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**Supplementary data**

"Data Supplement"

http://rsbm.royalsocietypublishing.org/content/suppl/2015/11/13/rsbm.2015.0025.DC1

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Elected FRS 1963

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John Lund’s life and career were rich in the unexpected. Although his early education was
deficient in science, he ultimately altered the character and practice of his adopted subject,
especially in Britain. Different traditions in systematic and physiological ecology were absorbed
from successive contacts with two leading authorities, and combined to good effect in his
main work on the ecology of freshwater planktonic algae. Insistence on factual specifics and
accuracy, and avoidance of over-generalization, were encouraged by a long wartime occupation
in forensic science with consequent legal evidence. He was forthright in his opinions; he
benefited and inspired a succession of younger scientists and assistants. Cooperative work with
senior scientists led to some ground-breaking innovations, including that with his wife, Hilda,
involving the extension of her mycological work to epidemics of chytrid parasitism in planktonic
population dynamics. In retirement he devoted much time to acquiring uncommon fluency in the
Russian language, which was put to good effect in private and official matters.

EARLY LIFE

John Lund, born in 1912, grew up within a professional family in northwest England.
Two ancestors were immigrants from Europe in the nineteenth century; one, John’s great-
grandfather, was a Polish Jew who came to England in 1819 and subsequently was prominent
in the Oddfellows group in Britain. The other was (probably, but unconfirmed) a Scandinavian
from whom the surname Lund was derived. His father, George Edward Lund, was a Manchester
solicitor; his mother was Kate, née Hardwick. They had three children, all boys, of whom John
was the youngest. His early education included a school near the Cheshire meres with which
his first publication was concerned (1)\(^\dagger\). In his teens he attended the well-known public school

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\(^\dagger\) Numbers in this form refer to the bibliography at the end of the text.
at Sedbergh in the western Yorkshire Dales, for which his memories were not affectionate. Military exercises in the Officer Training Corps earned his derision, and he was directed from a preferred science-based course to a classical one. (‘Well, Lund, it’s the classics that count in the after life. Latin can take you anywhere.’) But the fine mountainous surroundings were enjoyed; from one hillside he witnessed a solar eclipse in about 1928. Family fortunes were affected by the financial depression of the early 1930s. Soon after leaving school he had the prospect of an unexciting office job. A sympathetic uncle, a military man, noticed his interest in natural history—John then specialized in caterpillars, moths and butterflies—and suggested university enrolment in a biological subject. John acquired sufficient subject qualifications from a short course in a ‘cram school’. He entered the University of Manchester in 1931, where he specialized in botany—after a strained relationship with the professor of zoology.

**LATER EDUCATION: UNIVERSITY OF MANCHESTER**

His instructors included a young Irene Manton (FRS 1961), an exceptionally incisive character, who later co-founded the introduction of electron microscopy into botany. In one course she required students to microscopically examine freshwater algae that they had personally collected from some water body. Lund later recalled that his collection included some interesting forms and generated in him a lifelong attachment to the study of algae. After receiving his first degree of BSc (with first-class honours in botany) in 1934 he went on to a short period of research on the structure of a macro-alga, a brown seaweed, for which local support from W. H. Lang FRS was available. This he completed—but never published—for the degree of MSc awarded in 1935.

**UNIVERSITY OF LONDON: RESEARCH ON FRESHWATER MICRO-ALGAE**

His growing interest in algae led naturally to a research studentship (1936–39) under the pre-eminent authority F. E. Fritsch FRS, at Queen Mary College of the University of London. Fritsch’s influence was probably the most decisive in his scientific career. They later became close friends. He took up the taxonomic and ecological study of largely motile bottom-living micro-algae in several ponds within Richmond Park. Ecological aspects were largely linked to the behaviour of individual species. A rich assemblage of unfamiliar and partly new forms was uncovered and described in a PhD thesis and subsequent publications (2). His meticulous attention to specific detail earned the esteem of Fritsch. Fritsch had begun, for his own use, a collection of cuttings depicting individual freshwater species (figure 1). After Fritsch’s death the collection was gifted to Lund, who later extended and perpetuated this as the ‘Fritsch Collection’ at Windermere. Fritsch had earlier transferred to his keeping the first parts of a proposed British flora of freshwater algae, which was never completed.

