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THE ECOLOGY OF THE PLANKTONIC BLUE-GREEN ALGAE IN THE NORTH SHROPSHIRE MERES, ENGLAND

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The periodicity and development of planktonic blue-green algae in the Shropshire Meres are described; *Aphanizomenon* and *Anabaena* increase during spring, *Microcystis* and *Coelosphaerium* in the summer, responding to temperature, turbulence and nutrient concentration. Surface blooms occur frequently, and their formation is shown to be the result of redistribution of existing population in response to turbulence conditions. Blooms give a false impression of the abundance of the algae.

Blooms are a manifestation of the buoyancy possessed by the individual blue-green colonies, imparted by the presence of gas-vacuoles. Intraspecific variations in buoyancy are dependent upon the numerical density of the vacuoles, which may be altered by light conditions or by the growth rate. The potential flotation rates of different species are dissimilar; the same is true for the rates of sinking of algae in which the vacuoles have been artificially suppressed. Rates of rise or fall appear to conform to Stokes's Law.

Introduction

Planktonic blue-green algae have been the subject of a great deal of research, particularly during the last two decades. Investigations have been directed towards understanding the significance of two major aspects of their biology: the possession of gas-vacuoles, which confer upon the algae the property of buoyancy; and the production of large populations in response to eutrophication of lakes and reservoirs. The combination of these properties results in the phenomenon of dense water-blooms, which are potentially an expensive nuisance to those who manage reservoirs and recreational waters.

Much of the existing literature concerns laboratory studies, very often on cultured material. The results have made possible tentative interpretations of field situations, but there have been few long-term surveys of natural populations. The present paper deals with data collected over a three-year period on the group of meres near Ellesmere, Shropshire. These small, water-filled moraine hollows are naturally fertile and particularly prone to water-bloom formations during the summer and autumn months. Frequently, the blooms are so dense that algal scums may cover the entire lake surface to a depth of several millimetres. The intensity of the blooms, and the suddenness with which they appear, have earned the phenomenon a place in local folk-lore, where it is known as the "breaking of the meres" (Mary Webb, 1924).

The results presented here must be regarded as interim, and form the basis of further detailed investigations which are currently in progress.

The sites

The observations presented in the following account were made mainly at Crose Mere, White Mere, Cole Mere and The Mere, Ellesmered, uring the three-

year period, 1966–1968. The sites are described by Sinker (1962), and their waters have been investigated chemically by Gorham (1957). The phytoplankton was surveyed by Griffiths (1925), and Reynolds (1971) has investigated its seasonal periodicity. The "breaking" of these meres was first described in detail during the last century (Phillips, 1884).

Limnological data for the sites are set out in Table 1.

Table 1. *Limnological data for the four Shropshire meres investigated, with minimum and maximum concentrations of nitrate nitrogen and phosphate phosphorus in their surface waters, 1966–1968*

	Area (ha)	Max. depth (m)	Conductivity μmhocm^{-1}	Nutrient concentration mg l^{-1} (Surface waters)			
				O^{1}_{3}—N		PO_4^{111}—P	
				Low	High	Low	High
Crose Mere	15·2	9·2	311–396	indetect.	1·840	indetect.	0·160
Cole Mere	30	16	207–296	0·006	0·982	0·005	0·370
White Mere	26	14·5	166–225	0·006	0·938	0·051	0·600
The Mere, Ellesmere	47	19·5	229–279	0·071	0·940	0·252	1·100

METHODS

(i) *Field*

Measurements of environmental parameters in Crose Mere were made from a boat moored at the deepest part of the mere. Temperature was recorded by means of a calibrated resistance thermometer attached to a cable marked in half-metre divisions. A Mackereth oxygen probe was used to measure *in situ* dissolved oxygen levels.

Standard weekly collections included a 0-5 m. water column sample, obtained using a weighted polyethylene tube of the type described by Lund and Talling (1957). Several samples were combined in a suitable polyethylene jar, to give a volume of 4–5 litres. The water column method is particularly suitable for work with blue-green algae, since a more reproducible series of results can be built up week by week, without being subject to variations in vertical distribution of the algae.

Samples from isolated depths were collected by means of a 1-litre Friedinger water trap, and transferred to 1-litre screwcap polyethylene jars. Surface samples were collected in a similar jar, by dipping the neck just below the water surface.

