REVIEW ARTICLES

EXPERIMENTS WITH LAKE PHYTOPLANKTON IN LARGE ENCLOSURES

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The intrinsic characteristics of planktonic organisms (plankters) can be discovered by laboratory investigations. Examples are basic needs for growth and reproduction, the effects on growth rate of variations in the rate of supply of nutrients and the relation of total nutrient supply to yield. Generally, we are forced to study one organism at a time. In a few cases it may be possible to study two or more organisms in a defined medium or under defined conditions. However, any microcosm we set up in the laboratory in order to obtain essential basic data will be more or less remote – usually very remote – from the natural environment with its multitude of diverse species living in the same space, such as the plankters living in the open waters of lakes. Moreover we do not understand the natural environment fully and cannot follow all the changes occurring in space and time. This in no way implies a criticism of laboratory investigations, without which there is no hope of understanding natural events, but it does explain why ecologists may wish to carry out experiments with natural populations under conditions as natural as possible.

The present article is about the use of large plastic enclosures in one of our lakes as semi-natural basins for experiments, approximating to lakes within lakes. Most of the work has been with phytoplankton but these enclosures or 'tubes', as we call them, have been used for other investigations and are potentially usable for studies on virtually all kinds of communities or groups of organisms. One drawback of the size of these tubes is that the extra work involved in studying the enclosed water is equivalent to that of studying another lake. Apart from the consequent demand on manpower and resources, but arising from it, a second drawback is that it is impossible to have so many enclosures that experiments can be carried out with sufficient replication for statistical analysis. However, the belief that satisfactory experiments with phytoplankton could be carried out on small samples (e.g. 100 ml) of lake water proved to be fallacious, and so tests were made with larger and larger containers. While they were suitable for short-term experiments, they all proved too small for those relating to the longer periods of time involved in investigating the periodical phases of the plankton development typical of lakes. The relatively high ratio of surface area to enclosed volumes of lake water in these containers favoured attached or benthic algae more than the phytoplankton. This effect was more pronounced the longer the experiment lasted. Since the containers were not large enough to approach the desired situation of a lake within a lake, the decision was made to use very much larger enclosures holding over 18 000 m^3 of water. I do not believe that this

PLATE 3(a). Three Lund tubes in 'Grote Rug' reservoir near Dordrecht, Netherlands (Courtesy of Dr Jan G. Booij, National Institute for Water Supply). 3(b) Margin of a tube in Blelham Tarn.

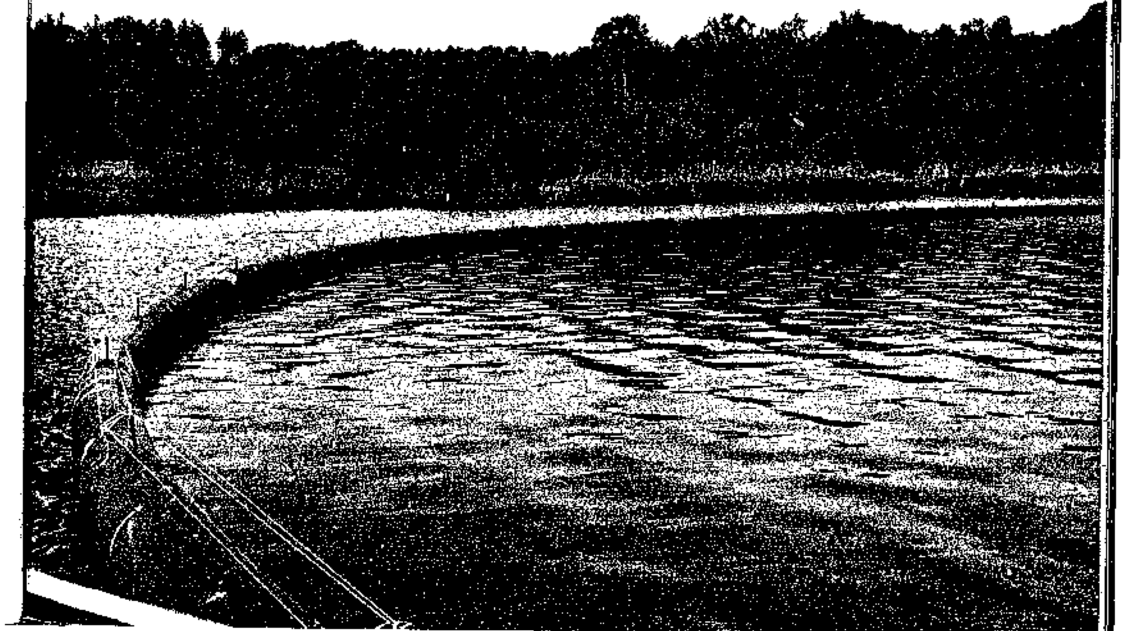
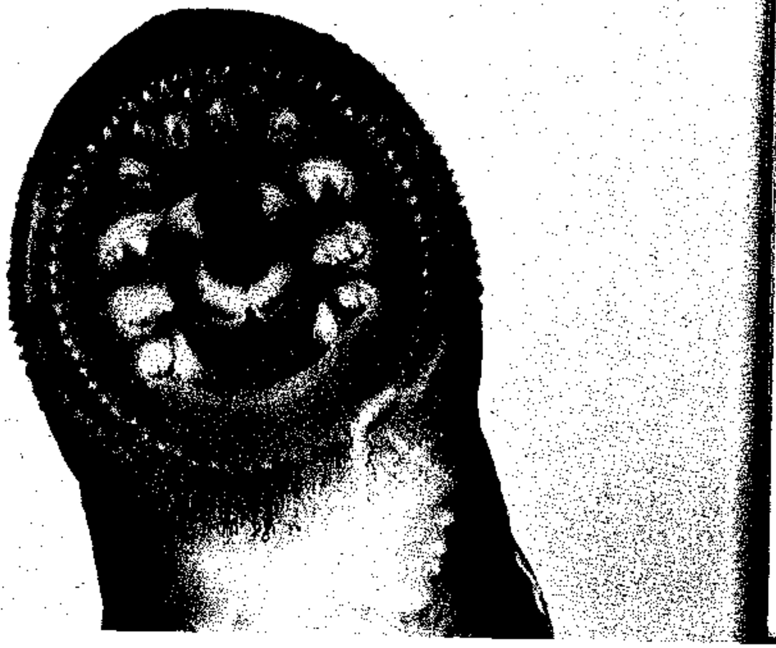