A second major influence came from another eminent scientist, W. H. Pearsall (FRS 1940). Pearsall combined plant physiology and ecology on an exceptionally broad front, which included pioneer work on the ecology of the English Lakes and their phytoplankton (Pearsall 1942). He was Lund’s external examiner for his PhD thesis—technically an insecurely bound file, which fell to pieces in Pearsall’s hands (money was short at that time). Lund later
described Pearsall as ‘a legend in his own time’. His challenging science inspired Lund’s later concentration at Windermere on ecological aspects of phytoplankton, as it had inspired two other early staff members (T. T. Macan and C. H. Mortimer (FRS 1958)) of the Freshwater Biological Association (FBA). This grant-aided research association ran an annual Easter course in freshwater science, which Lund attended in about 1937. Academic work continued for a short time, during which Lund was a temporary lecturer in the Department of Botany at Sheffield University.

**OTHER OCCUPATIONS: FORENSIC SCIENCE IN WARTIME BRITAIN**

In 1939 he was barred from war service by deficiencies of eyesight. After recommendations from others, he had entered (in 1938) a very different occupation, forensic science, at a leading forensic laboratory at Birmingham. It gave unexpected scope for his talents and expertise. He used microscopy to unearth clues—in part from soil-inhabiting diatoms—and later published extensively on soil algae (see, for example, (3)). He was an expert scientific witness in courtroom trials and learnt to distinguish between convincing and unconvincing evidence. He suffered adverse reaction from some judges with little respect for science. One summed up by advising the jury that they could neglect the scientific evidence! Later a former eminent judge, Lord Hailsham, visited the laboratory at Windermere, where Lund and he had a convivial discussion on such matters and personalities.
Having attended the Easter field course at the FBA, Lund had some familiarity with the laboratory and its staff. During 1944, with Fritsch’s encouragement, he took up the post of algologist with the FBA at the end of the year. The association then had headquarters and laboratories at Wray Castle, a domestic folly by the north shore of Windermere (figure 2). He lived in the castle for some time and took part in domestic activities. With Pearsall’s participation and support, the association had already made contributions to the study of algae; with Lund’s arrival, these were greatly enhanced. Laboratory facilities were cramped, the staff was small, and the situation could be regarded as a ‘backwater’ (he later said, ‘I like backwaters’). But, with some reservations, he took up the post.

His scientific projects were soon varied and in part novel. After contemplating his former subject of bottom-living algae—soon to be taken up by his student F. E. Round—he decided to concentrate on phytoplankton. He continued a programme of regular sampling on Windermere and several smaller lakes nearby, with attention to the changing phytoplankton and environmental conditions. He made wider collections and taxonomic study of other algae, with one broad investigation of Malham Tarn in the Pennines that showed his flair as a naturalist (11). Pioneer work with algal cultures had already been stimulated at Windermere (Storey 1944) by a Chinese visitor, S. P. Chu, well known to Lund personally. Lund spent much effort in developing their application to ecological problems, in which a modification of Chu no. 10 medium (Chu 1942) was much used. After the FBA moved from Wray Castle to the more capacious Ferry House, he came to preside over a large laboratory in which inverted microscopes, a multiplicity of iodized count tubes and cultures (figure 3) were richly represented. His work included a form of biological assay, by repeated use of nutrient-replete...
cultures suspended in lake waters with growth increment controlled by physical factors (4, 12). Thus both field exposures and laboratory experimentation were involved. Growth was typically measured as ‘cell divisions’ (doublings) to better accommodate its exponential nature. For the same reason he generally used logarithmic scales for graphs of change in natural populations (after Pearsall), which was then unusual but was thereafter widely adopted by others in Britain.