Aliquots of all samples were fixed in Lugol's Iodine. Additional samples for phosphate determinations were taken in polyethylene bottles whose walls were impregnated with iodine, as recommended by Heron (1962).

The collections at White Mere were also taken from a boat moored near the centre of the lake, where the water was 11 m. deep. Samples at Cole Mere and Ellesmere were collected from the shore, selecting in each case a part which was free of macrophytic vegetation.

In the experiments designed to determine changes in vertical distribution, a series of column samples were taken at hourly intervals: the sampling tube was used for columns over 1 m.; for columns of 200 mm. and less a simple perspex cylinder of 80 mm. diameter was employed: the ends were equipped with suitable bungs that could be placed in position under water.

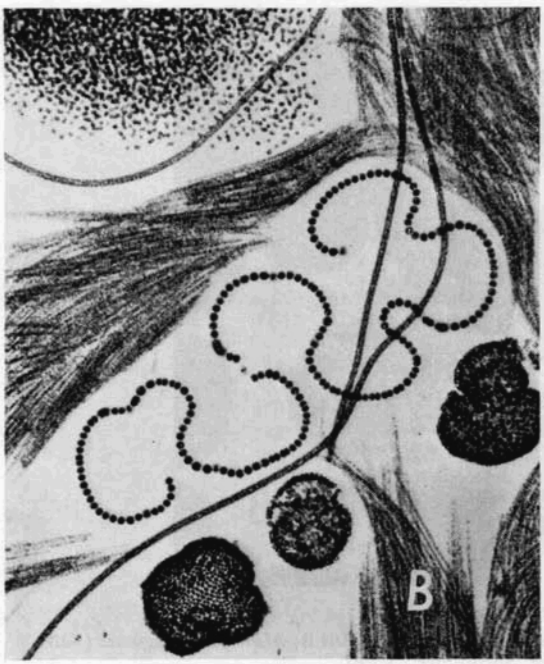

PLATE I.

A: Bloom of *Aphanizomenon* and *Microcystis* on Cole Mere, 7 August 1970; note the curious wrinkles in the scum caused by the disturbance of the surface tension. B: Blue-green algae from the plankton of Esthwaite Water, English Lake District. The bundles of filaments are *Aphanizomenon flos-aquae*, the broad isolated filaments are *Oscillatoria agardhii* Gom. var. *isothrix* Skuja, and the single squashed coil is *Anabaena* (?)*circinalis*; the coccoid colonies are *Coelosphaerium naegelianum* (Unger) Lemm. and part of a *Microcystis* colony is visible in the top left corner (×140). C: *Aphanizomenon flos-aquae* Ralfs ex Born et Flah. a small-celled form from Esthwaite Water (×140).

Photos by C. A. Sinker (A) and H. M. Canter (B, C).

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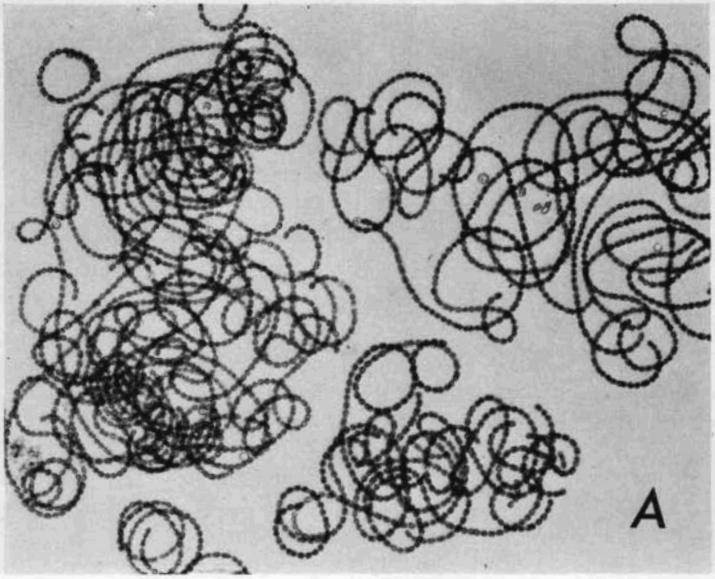


