

THE ECOLOGY OF PHYTOPLANKTON IN SHROPSHIRE AND CHESHIRE MERES

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This review summarizes the findings of five years' research (June 1970-June 1975) on the meres of the Shropshire-Cheshire Plain which was based at the Association's West Midlands Unit at Preston Montford, Shrewsbury. The long-standing proposal to establish a small group of scientists, working on various aspects of the biology of these productive lakes (see *Annual Report* 39), has still to be fulfilled; as yet, only the phytoplankton has been examined in any detail. Nevertheless, several members of the Association's staff have worked on material from the meres in the course of their projects, and their findings have contributed to our collective experience of enriched lowland lakes. At the same time, our ability to provide authoritative comment and advice in specific cases involving lake management and 'eutrophication' has been improved.

There are about seventy meres exceeding 2 hectares in area in the north-west Midlands (Fig. 1), the largest covering 60 hectares; most are less than 20 m in depth, and thus can be described as small, shallow lakes. All are situated in depressions in the thick mantle of glacial drift which was deposited in the region during the late Devensian period (some 14-16 000 years ago), and many basins are associated with terminal moraine formations. Some Cheshire meres, however, have been formed at a subsequent stage in the postglacial period, owing to subsidence in the underlying Triassic salt-bearing strata.

The present-day meres are supplied principally by ground water, whose chemical composition is influenced by the drift through which it is percolating. With few exceptions, mere waters are hard, with a dominance of divalent cations (Ca^{2+} , Mg^{2+}) balanced by an abundance of bicarbonate ions. Rainfall is uniformly low ($700-850 \text{ mm a}^{-1}$), and topographic catchment areas are rarely extensive; these factors combine to give characteristically long retention times (between one and six years where values have been calculated). However, slow percolation is compensated by chemical richness. Soluble phosphorus content is typically very high in the meres (up to 1.5 mg l^{-1}) and nitrate concentrations are moderately so (up to 4 mg l^{-1}), but there is evidence that the latter have been increasing significantly during the last two or three decades. Many meres are known to stratify in summer and, characteristically, their hypolimnia become severely depleted of oxygen. These meres may thus be described as 'eutrophic' in both the classical and modern senses of the word.

To some extent, ignorance of the fundamental characteristics of water and nutrient supply has restricted the evaluation of how chemical factors regulate algal production. Indirect evidence has been assembled from routine observations on lake temperatures, silicon analyses, water level