PLATE 4(a). The River Tees below Cow Green Dam.

PLATE 4(b). The suction disc and mouth parts of the river lamprey. Note the horny teeth around the mouth and on the tongue.

(Photograph by John Clegg).



is necessarily the ideal size for all purposes or places. That almost identical or similar enclosures can be of value elsewhere and for somewhat different purposes is shown by their use by the Water Research Centre in the Farmoor Reservoir 2 of the Thames Water Authority, in the Norfolk Broads (Nature Conservancy Council 1976) and in a reservoir in the Netherlands (Plate 3a). The tubes in the reservoir in the Netherlands, which have improved anchorages, have been successful despite its exposed situation (Booij & Vlugt, in press). There can be little doubt that modifications and special precautions are necessary in large waterbodies exposed to high winds. Moreover, a tube enclosed in a large piece of ice during a thaw would be in great danger with even a moderate wind blowing.

The construction and emplacement of the original models in Blelham Tarn are described by Lack & Lund (1974), the modifications for the two in Farmoor Reservoir 2 by the Water Research Centre (Anon. 1977a & b) and the three in the Dutch reservoir by Booij & Vlugt (in press). Basically the enclosures are tubes (Fig. 1) placed vertically in the waterbody. The top of the tube is inflatable and has compartments or, in the newer models, inflatable tubes within a covering. Our tubes in Blelham Tarn, English Lake District, have three such rings of inflatable compartments, one below the other and welded to the tubes themselves. Normally only the top ring is inflated. The bottom of the tube also has a hollow ring containing a heavy metal chain so that it sinks into the soft bottom deposits. That it has sunk into the mud is determined by a diver who treads round the edge of the bottom of the tube to ensure that it is as deep as or deeper than his legs can reach. The tubes are 15 m long but reach the bottom at about 11–12 m below the surface, their mean depth being a little over 11 m. The extra length of tubing allows for the rise and fall of the tube with changes in the