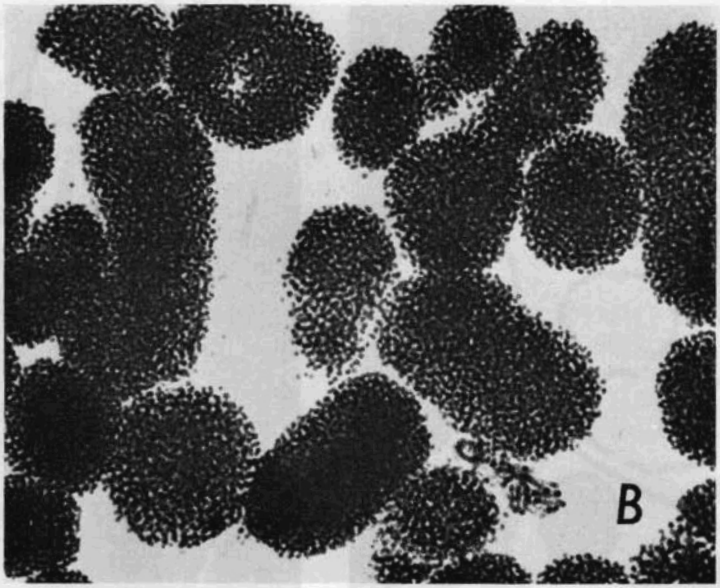


PLATE II.

A: *Anabaena flos-aquae* Breb. ex Born. et Flah. from Esthwaite Water (×140). B: *Microcystis aeruginosa* (Kutz.) Kutz. from Ellesmere, Shropshire (×140).

Photos by H. M. Canter.

(ii) *Laboratory*

Determinations of dissolved orthophosphate phosphorus and of nitrate nitrogen were carried out on the day following collection, after storage overnight in a cold, darkened cupboard. Analyses were carried out spectrophotometrically, using a Unicam SP.600 spectrophotometer.

Orthophosphate phosphorus was determined by the molybdenum-blue method of Stephens (1963); this method has recently been criticized in that it will detect phosphorus in radicals other than orthophosphate, which are not necessarily available to the algae (Rigler, 1968); however, since this method failed to detect a concentration of phosphorus on several occasions, it was concluded that what was being measured was being taken up and therefore was available to at least some species of algae.

Nitrate nitrogen was estimated by the method of Morris and Riley (1963), in which free nitrate is first reduced to nitrite, and subsequently determined. Nitrite controls were set up in parallel, but it was found that free nitrite was present in insignificant quantities.

Changes in the phytoplankton population were detected by means of counts, using the iodine-sedimentation and inverted microscope technique (Lund, Le Cren and Kipling, 1958). Parallel determinations of chlorophyll a, the dominant pigment in all groups of algae (Round, 1965) were carried out spectrophotometrically. The method employed was similar to that used by Richards and Thompson (1952): optical density of extracts in 90 per cent methanol were measured, and the modified formula of Talling and Driver (1963) was used to derive the original concentration of chlorophyll in the sample.

Results quoted from a parallel study of photosynthetic rates were derived from experiments employing the oxygen light and dark bottle technique (Lund and Talling, 1957; Soeder and Talling, 1969); oxygen concentrations were determined by Winkler titration, using N/400 sodium thiosulphate.

