inapplicable to mobile populations subject to major and age-related loss processes, but often usable with attached macrophytes (e.g. Westlake, 1963). In many invertebrate and fish populations, information on component biomass-age distribution was the basis for some production estimates (as by the ‘Allen-curve method’: Allen, 1951; also Ricker, 1968). In some cases the relative frequency of critical developmental stages in a phased life history could be utilised to estimate production rates, as applied to egg-bearing zooplankters (Elster, 1955; Edmondson, 1960), the frequency of division-stages in unicells (e.g. Heller, 1977), or that of successive stages of known duration (e.g. Gras & Saint-Jean, 1983).
Production ecology thus had many ramifications, with roots in various other lines of enquiry – such as the nine illustrated by Talling (1984) for primary aquatic production.

Carbon contributions from terrestrial production were also traced, as in the utilisation of detrital particles by filter-feeders of streams and in transfer from marginal macrophytes. The question of utilisation of dissolved organic matter by aquatic animals had a controversial early history, linked to the ‘Pütter hypothesis’ (Jørgensen, 1976); later the microbial utilisation led to much discussion – shared with marine science – of the ‘microbial loop’.

Community structure also developed general interpretations, in which decisive elements were interspecific competition and food/feeding relationships – e.g. of fish upon limnetic zooplankton (Hrbáček et al., 1961) or upon stream zoobenthos (Elliott, 1967). Food relationships were used to distinguish functional groups or guilds in the zoobenthos of streams – as in relation to the relative size of particles (microphages, macrophages), to the degree of dispersion or compaction (plantivores, scrapers, shredders), and activity of the consumer (filter feeders, substratum ingesters, ambush predators, pursuit predators). For the deep zoobenthos of lakes, attention was given to the use of sediment detritus and inputs from the planktonic production above (Jónasson, 1972).

Ecophysiology applied physiological knowledge and techniques to the tolerance and activities of organisms under varied environmental conditions. Examples included response to salinity and oxygen depletion (Harnisch, 1951), ion uptake (Beadle, 1943), photosynthesis (Talling, 1961) and nitrogen fixation (e.g. Dugdale & Dugdale, 1962). A uniquely wide-ranging combination of plant physiology with hydrobiology appeared in the two-volume work *Hydrobotanik* by Gessner (e.g. 1955).

Palaeolimnology aimed at the reconstruction of past aquatic environments and their biota. Use was made of the remains in layered sediments of lakes, bogs and fens. There had been notable pioneer studies on Swedish and Swiss lakes in the 1920s, with many applications elsewhere after 1940 (e.g. Pennington, 1943). Investigations have continued to develop both in scope and techniques to the present day.

Geographical extension of fieldwork brought new material and problems from regions beyond the long-studied ones of Europe and North America. Contrasts emerged especially from the tropics (Ruttner, 1931; Beadle, 1932, 1974; Beauchamp, 1939), arid regions (Cole, 1968), high mountains (Löffler, 1964) and isolated land-masses like Australia (De Dekker & Williams, 1986). Environmental novelty stemmed from climate and geology, biological novelty from environmental response and restricted geographical distributions. By 1965 there was a broad foundation for tropical studies. Included were some major rivers, notably the Nile and Amazon, for which this and later work was summarised in monographs (Rzóska, 1976; Sioli, 1984). Expeditions – pre-eminent among which was the German Sunda Expedition of 1928–29 (Göltenboth, 1996; Talling, 1996) with Thienemann and Ruttner as participants (Fig. 4) – had a major role. This is exemplified by the personal histories of two pioneers, L.C. Beadle and R.S.A. Beauchamp:

‘With the death of Leonard Beadle in September 1985, the world of freshwater biology lost a major pioneering spirit. He had a life-long interest in the tropics which began in the middle of his undergraduate studies at Cambridge University with his participation in an expedition to South America, in 1926. Four years later he arrived for the first time in Africa, as a member of a Cambridge University expedition to the East African lakes. Thereafter he returned to Africa three times: to Algeria in 1938 to work on the biology of saline waters and oases, to Uganda in 1949 where he was head of the Zoology Department of Makerere University and Trustee of Uganda National Parks until his retirement in 1966 and, finally, as advisor to the Royal Society International Biological Programme project on Lake George in Uganda...