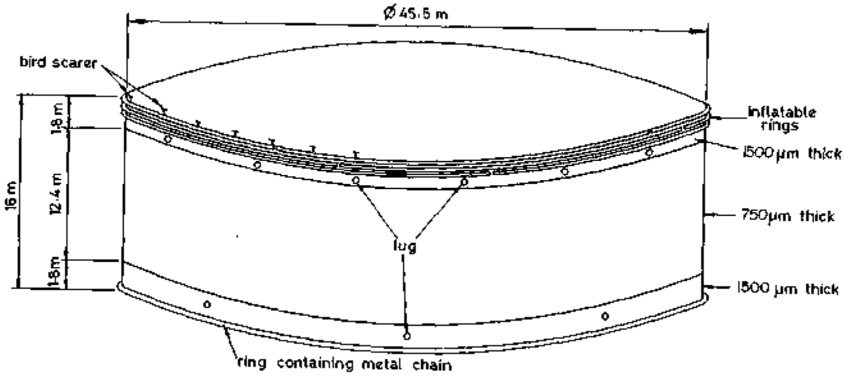


FIG. 1. Diagram of a Blelham Tarn tube.

lake level. The Farmoor tubes are fixed to the bottom of the reservoir (Anon. 1977a, b). All the tubes are constructed of butyl rubber (Esso Butylite).

Though these enclosures do behave like lakes within lakes (Lund 1972, 1975; Lack & Lund 1974), those in Blelham Tarn have a mean depth over four metres greater than that of the lake itself (6·8 m) and they are artificial in that they do not have any shallow water in them. A third tube now under construction will be placed in a more marginal area of the lake so as to enclose also a shallow, littoral region.

The tubes were installed in 1970 and the fact that they appear to be good for another 7 years attests to the durability of butyl rubber. Entry into them is made by rowing a keel-less boat up to the tube as fast as possible. The boat then slides up and over the inflation collar. Even in the regions of entry the original butylite is still in use.

A preliminary experiment, which had to last over a year in order to answer the questions posed, showed that a natural phytoplankton would be maintained for an apparently unlimited period and that thermal conditions, such as the degree of stratification, were very similar to those in the lake outside (Lack & Lund 1974, Figs 4–6). This experiment also showed that enclosure of lake water, and so prevention of renewal of nutrients by the inflows of the lake, caused the phytoplankton to change rapidly from that of a moderately eutrophic lake to a very oligotrophic one. Both quantity and quality of the phytoplankton altered (Lund 1975). This in turn suggested that eutrophication of the lake during the last 25 years had not (as has been recorded for some other lakes) so enriched the bottom deposits that an immediate improvement in water quality could not be effected by regulation of the sources of enrichment. Six years later, a similar experiment using the same tube did not cause such a marked diminution of the algal populations as in 1971, nor was the composition of the phytoplankton the same. These differences may be caused by the enrichment of the deposits in this tube as a result of the fertilizers added in experiments during the years 1972-1976. If so, a similar condition may arise in the lake itself if enrichment from farming and sewage (Lund 1971, 1978) continues, as indeed it may well do. It is also possible that this change, in part at least, was the result of the growth of algae derived from the previous year's phytoplankton. In that year fertilizers were added to the tube and both vegetative cells and spores of the plankters which then were abundant could have sedimented on to the bottom deposits and so formed an inoculum for the 1977 phytoplankton.

The fertilization experiments were carried out at all times of year. Laboratory bioassay was carried out during much of the period, using the technique of Lund et al. (1971) and the results for the lake water have been published (Lund et al. 1975). Before an experiment started, the tubes were opened by deflating some of the compartments of the inflation collar so that the tube water would equilibrate with that of the lake or, in summer, with the lake's epilimnion. Each experiment lasted several months, though it might include more than one fertilization. Only a few general descriptions or comments on some of the experiments carried out so far can be given here.

Apart from winter, when physical conditions control algal growth, a single addition of phosphate will produce an increase in the phytoplankton, suggesting that phosphorus is the major element limiting algal growth in Blelham Tarn. For diatoms, as expected, silicon has to be added at certain times. The anaerobic part of the hypolimnion is enriched with both elements but the amount of regenerated silicate is, in total, small compared to that added by the inflows to an equal volume of lake water. Phosphate returns in variable amount from the bottom deposits each autumn, even in the absence of fertilization, but decreases during winter. The phosphate concentration in the lake water will remain similar or increase during winter. It may be that much of the recycled phosphate in the tubes is attached to ferruginous particles, because the total iron concentration also falls during winter.

Laboratory bioassay using *Asterionella* showed that for four years it was necessary to add only sodium silicate, potassium dihydrogen phosphate and the ferric complex of ethylenediaminetetraacetic acid (EDTA), separately or combined, in order to promote good growth of the diatom at times when it would not grow in unenriched lake water. Experiments in the tubes support the view that silicon and phosphorus are two of the major limiting factors for the growth of this and other diatoms. Experiments with adding iron to the tubes as the ferric complex of EDTA have given somewhat contradictory results.