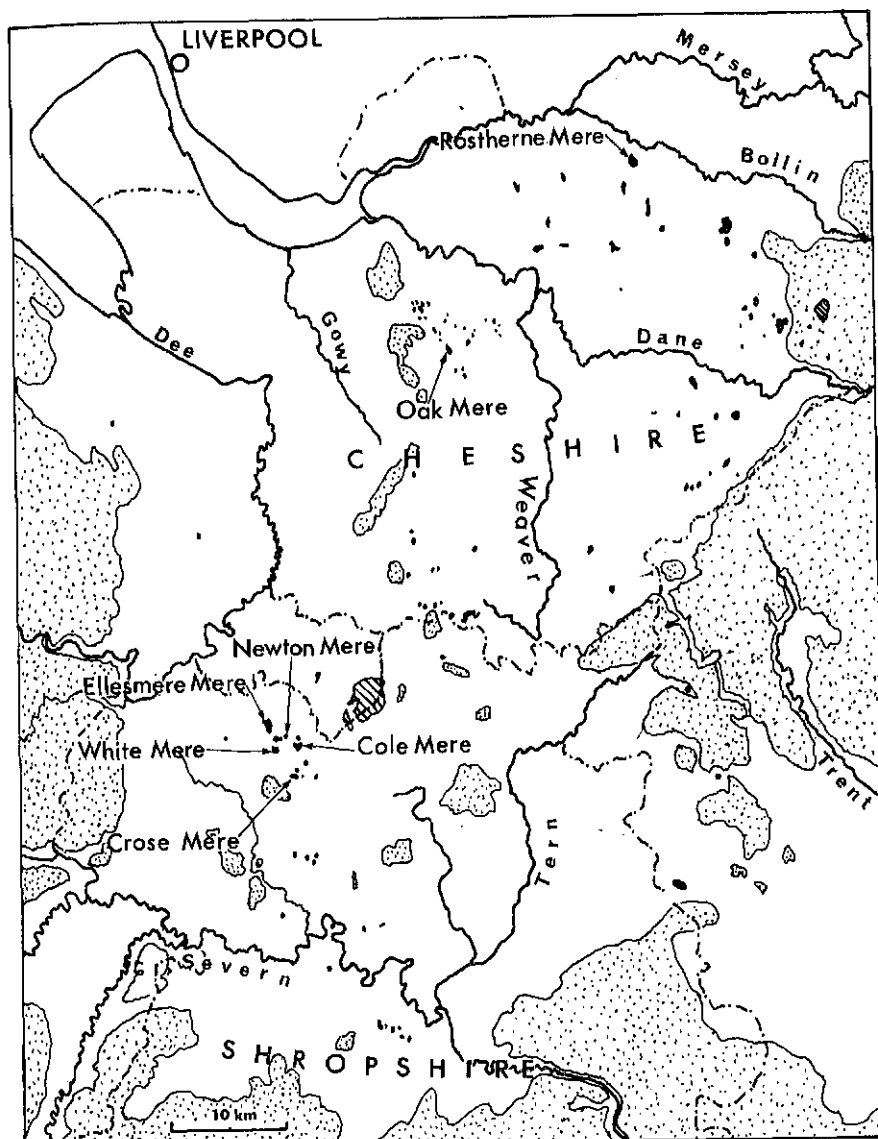


FIG. 1. The Shropshire-Cheshire Plain showing the clustered distribution of the meres and related peat-filled hollows (the mosses: larger sites shown by hatching). Higher ground (approximately >125 m above O.D.) shown by stippling.

and discharge which suggests an annual rate of ground water influx into Crose Mere not dissimilar to a theoretical figure derived for the topographic catchment (Reynolds 1975). If augmentation of the dissolved phosphorus and nitrogen concentrations in the lake is attributed solely to the influx of ground water (thus ignoring the contribution from sediment re-solution), the following loading rates may be approximated for the mere: $0.5-1.3 \text{ g P m}^{-2} \text{ a}^{-1}$; $6.2-8.5 \text{ g N m}^{-2} \text{ a}^{-1}$.

In the context of lake eutrophication, these loading rates might be classed as 'dangerously high'. Yet much of the nutrient income of the meres must be due to a natural process of leaching in the permeable drift, rather than to artificial enrichment. Moreover, it appears that the meres support healthy, balanced ecosystems which are highly productive at all trophic levels. Admittedly, the communities present are those of 'eutrophic' biotopes, characterized by large populations of relatively few species.

This is certainly true of the phytoplankton, where only a dozen or so species ever comprise over 50% of the plankton biomass. Large and relatively pure populations of algae lend themselves well to ecological study: increases in population are readily detectable from cell counts while significant changes in vertical or horizontal distribution are conveniently identified. At the same time, buffering by bicarbonate reduces the likelihood of either direct carbon limitation of photosynthesis or wide fluctuations in pH; moreover, the advantages of contending with a low throughput of water, which simultaneously ensures that the rate of nutrient replenishment is predictable and that outwash losses are negligible, will be immediately apparent to those who have attempted to 'model' the dynamics of phytoplankton growth and nutrition. The mere system provides great scope for general ecological research which so far, has been barely exploited.