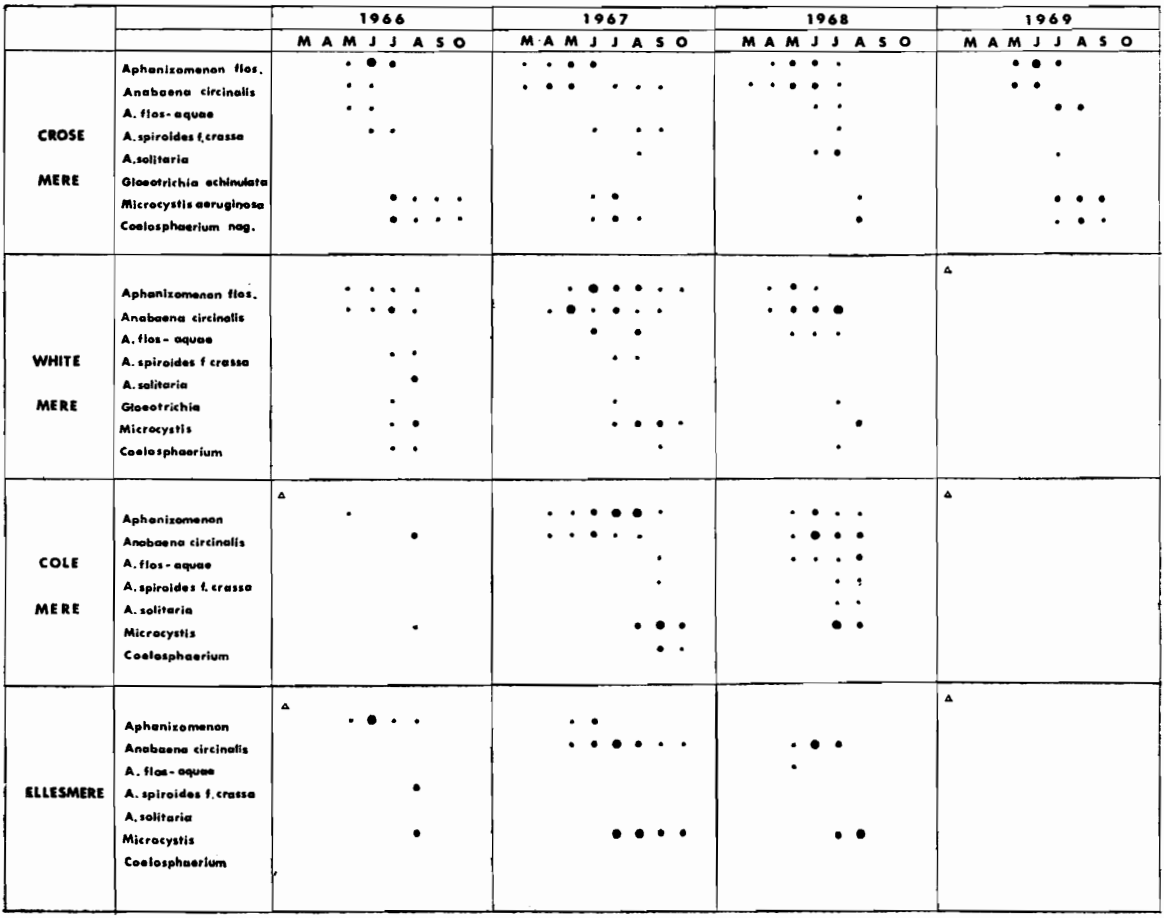
In the following account, the taxonomy used follows Komarek (1958) except that the more familiar names *Microcystis* and *Coelosphaerium naegelianum* are used instead of *Diplocystis* and *Gomphosphaeria naegeliana* respectively.

Periodicity

The most frequently occurring blue-green algae were (Plates I and II):
Aphanizomenon flos-aquae Ralfs ex Born et Flah.
Anabaena circinalis, Rabenh. ex Born et Flah.
A. flos-aquae Breb. ex Born et Flah.
A. spiroides Kleb., f. *spiroides*.
A. spiroides Kleb., f. *crassa* (Lemm.) Elenk.
A. solitaria Kleb., f. *planctonica* (Brunnth.)
Microcystis aeruginosa (Kütz.) Kütz.
Coelosphaerium naegelianum (Unger.) Lemm.
Gloeotrichia echinulata J. E. Smith.

Populations were rarely unialgal, but were normally dominated by one or two species. The seasonal occurrence of these algae in four Shropshire meres is represented in Table 2.

Table 2. *Periodicity of the more common species of planktonic blue-green algae in four Shropshire meres, 1966–1968*



Δ –indicates data incomplete over season concerned

The size of dot indicates the maximum population achieved during the calendar months given by the common species:

filamentous forms		coccoid forms
1–100/ml	•	0·5 – 5 cols./ml
100–1000 "	•	5 – 50 "
over 1000 "	●	over 50 "

Periodicity in Crose Mere

Surface blooms occurred from time to time in Crose Mere, though less frequently than in some of its neighbours. Even so, discontinuity in vertical distribution can give a false impression of the abundance of an alga; to maintain the comparative value of the data, all population determinations for the lake are based on counts from 5 metre tube samples. Samples collected from Crose Mere during 1969 are also included.