He gave especial attention to the ecology of diatoms, and after a few years at Windermere now-classic papers were published on the contrasting seasonal cycles of *Asterionella formosa* and *Melosira italica* var. *subarctica* (later *Aulacoseira subarctica*) (4, 5, 7). Others in the FBA had appreciated the practical prominence and theoretical potential of the spring *Asterionella* maximum (Mortimer 1939; Storey 1942, 1944), and two—F. J. M. Mackereth and C. H. Mortimer (FRS 1958)—later cooperated with Lund in an exceptionally detailed investigation of its spatial distribution and associated chemical characteristics in Windermere North Basin during 1947 (14). This work, combining hydrodynamics, chemical distributions (extended by Mackereth (1953)) and population ecology, was a landmark of freshwater science in Britain.

The *Asterionella* work made use of long-term records by others in the 1930s and 1940s (see, for example, Storey 1944). As more years passed, Lund added other long-term studies, notably from his work on small centric diatoms (15), the neglected flagellate *Rhodomonas minuta* (later *Plagioselmis nanoplanktica*), very small ‘µ-algae’ (16) and desmids (17). Methods of study were improving, and with a colleague he published a review that incorporated local and worldwide work in limnology (8).

Soon after his arrival at Windermere he entered a new field. Hilda Canter (figure 4) took up work at the FBA, through the aegis of her professor, C. T. Ingold of Birkbeck College, London, to study the parasitism of algae by chytrid fungi. It often involved epidemics that could greatly reduce algal populations. She eventually became the leading authority on the
subject, in work that continued for more than 40 years. She collaborated with John Lund in this then novel field. She became his wife in October 1948.

After 1950 Lund became interested in the potential application of plastic enclosures to contain large delimited samples (mesocosms) of natural phytoplankton communities that were amenable to experimental modifications. There were related interests in the FBA about 1960: the use of samples in plastic bags, which Lund used at first in the lake Buttermere, or surface-open lake partitions in the small lake Blelham Tarn that could be subjected to chemical modification or vertical hydraulic mixing by ‘bubble-guns’ (project ‘Swizzlestick’). Lund championed the use of large circular plastic (butyl rubber) enclosures that unlike small bags could maintain phytoplankton communities of natural composition. Eventually ‘Lund tubes’ holding about 18000 m³ were developed, situated in Blelham Tarn, and continued in use until 1984 (figure 5). This involved much extra manpower and also local permission. Lund himself was actively engaged in the earlier stages (19), but later—approaching his retirement—the work was largely continued with a team of ecologists led by his ex-student C. S. Reynolds (Reynolds et al. 1982) and allowed some most profitable experimentation (22).

Throughout his career Lund was greatly helped by assistant staff, including research workers and secretaries. Secretarial assistance made feasible his wide range of activities. These included service with some chairmanships in national and international projects outside the FBA, such as those of the International Biological Programme on Loch Leven and the African Lake George, work on the productive lowland meres (Reynolds 1980) and advice to the water industry. Participation in affairs of the Royal Society—of which he was elected a Fellow in 1963—involved many overnight train journeys to London. He enjoyed exceptionally good relations with three successive helpers, Margaret Thompson, Gina Devlin and Elaine Monaghan. He gave much support to his ex-students, notably...
F. E. Round, J. F. Talling (FRS 1968), Barbara Douglas, C. S. Reynolds and A. E. Bailey-Watts, who extended his work into related fields. Two—Talling and Reynolds—became colleagues at Windermere; other research colleagues there with primarily algal interests were Brenda M. Knudson, J. H. Belcher, Erica M. F. Swale, Elizabeth Y. Haworth, Kathleen Atkinson and S. I. Heaney.