The Cambridge expedition of 1930 must have gone to Africa in very much the spirit of Burton and Speke. The Livingstone era had ended only some sixty years previously and tropical Africa was still largely unknown to the professional biologist. The old excitement generated by the continent, the exceptional diversity of freshwaters and one suspects, the lure of the metaphorical “grey, green, greasy Limpopo river, all set about by fever trees”, evidently
persisted throughout the next 40 years of his career. His book entitled “The Inland Waters of Tropical Africa”, first published in 1974, represents the distillation of his personal experience and enthusiasms over this long period and it is now a classic in its own field. This work centred largely on water chemistry and the ionic and respiratory adaptations of animals in swamps and saline waters; and reflected the fact that he had devoted much of his own research effort to the study of osmotic regulation and physiology in aquatic animals and that he was an acknowledged authority in these fields. He was a gifted experimentalist and he maintained his skills throughout an active research career.’

(from McLachlan, 1987)

‘Beauchamp, Director [of the East African Fisheries Research Organisation, later EAFFRO] from 1947 to 1960, was another of the “Cambridge School” of African limnological research. Before World War II he had laid the foundations of our knowledge of the Rift Lakes Tanganyika and Nyasa. This included making a truly epic voyage down the length of Lake Tanganyika in a four-metre boat, sleeping under trees near the beaches and equipped only with a hand-operated winch and three quarters of a kilometre of hydrographic wire and a reversing thermometer. Lowering and hauling this took half an hour or more to get a single temperature reading, yet, with this simple equipment, Beauchamp accurately obtained the first-ever data on the existence of the separate water layers and the thermocline between them (Beauchamp, 1939). When one thinks of the millions spent on such research today, the tiny investment in his work yielded incalculable dividends.’

(from Jackson, 2000)
Universities developed strongly in many tropical and subtropical lands after 1945, with pioneers who were often expatriate staff members. In much of his later life Beadle was one. Two further notable examples serve to illustrate the endeavours, both earlier and later.

G.E. Hutchinson (University of the Witwatersrand, Johannesburg):

‘A group of very large pans, most of which are now perennially filled with water, is found in the Ermelo district of the Transvaal. This group consists of Lake Chrissie, Lake Banagher, Magdalenasmeer, Eilandspan, the Blaauwater pans, and some others. They looked particularly attractive and several of us from the university visited them in February and May of 1928. A number of smaller pans nearer Johannesburg were also studied. Though we had makeshift equipment and no boat, except on Lake Chrissie, it was possible to learn a great deal about these extraordinary basins.

They varied in an astonishing manner. One basin contained fresh, soft water with a rich flora of desmids; at the other extreme there was saline eutrophic water, soupy with the blue-green alga _Nodularia_. Most typically the lakes were slightly saline and alkaline and were either very turbid with suspended mud and colloidal silica or had sepia-colored water, apparently due to the accumulation of a peaty extract of decomposing wind-blown grass. Nothing like the last-named type of lake had been described in the limnological literature; of this I knew nothing at the time...

When I returned to Cambridge on my way to America, Penelope Jenkin, whom I had known as a student, and who has since done most beautiful work on the limnological aspects of flamingos, showed me August Thienemann’s newly published _Die Binnengewässer Mitteleuropas_. Reading this, I learned how the Lake Chrissie pans fitted, as new categories, into the scheme of classification that was being developed in Europe. I also came to see, reading this book after Elton’s _Animal Ecology_, how all the ways of looking at nature that I had acquired in a random, disorganised way could be focused together on lakes as microcosms. I had, in fact, become a limnologist.’

(from Hutchinson, 1979. The information from the pans was published in Hutchinson et al., 1932.)

J. Rzóska (University College of Khartoum):

‘Wartime experiences followed, severing him from his native Poland. ... Apart from two essays on historical topics (1942, 1943), hydrobiology did not return until 1946 with his appointment as lecturer and later Reader in zoology at the University College of Khartoum, Sudan. There his imagination was captured by the great Nile river, and with official encouragement and some devoted colleagues he built up from small beginnings a well-equipped and mobile Hydrobiological Research Unit. By vacation cruises – often exceeding 2000 km – and by land treks, this Unit surveyed many features of the ecology of the Blue and White Niles. Emphasis was given to longitudinal and seasonal differentiation in relation to water flow, but he also made various more specialised and intensive studies – as on the colonization of temporary rain-pools (1961) and the diel distribution patterns of zooplankton (1968). His sustained quantitative work on zooplankton was then virtually unique for African fresh waters, and the same can be said for the immense longitudinal river-surveys.’