Periodicity of the phytoplankton

The wax and wane of successive algal populations, whose study has formed the basis of the Meres Project, have been followed mainly in Crose Mere, Shropshire. Here, the diatoms *Asterionella*, *Fragilaria* and *Stephanodiscus* are typically dominant in February and March, green algae (especially *Eudorina*) in April and May, blue-green algae *Anabaena*, *Aphanizomenon* and *Microcystis* in early summer, and the dinoflagellate *Ceratium* in late summer. Diatoms (*Melosira*, *Fragilaria*) often produce large or even dominant populations during the summer. Cryptomonads nearly always form a significant portion of the standing crop, though they are rarely dominant. This pattern of seasonal succession (represented in Fig. 2) is broadly similar from year to year, and has been suggested to be representative of a 'regional type' (Reynolds 1973a). It is also similar to that described for many of the world's mildly eutrophic temperate lakes, though it is worth emphasizing the points of difference which include the early commencement of the spring diatom maximum,

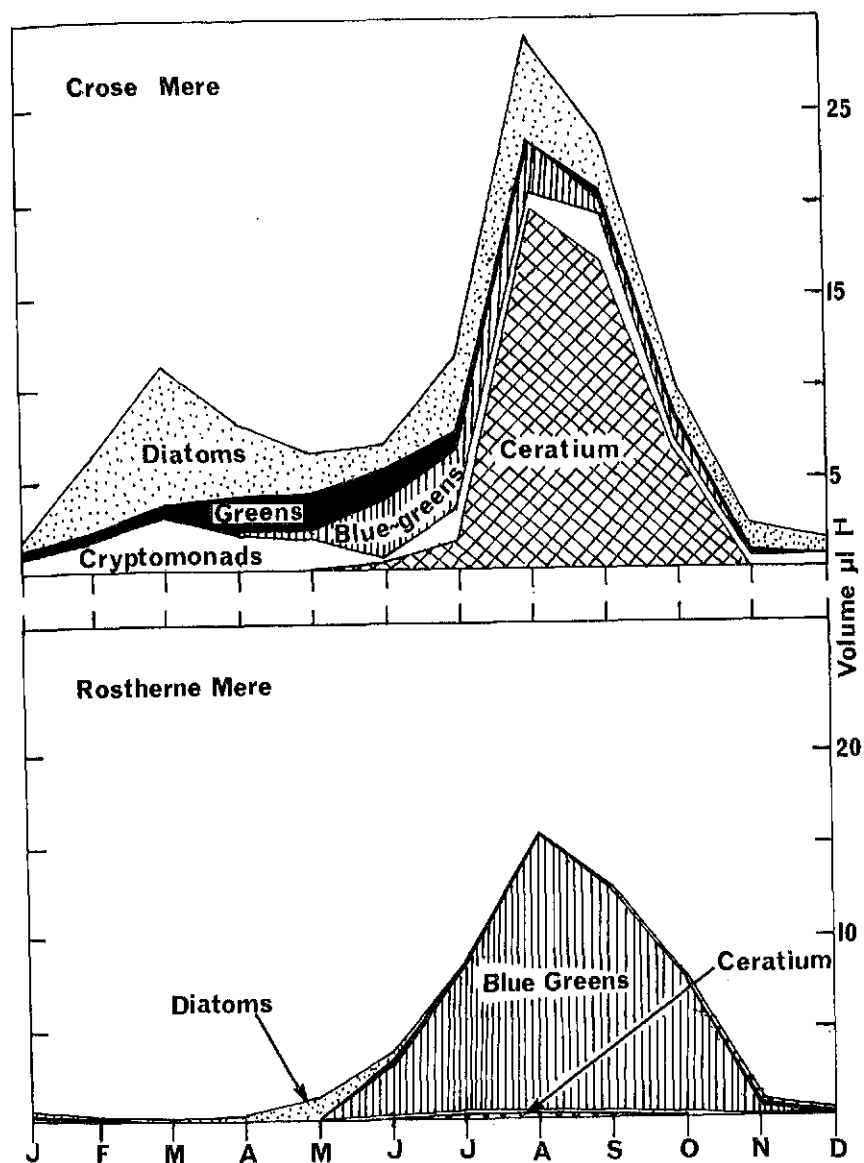


FIG. 2. Mean monthly cell volumes of the major components of the phytoplankton of two meres. Based on 0-5 m (Crose Mere 1966-1971) and 0-4.5 m (Rostherne Mere 1972-1973) tube samples.

the relatively poor growth of chrysophycean algae and the irregular phases of rapid diatom growth which occur in summer.