The periodicity of three algae, *Aphanizomenon*, *Anabaena circinalis* and *Microcystis*, together with the surface temperature, and the epilimnic concentrations of nitrate nitrogen and phosphate phosphorus, is presented in Figure 1. It is evident from

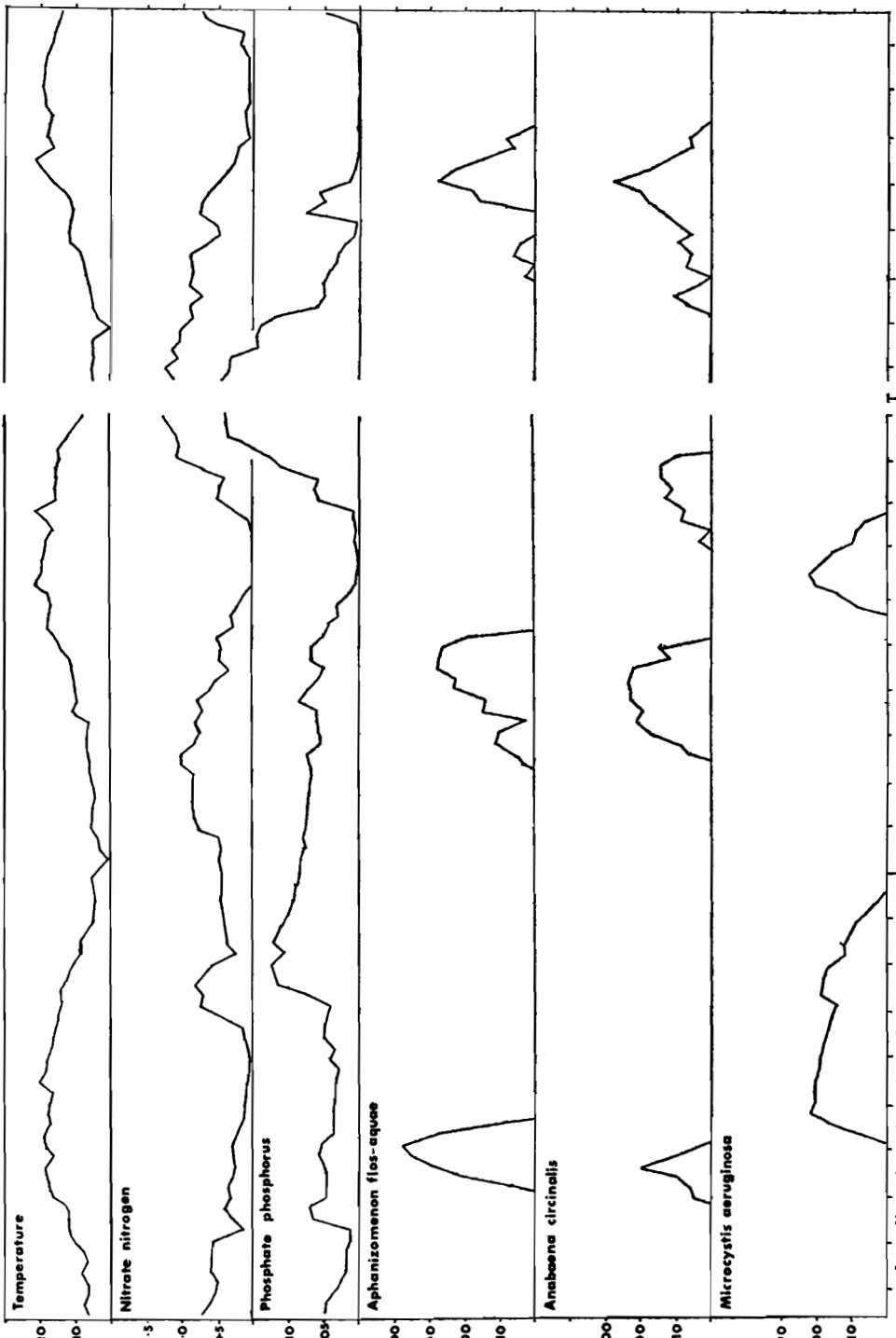


FIG. 1.
Seasonal variations in surface temperature, in the concentrations of dissolved nitrate nitrogen and phosphate phosphorus, and the periodicity of three species of blue-green algae, in Crose Mere.

these data that *Aphanizomenon* and *Anabaena circinalis* tend to be most abundant in the late spring, and *Microcystis* in the summer, though the size of population, the relative abundance, and the duration of dominance vary in each of the years.