(from Talling, 1985)

Later much research, especially on lakes of Africa, was linked to the support of fisheries – although divergences of opinion could develop. A major disagreement concerned the desirability of introductions, especially of a large predator fish, the Nile perch. In his memoirs, Jackson (2000) recounts the circumstances that led to the presumed extinction of many endemic fishes of Lake Victoria – possibly the largest event of vertebrate extinction in recent times:

‘I will never forget the look of incredulous horror on Vernon van Someren’s face, when Rhodes, in giving Uganda’s report, mentioned he had imported some carp to try as fishpond fish. Van Someren, of Scottish extraction, but Kenyan to the core, came from a distinguished family which had served East Africa well... Later, on Beauchamp’s retirement, he briefly became director of EAFFRO before his untimely death. His speciality was aquaculture, especially of trout and tilapia.

Once sure that he had heard aright, he began to upbraid Rhodes for doing such a thing without consulting the other territories, stressing that these fish might wreak havoc among trout and indigenous fish, should they escape
or be introduced by unscrupulous folk. Unconscious of wrongdoing, Rhodes replied with spirit......

The introduction of Nile perch, Lates niloticus, to Lake Victoria can also be laid at the door of Kinloch and Rhodes. They claimed that this famous game fish would enhance the lake’s tourist value by attracting sport fishermen, and would benefit commercial fishermen with long lines. As for the lake’s small endemic haplochromines, they considered them ‘trash fish’ (Kinloch, 1972), possibly of some zoological interest, but of no commercial importance. Informed opinion had not adequately considered the question when the tilapia had been introduced earlier, but the Nile perch proposal encountered much opposition from alerted researchers. Beauchamp spoke against it at board meetings; Fryer (then an EAFFRO staff member) put forward counter arguments in a cogent paper (Fryer, 1960), while I opposed it as a board member (Jackson, 1960). The Fisheries Departments of Kenya and Tanganyika, intimately involved since most of the lake belonged to them, were either lukewarm in support or actively rejected the proposal.

But, in the teeth of all opposition, the wishes of Rhodes and Kinloch prevailed. They secured the compromise that Nile perch biology should be studied in fish-ponds before introduction was sanctioned. This job was assigned to Eric Hamblyn (1966) of EAFFRO, but, before he had completed his studies, Nile perch were recorded from Lake Victoria. The first were allegedly escapees from fish ponds within the lake catchment in Uganda, but reliable sources intimated that direct stocking was done clandestinely in about 1956 near Entebbe. It matters little; to keep such fish in ponds within a catchment is as reprehensible as putting them in the water directly.’

Endemism was charted in a few ancient lakes of tectonic origin (Brooks, 1950) like Baikal (Kozhov, 1963) and Tanganyika (Coulter, 1991). The background situation (with prolonged isolation) for another, Victoria, is still debatable but the belief that the entire species flock of hundreds of species of cichlid fishes evolved in about 15 000 years subsequent to the lake drying out is clearly untenable (Fryer, 2004). Evidence was obtained on finer intraspecific differentiation in some temperate species, such as the charr (Frost, 1965) among fishes. Nevertheless, for smaller species of inland waters the predominant impression was of a tendency (noted by Darwin) towards cosmopolitanism. There were, of course, restrictions over latitude and altitude due to environment, and indications of the persistent influence of major historical events such as the Quaternary Ice Ages (e.g. Thienemann, 1950) and desertification (as from aquatic relics in the Sahara: e.g. Daget, 1959).

**Later period (1970–present)**

In this period there was much extension of the individual lines of enquiry outlined above and development of new ones. This was aided and augmented by three sorts of stimuli.

Advances in the physical sciences, and the resulting technology, opened up new techniques. Among them were remote sensing applied to spatial distributions; electronic digital recording and computing; developments of electron microscopy; new sensors for environmental variables; and advances in chemical methods such as spectrophotometry, atomic absorption spectroscopy, liquid and gas chromatography, and isotope ratios. Also, we should include the use of fluorescence as a physiological tool, e.g. in work on photosynthetic production. There were also consequences from new methods in the biological sciences. Those of molecular biology were applied to the fine genetic analysis and differentiation of populations (e.g. Reid et al., 2000) – including bacteria (e.g. Pickup, 1991), for which there were now improved methods of enumeration from the replacement of plate-counts by direct count methods based on fine filters and epifluorescence microscopy (Jannasch, 1958; Hobbie et al., 1977) – as well as applications of microbial physiology and chemistry (Kusnezow, 1959; Brock, 1966). Production biology continued to flourish, but with attention more centred on mechanisms (e.g. Falkowski & Raven, 1997) than numerical characterisation. In parallel with marine discoveries, it was recognised that a very small-celled, autotrophic picoplankton is widespread in inland (as in marine) waters (Stockner, 1988; Reynolds, 2006). Investigations of relatively remote areas – including the Arctic and
Antarctic (Fogg, 1998) – increased, aided by supporting air transport and means to operate in extreme environments.