Some attempt has been made to identify the critical factors that determine the seasonal periodicity in Crose Mere. The annual recurrence of specific maxima has provided some clues. Thus, the abrupt onset of spring diatom growth, which commences almost within the same calendar week each year, has been related primarily to the interaction of day length, and relative penetration of light into the well-mixed water; it is hardly influenced by water temperature, rainfall or nutrient concentration. Similarly, light is usually the factor that controls the eventual population maximum, which is equivalent to a content of 170–220 mg chlorophyll *a* per m³ of the illuminated (euphotic) layer (Reynolds, unpublished). Diatom dominance is subject to modification by parasitic attack and possibly by extended periods of ice cover. It is the rarity of continuous frosts coupled with the overall shallowness of the mere which probably contribute to the early onset of diatom growth.

Diatoms continue to be abundant until the lake stratifies; thereafter populations may be more or less rapidly reduced. This seems to be partly due to sedimentation as average turbulence declines. The green algae, blue-green algae and *Ceratium*, whose maxima occur during the summer stagnation, all have some means of remaining in suspension. Water temperature, day-length and selective influences of grazing, parasitism and growth-inhibiting substances are often cited as causal factors in the summer succession of phytoplankton. However, it has been observed repeatedly in Crose Mere (e.g. Reynolds 1972, 1973b) that although nutrients rarely, if ever, limit spring growth, uptake in the newly formed epilimnion considerably exceeds renewal and often results in early exhaustion (of nitrogen especially). Further, these changes are accompanied by shifts in algal dominance: the maximum of green algae continues only so long as inorganic nutrients remain plentiful in the epilimnion. Dominant populations of blue-green algae apparently tolerate lower epilimnetic concentrations of phosphorus and nitrogen, but *Ceratium* populations have developed to light-limited densities even when concentrations of inorganic nitrogen have been undetectable in the epilimnion. It is also apparent that the populations of species dominant in the early part of the year have significantly faster rates of growth than those which follow later in the season. The only exception is provided by the diatoms *Fragilaria* and *Melosira* which, at temperatures of 16–18°C, are able to double their numbers faster than any of their major competitors. These observations, made over a number of years, suggest that the succession progresses from those species capable of rapid growth to slower-growing species which are perhaps more tolerant of conditions of nutrient stress. However, it has been calculated that the minimal nitrogen requirement of the largest *Ceratium* populations (up to 1000 individuals ml⁻¹) is equivalent to about 700 µg N l⁻¹. How they continue to grow in spite of persistently undetectable epilimnetic nitrate

and ammonia levels is a fundamental problem still requiring a considerable research effort.

The periodicity of the phytoplankton in several more or less similar meres has been followed in less detail. Cycles in Cole Mere and White Mere (Shropshire) are similar to that in Crose Mere. Certain other less rich meres (e.g. Newton Mere) tend to have fewer 'eutrophic' species, while some richer Cheshire meres (e.g. Great Budworth Mere) have relatively larger crops of green algae. Oak Mere continues to support a plankton which is unlike that of any other mere (see Swale 1968). Two deeper meres (Ellesmere Mere, Rostherne Mere), in which epilimnetic concentrations of nitrogen and phosphorus do not become exhausted, support dominant *Microcystis* populations throughout the summer (Fig. 2). Recent work on Rostherne Mere (Reynolds & Rogers 1976) confirms the earlier observation of Belcher & Storey (1968) that blue-green algae have increased during this century; populations now appear to be light-limited.

Buoyancy of phytoplankton

For most non-motile algae, maintenance of their position in the plankton is dependent upon vigorous vertical mixing of the water, and a relatively slow rate of sedimentation. Motile algae are also affected by turbulent water movements but, potentially, they can swim to particular depths when turbulence subsides. Vertical movements of algal populations in Crose Mere have been detected when, as often occurs in summer, stable, 'microstratified' conditions rapidly become established in calm periods (Reynolds 1971, 1972). Predictably, diatoms have been found to sink at such times, and they do so at rates comparable with those observed in laboratory vessels ($0.2-1.0 \text{ m d}^{-1}$) (data in press). Routine measurements show that sinking rate is related not only to specific gravity and colony or cell size, but also to the physiological condition of the alga: dead, resting or simply non-growing cells sink at up to four times the rate of growing cells. The reasons for this effect, which has been observed by other workers, are still unresolved and are now being sought.