ACTIVE RETIREMENT, 1977–2015

A long retirement, initially very active, began after his 65th birthday. The occasion led to the presentation of a Festschrift volume of contributions from former colleagues and friends, published by his first student, F. E. Round (Round 1988). For some years he continued to supervise the Fritsch Collection of Algal Illustrations, work that was later taken over by his colleague Elizabeth Haworth. He cooperated with others in the publication of original work, such as that with S. I. Heaney on the dinoflagellate Ceratium (24) and with the Czech J. Komárek on the blue-green Spirulina platensis. He published some thoughtful bibliographic essays such as those on Fritsch (27) and, with Elaine Monaghan, on Penelope Jenkin (28), a pioneer worker at the FBA, and provided a video tribute for the valedictory celebration for S. P. Chu in Qingdao, China. In his eighties he completed the text of a book designed to present his wife Hilda’s unrivalled assembly of photomicrographs of freshwater algae (26), giving much general information on these algae. It won an American (Gerald W. Prescott) award.

He had already made efforts to improve his knowledge of the Russian language, with both scientific and social applications. For this an elderly Russian emigrée living at Ambleside, Mrs Thompson, was most helpful. He also participated in a ‘Russian circle’ of other learners at Windermere. During retirement he devoted much time to learning Russian and had a long
correspondence with families of colleagues in Russia. Up until his 101st birthday he was still taking lessons in Russian, and he maintained his interest in the modern usage of the language. Lund's ability also helped some aspects of Russo-British cooperation, as on issues of eutrophication of enriched inland waters. He travelled widely in Russia on several occasions.

The death of Hilda after a distressing illness, and his deteriorating eyesight, marred the final decades of his life. Adaptations for limited sight, and secretarial and other help, were available, but although complete blindness eventually followed he was able to celebrate his 100th birthday with family and friends at Ambleside.

**FAMILY AND HOME LIFE**

John Lund's earlier years as a staff member of the FBA involved residence in Wray Castle. After marriage to Hilda he acquired an old capacious house set above the neighbouring village of Ambleside. Its agreeable surroundings included an exceptionally large garden. Both he and Hilda were enthusiastic gardeners, and the remoter regions were initially partly cleared with a machete. A traversing stream was also tended and yielded a pond, with plant life that included an algal stonewort. Hilda was especially assiduous in tending colourful plants, in consequence of which holidays elsewhere tended to be limited. John took a partly professional interest in several distinctive garden inhabitants, notably a large *Gunnera* species that harboured blue-green algae of a symbiotic association in stem-nodules. Other plants were reared indoors, including a species of the green alga *Cladophora* that formed discrete unattached 'lake balls' at the upland Malham Tarn, of which he was very proud. Hilda had a deep-seated attachment to colourful plant illustrations, which appeared as cut-outs on a screen and later as her own photographic products in a book. Each had a study for writing and occasional microscopy, for which Hilda acquired an advanced microscope by means of a grant from the Royal Society.

The family was enlarged in the 1950s by two children, Richard and Hilary. Their upbringing reduced the time that their mother could give to science, but later she returned to work at home and the FBA. John took pains to check their subsequent local schooling. Later Richard left university education and entered the Civil Service. Hilary first took up work (like John) in forensic science, but later moved to study marine chemistry and a lectureship in marine biochemistry at Bangor University. Both later married, and made frequent visits to their parents at Ambleside. There was also a grandchild, Sarah, who spent a week of her summer holidays each year visiting 'Grampy' at Ambleside.

**SCIENCE: WIDTH AND PENETRATION**

Lund's wider influence in his field, nationally and internationally, is incontestable. It was based on an interest in specifics rather than generalities. Algal diversity always impressed him, and averages could be misleading. Analyses at the species level were preferred. Aggregate measures such as chlorophyll *a* were at first avoided, except for dry weight summed from estimates on individual species (20). He sought to isolate the action of individual factors (16), but in an early joint work at Windermere (6) also explored factor interaction. He made possibly the widest integration of his science under the heading of
eutrophication (for example (18)). He wrote several major reviews (for example (16)) and contemplated several books, including a monograph on Asterionella; finally a single book was produced jointly with his wife (26).