Second, there was extension of principles and theory within each of the contributing disciplines that derived from situations other than those of freshwater science. This brought to bear much knowledge, experience and theory generated elsewhere and also led to disputations (e.g. Lehman, 1986; Peters, 1986). It involved, however, the paradox of an aquatic science that was simultaneously enriched but also – detrimental to the science – more often regarded as a mere association of separate and multiplying specialities, despite increasing evidence of their interaction.

Third, the practise and content of freshwater science was increasingly influenced by external funding organisations and currently favoured applications. The latter tended to change with time and geographical region. Thus in the 1960s production quantification had been foremost, followed in the 1970s by nutrient enrichment (eutrophication) with its consequences, and subsequently conservation and the assessment of biological diversity. In developing countries, as within tropical Africa, most work was underpinned by fishery science and water supply. There and elsewhere much depended upon large internationally supported projects that included the broad, and latitudinally extensive (e.g. Carmouze et al., 1983), International Biological Programme of 1964–74 (results summarised in Le Cren & Lowe-McConnell, 1980). Larger scale collaboration also appeared within the initiatives of individual countries. All this contrasted with the situation early in the 20th century, which was marked by the individual contributions of university-based scientists, field stations or institutes (as at Plön in Germany, Lunz in Austria, Aneboda in Sweden) and gifted amateurs like Scourfield and Boycott in Britain.

The preceding 1930–1970 period saw the establishment of three major quantitative approaches to general ecological-environmental science – production ecology, population dynamics, and biogeochemistry with physical dynamics in ‘ecosystem science’. For these, well-delimited inland water-bodies offered some special advantages. All three were interconnected to varying degrees. Thus primary aquatic production was linked to biogeochemical circulation with photosynthesis adopted (especially for plankton) as an accessible ‘rate-meter’; secondary production depended more on variables resolved in population dynamics. Physical dynamics can be viewed as the ultimate limiting framework. In production ecology, a former unspecific use of ‘turnover time’, as by Juday (1940), was replaced by summarising production/biomass (P/B) ratios and, more analytically, prediction of population change with exponential rate constants and the separation of gain and loss rates (e.g. Reynolds et al., 1982). Isotopically labelled constituents gave much useful information. Boundaries between physical, chemical and biological approaches to the science became increasingly ill-defined and the total span impressive. This is evident in a recent synopsis of 20 major components of advance (McCullough et al., 2007), which can be listed as:

- Lake hydrodynamics
- Basic chemical kinetics and reactivity
- Major ionic components
- Bacterial activities and distributions
- Nutrient limitation of primary biological production
- Aquatic photosynthesis
- Solute – including nutrient – dynamics in running water
- Population dynamics
- Food-web interactions and community structure
- Ecophysiology
- Dynamics of large rivers and lakes
- Biodiversity, taxonomy and the fine genetic structure of populations
- Indicator organisms and assemblages
- Reconstruction of past environments and biota
- Consequences of reservoir creation
- Human constraints upon change – conservation
- Tropical freshwater science
- Mathematical modelling
- Consequences of climatic changes
- Subject surveys and syntheses.

The accumulating body of observations facilitated two general approaches – the analysis of long-term datasets and the comparative treatment of examples within wide-ranging surveys. Less positively, it tended to promote increased specialisation among practitioners.
Preoccupation with the benefits of applied freshwater research rather than its fundamentals is not without its dangers. This has been expressed by Lampert (2007), in relation to the current closure of limnology at the Plön institute: ‘We have many problems that must be solved quickly. But I am afraid that the concern expressed by Pete Jumars already in 1990 is still valid: “Although the need for applied limnology is obvious, it is arguably less obvious that it is impossible to apply knowledge that one does not yet have: sound understanding of basic limnology is prerequisite to sound management”. Does the declining interest in fundamental limnology mean that we already have the “sound understanding”? Do we train our students with the perception that limnology no longer has surprises and discoveries to offer? Sometimes going to conferences I get the impression that this is an agreed opinion. If this is the case, then limnology is in fact no longer a subject for the Max Planck Society, and nobody should complain about the end of an era at Plön.’