Flagellates, and especially *Ceratium*, often take up station in the depth range 0.5-2.0 m, though they may disperse into deeper water at night. Even small cryptomonads have been observed to accumulate in the lower epilimnion (in summer) or near the lake surface (in winter). But it is the blue-green algae which produce the most striking migrations when, in quiet weather during early summer and autumn, they form surface scums or 'blooms'. Indeed these are sufficiently spectacular to have acquired a local descriptive term, 'the breaking of the meres'. This term has been in use for well over a century, which shows that blue-green algal blooms are no new phenomenon to the meres.

Blue-green algae have no means of swimming, but many planktonic genera possess gas vacuoles in their cells which lower the specific gravity of the alga. Thus blooms occur when the algae are sufficiently buoyant to

overcome turbulence, as may happen under still conditions. Although gas vacuoles are almost always present in the vegetative cells of bloom-forming species common in the meres (*Anabaena*, *Aphanizomenon* and *Microcystis* spp.), it has been shown that their relative abundance, and hence the buoyancy which they impart, are conspicuously variable. At times cells may be negatively buoyant, i.e. the alga sinks (Reynolds 1972, 1973b); the popular assumption that blue-green algae are always buoyant is incorrect. Indeed, by controlling their gas vacuole content, blue-green algae can regulate their buoyancy and, potentially, are independent of turbulence for suspension in the plankton.

The mechanism by which buoyancy is adjusted was proposed and later substantiated by Dr A. Walsby and his co-workers (for a full review of gas vacuole structure and function see Walsby (1972)). Gas vacuoles are built up of regular, cylindrical sub-units (gas vesicles) which have self-erecting proteinaceous walls. Walsby showed that the enclosed spaces fill with gas in equilibrium with that in external solution. As gas vesicles are assembled, so the cell becomes increasingly buoyant. In healthy, growing cells the assembly of new gas vesicles may not keep pace with cell division. In addition, turgor pressure can rise as a result of an increase in osmotically active sugars produced by photosynthesis, and the rise may be sufficient to collapse the weaker gas vesicles present. The algae lose buoyancy and sink. In deeper, darker water, growth rate and turgor pressure fall, enabling the alga to increase its gas-vacuole content and to recover its buoyancy. The involvement of photosynthesis ensures a relatively rapid adjustment of buoyancy and the means to maintain station at a favourable position in the light gradient.

By applying some of Dr. Walsby's methods to the natural populations of blue-green algae occurring in the meres, it has been shown that, during growth, buoyancy and turgor pressure are roughly in inverse relation, and the algae remain approximately neutrally buoyant (Reynolds 1972, 1973b). Under stable conditions, the algae themselves stratify, or attempt to do so, in the lower part of the euphotic zone (Reynolds 1973b, and data in press). Efficient buoyancy regulation thus enables the algae to remain in suspension, to accommodate sudden changes in wind-mixing and, at times, to descend to the bottom of the illuminated zone where nutrient concentration may be higher. Loss of buoyancy in the autumn causes *Microcystis* to migrate to the sediments of Rostherne Mere, where it is found in winter (Reynolds & Rogers, 1976).

Why, then, do these algae come to the surface at all? In fact, the meres rarely 'break' during the period when blue-green algae are increasing. When they have done so, blooms have formed after abrupt ending of windy weather. It seems that the algae respond to poor average light conditions during mixing into dark water by becoming more buoyant. As the turbulence subsides, the algae float upwards and some may reach the surface before they can develop the turgor necessary to reverse their buoyancy. If it becomes calm overnight (as is often the case), there is no

way in which the algae can prevent their passage to the surface. Most blooms occur, however, after the population maximum, when the algae have lost their physiological vigour and again, perhaps as a result of nutrient exhaustion or carbon limitation, they are unable to regulate their buoyancy.