Some personal scientific features seem improbables. He was interested and skilled in taxonomy and systematics, as shown in his numerous publications under the title ‘Contributions to our knowledge of British algae’ and in some surveys of algal groups such as the Chrysophyceae (13). However, he tended to despise mere species lists, except in exploratory records such as for some Irish waters. Though poorly schooled in physics and chemistry, he saw their application to ecological issues as crucial, with support from plant physiology in the tradition of Pearsall. He greatly expanded the ecological application of experimental cultures of ecologically important species. Although a committed and versatile field naturalist, he avoided regional descriptions—with the exception of favourite sites, a Cheshire mere (1) and Malham Tarn (11). He made much use of chemical budgets for assessing possible nutrient limitation, but did not enter rate considerations of chemical kinetics. An early discounting of limitation of Asterionella by a deficiency of carbon dioxide due to the large atmospheric reservoir neglected limitations that were later investigated in detail at Windermere (Talling 1976; Maberly 1996). He did not seriously explore animal grazing on phytoplankton except at the microbial (protozoan) level, and relationships with associated zoologists were few (see, for example, (25)). One was with the eminent visitor W. T. Edmondson (Edmondson 1965). Lund defended and made use of an exceptionally long series of routine (repetitive) sampling (see, for example, (21, 23, 25)) that was unrivalled in the world.

His absence from some fields actually stimulated their exploration by several of his students and other associates. Thus partly philosophical issues involving other subjects (such as community succession and primary production) were taken up by ex-students C. S. Reynolds (see, for example, Reynolds 1997) and J. F. Talling (Talling 1993). Physical and physiological topics of algal flotation and sinking were explored in depth by A. E. Walsby (FRS 1993) (see, for example, Walsby 1988), with acknowledged guidance from an early paper by Lund (10) on these matters. Many major later advances in studies of micro-algae were made possible only by new techniques of electron microscopy and genetic analysis that remained outside his personal expertise. He did introduce some new methods into phytoplankton sampling and study, and removed much regional neglect of some older ones (9).

**PERSONAL QUALITIES**

He immediately impressed by his quick-wittedness and his ability to see humour in a situation. Tolerance of other viewpoints increased somewhat with age, but this did not extend to half-truths and euphemisms. As a senior scientist he made privileged use of many of the institute’s facilities. In his youth he openly contested national imperialism and jingoism. He had some distaste of abstractions, preferred concrete reasoning, and respected practicalities including the financial.

He evoked loyalty and friendship in his many assistants. These extended to other colleagues with similar professional interests, although naturally there could be competition within the institute. Influential phases of shared interests existed early with several senior colleagues, with whom there was active cooperation, but later their interests tended to diverge.
In conversation he was generally entertaining. Included was a tea club in one laboratory, where he might criticize the FBA director, H. C. Gilson. Later opinion mellowed; ‘we were lucky to get him’.

He had a penetrating insight into many difficult human situations. Forensic work and police courts introduced the seamier side of much human behaviour. In old age he was approached by a group seeking to gather memories of former times and personalities in Ambleside, his home village. They were impressed by the clarity and range of his recollections.

AWARDS AND APPOINTMENTS

1934  BSc, University of Manchester
1935  MSc, University of Manchester
1939  PhD, University of London
1957  President, British Phycological Society
1961  DSc, University of London
1963  Fellow of the Royal Society
1967  President, International Phycological Society
       Vice-President, Freshwater Biological Association
1975  CBE

ACKNOWLEDGEMENTS

We are indebted for helpful records kindly supplied by Keith Moore of the Royal Society, by Elaine Monaghan, and by Ian Pettman, Elizabeth Haworth and Tamsin Vicary of the Freshwater Biological Association, who also supplied material used in the figures.

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REFERENCES TO OTHER AUTHORS


**Bibliography**

The following publications are those referred to directly in the text. A full bibliography is available as electronic supplementary material at http://dx.doi.org/10.1098/rsbm.2015.0025 or via http://rsbm.royalsocietypublishing.org.

Biographical Memoirs