Large-scale summary and outlooks

The interrelation of findings within inland water science has been considered in numerous reviews of component topics. Broader accounts over the subject as a whole are fewer. Considered in the time-sequence of their publication, they represent both the increasing amount of factual knowledge and changing working attitudes (paradigms) to this knowledge. The last point is brought out, for example, if the 1910 evaluation by Wesenberg-Lund (‘Summary of our knowledge regarding various limnological problems’) is compared with the present-day climate of ideas. Well-placed, however, was his impatience with over-descriptive contributions:

‘During the last ten years we have obtained from different countries a number of lake descriptions... We find in these papers a pot-pourri of very many different branches of science: physics, chemistry, geology, meteorology, zoology, botany, all treated and finished off in one or two hundred pages. The starting point for these publications is that a lake is a sharply limited piece of nature with its own laws... The great model is Forel’s excellent monograph, Le Léman.

All these papers deal with the regular annual variation in temperature, the transparency of the water, a little in regard to environment and a list of organisms – never complete and only thoroughly carried out for those groups which most interested the author. In the biological parts we find casual remarks, but really the only remarks of scientific value. All the papers finish with a chapter giving the results of the investigations... intended to give us a clear understanding of this one lake as different from other lakes. These chapters are almost identical in all the papers.’

There has been a divergence between outlooks more influenced by classical systematics and those that reflect attention to quantitative issues of ecosystem and population dynamics. Further, some national traditions can be detected. These could be exacerbated by political events or modified by international contacts, as illustrated in the scientific autobiography of Rzóska (1982):

‘A university was created in Poznań and at last we could study under Polish professors who arrived mainly from the Austrian part of Poland, where a class of intelligensia had been created previously.

My parents wished me to study medicine because that and law were the only careers open to a Pole in the German occupied territory. To their displeasure I opted for zoology. It was only from the years of 15 and 16 I was interested in biology and with the help of a small microscope and an aquarium I began to study pond life. Mentally, I was under the influence of German thought and pantheism and also Goethe. These juvenile notions changed quickly as my knowledge of the spread of zoological information increased.

I began to work on the biology of lakes and other standing water in Western Poland and wrote some research papers on these subjects. Soon I realised the complexity of nature and began to wonder about the problems of the relation between terrestrial and aquatic fauna. A visit was made to the Austrian limnological station and contacts made with Austrian advanced biologists... Later on, with broader interests, I spent two summers at the Swedish Station of Aneboda; that extraordinary man Einar Naumann lectured to a group of students, but for my benefit, often spoke in German.’
Over the years there has been a succession of general surveys, written by distinguished practitioners. These blended physical, chemical and biological approaches in varying degrees. Early classics, influential in their time, included the *Handbuch der Seenkunde* of Forel (1901), *Das Süsswasserplankton* of Apstein (1896) and *The Microscopy of Drinking Water* by Whipple (1899). More detail is available through the excellent early bibliography of Chumley (1910). Notable later expositions included those of general limnology by Welch (1935), Ruttner (1940), Macan (1963), Dussart (1966), Cole (1975), Golterman (1975), Wetzel (1975), Moss (1980), Goldman & Horne (1983), Margalef (1983), Lampert & Sommer (1997) and Kalff (2002), and of running water studies by Hynes (1967) and Allan (1995). Most outstanding for lakes in its scope and erudition was the four-volume *Treatise on Limnology* of Hutchinson (1957–1993). Here the historical dimension is abundantly represented in specific detail, although (as in the other general works) not in a more integrated survey.

It is impossible to overestimate the influence of relatively abstract attitudes and approaches in the history of the subject. Paired contrasts can be listed: holism versus reductionism; preference for inductive versus deductive reasoning; the supremacy of tracing causality (Lehman, 1986) or testing prediction (Peters, 1986); the water-body as a microcosm (Forbes, 1887) or as a channel in wider flux; emphasis on consequences of species differences (Lund, 1949) or more composite ‘envelope ecology’ (Talling, 1993); formulation of the ecological strategy of an organism (Kilham & Kilham, 1980) or its teleological ‘absurdity’ (Beever, 1993); the attraction of ‘higher level’ generalisations versus the difficulty of feasible refutation (Rigler & Peters, 1995); the importance of unifying concepts or their practical irrelevance (Rigler, 1975); the gains in creating quantitative test-models versus possible defects in the rigour of their foundations; the supreme importance of individual ‘facts’ or of emphasis on their wider significance (‘Hutchinson school’); the value of long-term series of observations versus their predominant repetitiveness; the merits of a core of ‘hard science’ versus secondary areas of more familiar ‘soft science’; and the modern significance or outdated insignificance of old interpretations. An element of real value probably attaches to each side of these contrasting alternatives.

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