Aphanizomenon appeared at the end of May 1966, whilst the mere was still isothermal, at 9°–11 °C., and continued to increase during a warm, sunny spell at the beginning of June, when the surface water temperature was increased to 16 °C., and stratification was induced. A maximum of 5,900 filaments/ml. in the 5 metre tube was recorded on 4 July. The end of the maximum coincided with the presence of a rapidly multiplying rhizopod (tentatively identified as *Pelomyxa* sp.), individuals of which were seen to be packed with blue-green coloured vacuoles, and recognizable *Aphanizomenon* heterocysts; numbers were drastically reduced to less than one filament/ml. by mid-July.

Aphanizomenon appeared again in March 1967 after the water temperature had exceeded 6 °C. A period of slow increase followed but, after several warm sunny days in mid-April had raised the surface temperature above 10 °C., the rate of increase was considerably accelerated. A maximum of 600 filaments/ml. was recorded on 15 May. The population progressively declined to less than 1 filament/ml. by 12 June.

In 1968, the same alga appeared in early April, after the temperature had reached 7 °C., and continued to be present in numbers less than 10/ml. until mid-May. Warm sunny weather at the end of May, increasing the temperature from 10 to 16 °C., again resulted in a more rapid increase to 900 filaments/ml. by 3 June. The population declined during June, when a series of surface blooms removed the majority of algae to the lee shores.

Anabaena circinalis was also present in all three years, though it failed to produce a maximum in 1966, remaining at less than 100 filaments/ml. throughout the early summer. In the following year, however, it appeared during March, at about the same time as *Aphanizomenon*, increasing progressively in water temperatures between 6–9 °C. to 140/ml. by mid-April, and reached a maximum of 250 filaments/ml. in early May. The population had declined to less than 1 filament/ml. by 1 June. It reappeared towards the end of July and persisted through August, but numbers only exceeded 10 filaments/ml. during September after phosphorus and nitrogen concentrations in the epilimnion had been increased during seasonal mixing.

In 1968, *A. circinalis* appeared during March, when the temperature was 5 °C., and increased gradually to 15/ml. by the beginning of May, when the rate of increase accelerated, producing a maximum of over 600/ml. by the end of the month. Numbers declined considerably during the period of surface blooms in June, but small numbers persisted until the end of July.

Microcystis aeruginosa appeared in each of the three years, but in 1968 it failed to develop into a large population. It increased during 1966, between 4 July and the beginning of August, to 140 colonies/10 ml., after the surface water temperature had increased to 16°–18 °C. It persisted in small numbers (50–100/10 ml.) until the end of October, but it did not finally disappear until January 1967.

The alga reappeared in June 1967 and reached 150 colonies/10 ml. by mid-July. The surface temperatures during this time were in the range 17–21 °C. The population progressively declined towards the end of the month, and fell below 1/10 ml. in August, though the temperature remained in the same range, but nitrogen and phosphorus had fallen to very low concentrations indeed: nitrogen to less than 1 μg/l, and phosphorus to 0·4 μg/l.