The algae which have become abundant when tubes were fertilized have included most of the major plankters of the tarn. However, a few of the important plankters in the lake have never grown well in the tubes, the most notable examples being the flagellates *Ceratium hirundinella* O.F.M. and *Mallomonas caudata* Iwanoff. It can be very striking to have three different but abundant plankton populations in the lake and the two tubes at the same time, for example diatoms, green algae and blue-green algae.

Clearly, in an experiment lasting several months, the effect of fertilization will differ qualitatively, if not quantitatively, according to the season, the meteorological conditions and the effects of grazing and parasitism. A feature of our climate is its wetness, notably in autumn and winter when, moreover, there is more inflow from a given amount of precipitation because of the lower rate of evapotranspiration. One effect of a drier winter is suggested by analysis of the data on the start of the spring diatom bloom during the last 33 years (Lund 1978). This effect can be carried in a tube to the extreme condition of the waterbody receiving only direct precipitation. When a tube was fertilized in autumn with phosphate, silicate and the ferric complex of EDTA, the normal 'vernal' diatom maximum was reached in February when the vernal increase in the lake outside was only just beginning (Fig. 2). This result shows how the winter minimum of phytoplankton is determined by outflow as well as by light. Another change from the lake's spring bloom was produced by adding silicate, phosphate in late summer and further phosphate in autumn.

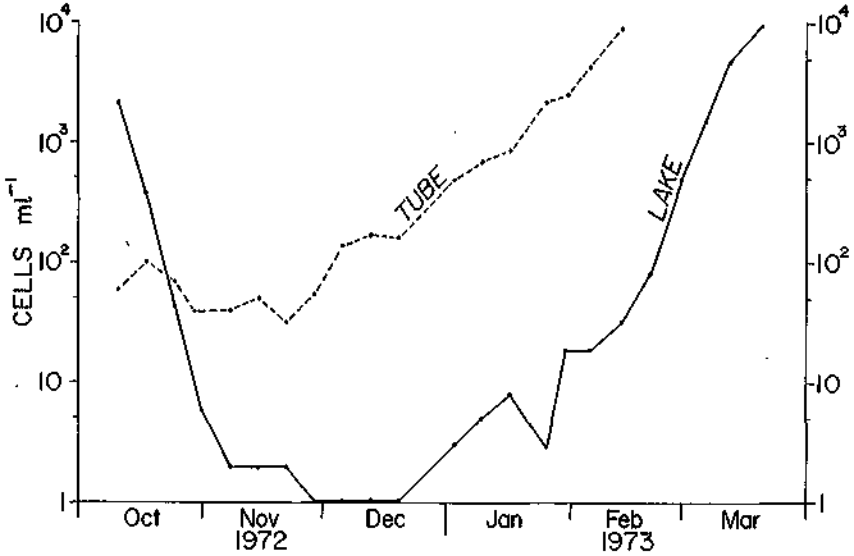


FIG. 2. Planktonic diatom populations in a tube fertilized in September 1972 with silicate, phosphate and the ferric complex of EDTA compared with that in the lake water outside. Vertical axis: cells per ml, logarithmic scale.

Adding silicate alone in August had no effect but when phosphate was added in early September, a diatom bloom arose, together with one of blue-green algae (Fig. 3). The further autumnal addition of phosphate had little effect because of fungal parasitism, grazing and short winter days. However, in the succeeding spring a very large population of the blue-green alga *Oscillatoria agardhii* Gom. var. *isothrix* Skuja arose to form the spring maximum. This waterbloom in the tube could be seen from far away as a greenish disc on the surface of the water. Further details of these experiments are given by Lund (1978).

The single addition of a nutrient at a given moment is not a natural event. In nature, nutrients are entering the water at all times to a greater or lesser extent and being regenerated within the waterbody. In 1975, from spring to early winter, nitrogen as nitrate plus ammonium nitrogen, phosphorus as phosphate and silicon as sodium silicate, were added to one tube in amounts corresponding to those brought into the lake each week by its inflows, as judged from weekly analyses. The same additions were made to the other tube plus an extra addition of phosphate, that is it received twice as much phosphorus. Neither tube produced larger crops, expressed on a chlorophyll *a* basis, than the lake, after due allowance had been made for losses of lake plankton by outflow. However, this would not be equally true if, for example, carbon was used as a measure of phytoplankton abundance since the carbon to chlorophyll *a* ratio is not the same in all algae (e.g. for blue-green or green algae). The populations in the tubes also showed marked qualitative differences from those in the lake. The tube receiving double the amount of phosphorus was also fertilized once in early September with the ferric complex of EDTA, after which, until late October, it had a population producing waterblooms and dominated by *Microcystis*. It is interesting to note that Dr C. S. Reynolds carried out an experiment in 1977 based on weekly additions of nitrogen, phosphorus and silicon. These fertilizations were designed not just to simulate the weekly supplies of nutrients to the lake but to replenish the nutrient contents in a tube, when necessary, so that their concentrations reached certain levels. The results of his experiment show considerable quantitative and qualitative differences from those of 1975. In both the 1975 and 1977