It is probably the scums and strand lines of moribund, putrefying algae which are the most offensive aspect of blue-green algal growth in lakes, and thus, the cause of widespread concern. This is in spite of the fact that even quite modest populations can produce surface blooms which give grossly exaggerated impressions of algal abundance (Reynolds 1971). Nevertheless, if the growth of blue-green algae is to be prevented, it is essential that the significance of buoyancy regulation is properly assessed in relation to the physical and chemical environment. These essentially simple observations on the behaviour of populations in the meres may be viewed as a step towards such an assessment and as a basis for future experiments.

One conclusion to be drawn from the heterogeneous vertical distribution of algae in shallow lakes is that buoyancy (or the lack of it) and its interrelationship with water movements may greatly influence, if not account for, the seasonal succession. Further evidence has come from observations on vertical distribution in the mere, and the results of

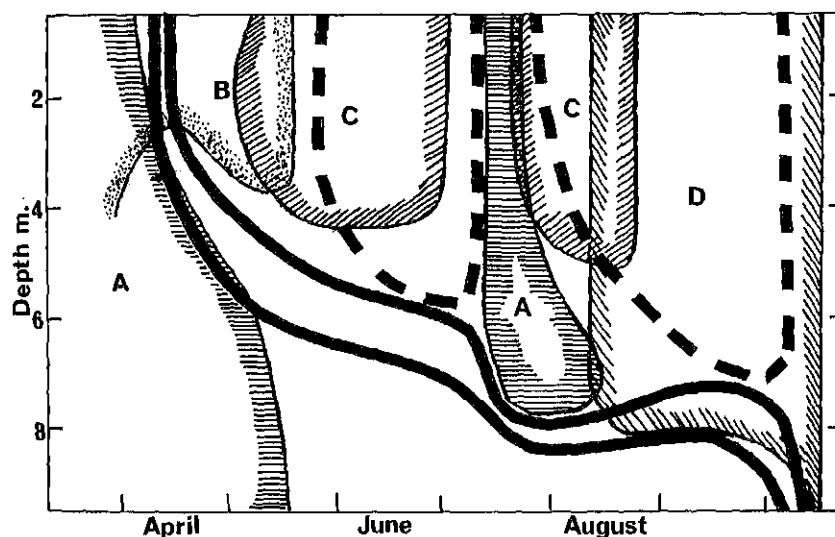


FIG. 3. Stylized depth-time distributions of four major phytoplankton components in Crose Mere: diatoms (A), green algae (B), blue-green algae (C), and *Ceratium* (D). The heavy solid lines represent the thermocline; the areas enclosed by heavy, pecked lines represent the extent of nutrient stress conditions.

trapping experiments designed to demonstrate the depth ranges within which motile algae actively confine their movements. These have shown that, after the onset of stratification, when diatoms ceased to be maintained in suspension, the successive dominants extended their vertical ranges progressively deeper into the lake. Once the epilimnion became depleted of nutrients, the faster-growing, high-light demanding green algae were succeeded by slower-growing, low-light tolerant blue-green algae. Dinoflagellates, which are capable of descent beyond the photic zone where nutrients are still abundant, ultimately replaced the blue-green algae. Diatoms exploited disturbances of stable stratification and the release of free nutrients from hypolimnetic water mixed into the deepened epilimnion. This summary of succession in Crose Mere is shown in stylized form in Fig. 3. It may well be applicable only to certain meres, although the scheme can be extended to accommodate differing chemical conditions in other meres. In shallow lakes, additional nitrogen (and perhaps organic matter) may permit the prolongation of green algal dominance. In the optically deeper meres (e.g. Rostherne Mere), epilimnetic nutrient reserves may have led to the relative dominance of blue-green algae. Again, diatoms have remained dominant for longer in the season in those years during which stagnation was delayed, or once established, was less stable. The next step will be to test these hypotheses in experimental situations, and to see if they might be applicable to other lakes.

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