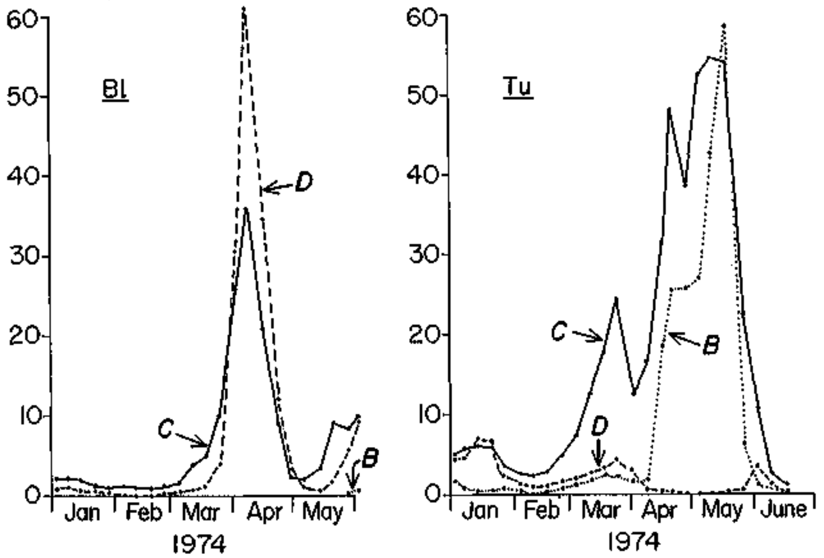


FIG. 3. Phytoplankton of Blelham Tarn (Bl) and of a tube (Tu) in the first half of 1974. The tube fertilized with silicate and phosphate, August, September and November 1973. Vertical axis: Chlorophyll a μg l^{-1}, without allowance for phaeophytin; blue-green algae, filaments, mm (100 μl)$^{-1}$ and diatoms, cells (5 μl)$^{-1}$ in the 0–5 m water column. B, blue-green algae; C, chlorophyll *a*; D, diatoms.

treatments natural planktonic successions took place. Both experiments in which additions of fertilizers are made at short intervals (e.g. weekly) and those in which a single addition of one or more fertilizers is made are valuable. Each experimental system has its advantages and disadvantages.

Apart from experiments done and observations made by other FBA groups (Jones, 1973, 1975, 1976; Smyly 1976; Willoughby 1974), we have cooperated in two major investigations which have been carried out by the Scottish Marine Biological Association and the Department of Biological Sciences of Dundee University on the kinetics of nutrient depletion of a natural phytoplankton and on the uptake and transformations of nitrate nitrogen (using ^{15}N as a tracer) respectively. The latter study in particular illustrates the advantage of working with a hydrologically closed system in which the fate of planktonic production and transformations of matter can be followed. Such a system is specially useful also for studies on the sedimentation of live or dead algae, their incorporation into the bottom deposits and possible resuspension therefrom.

The experiments described above are only a few of those that have been carried out and the detailed quantitative significance of many of them have yet to be fully analysed and interpreted.

Though the value of such tubes is clear, in our work, as is almost invariably the case, a new approach to studying a problem, in this case the ecology of the phytoplankton, has uncovered others or exposed deficiencies in the work up to now. An example has been mentioned, namely the importance of studying the physical, chemical and biological interrelationships between shallow and deep water regions. The present location of both tubes in deep water makes the tube 'lakes' too different from Blelham Tarn as a whole. The results of the work of Dr Reynolds's team with an additional tube enclosing both shallow and relatively deep water will be of great interest.

Many members of our Windermere laboratory have taken part in the development and use of the tubes. The National Trust kindly permitted us to put them in its lake. Atlantic Rubber Ltd., Altrincham, Cheshire constructed these and the other tubes mentioned in this article. We are grateful to the Department of the Environment for financial support.

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