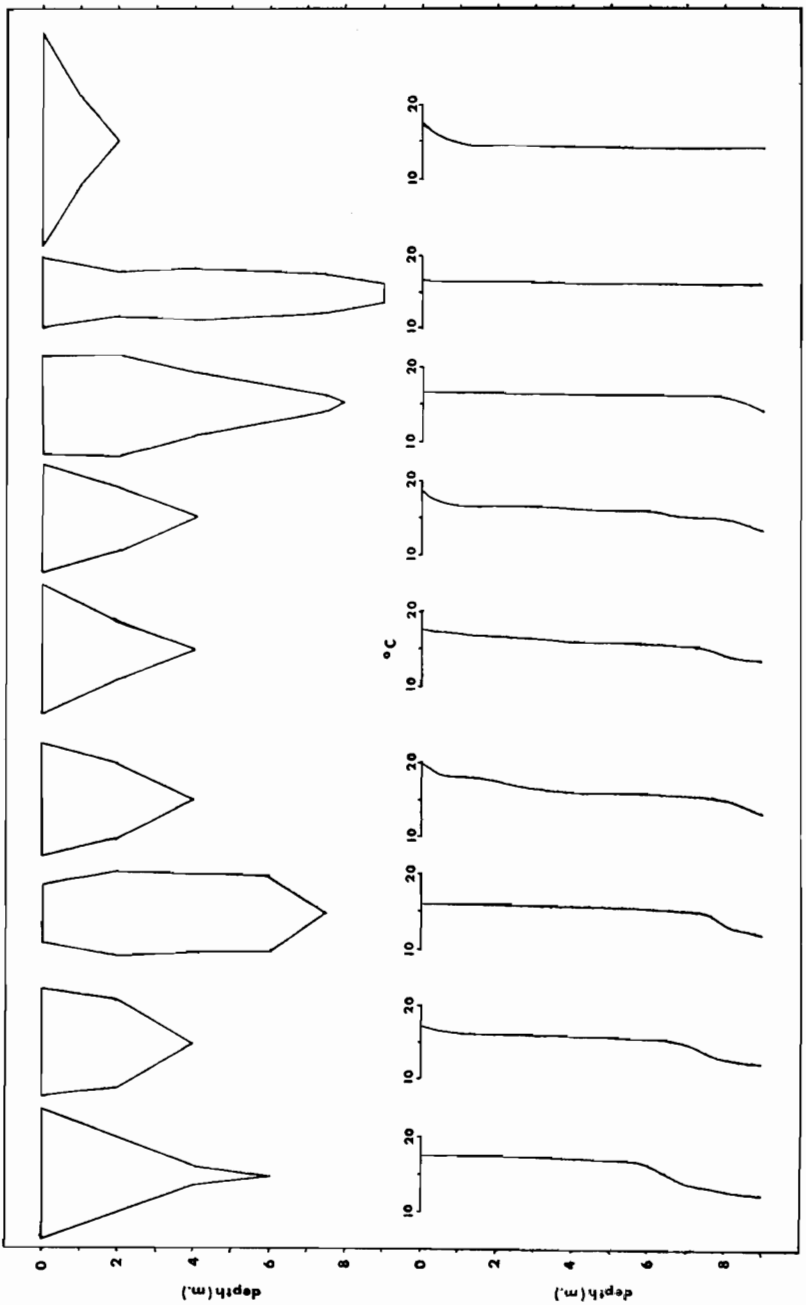


FIG. 2.
Vertical distribution diagrams of *Microcystis aeruginosa* in Crose Mere during summer, 1966. Diagrams are constructed as "cylindrical curves", the horizontal axis at each depth being equivalent to the cube root of the number of colonies recovered at that depth. Corresponding temperature profiles are shown for each sampling date.

In 1968, colonies of *Microcystis* were frequently recovered in townet collections from mid-June onwards, again after surface temperatures were in excess of 17 °C., but numbers were insufficient to be recorded in 10 ml. samples. The temperature through June to August was consistently in excess of 16 °C., but by mid-June the phosphorus concentration had fallen below 2 μg/l., and remained very low (0·5 μg/l.—indetectable) until mid-September; nitrate concentration, however, was 246 μg/l. in mid-June, and its minimum was 45 μg/l., during August.

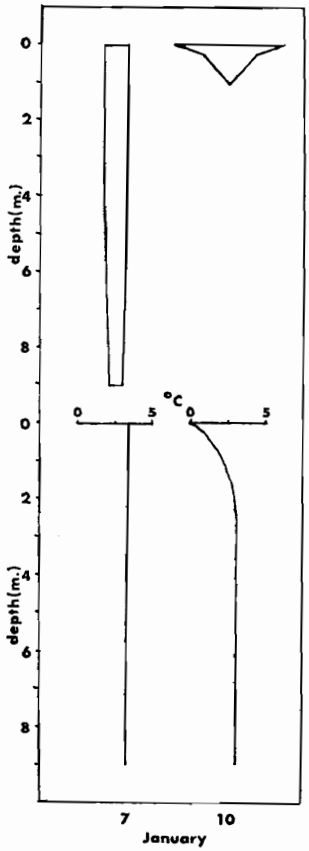


FIG. 3.
Vertical distribution of *Coelosphaerium nagelianum* in Crose Mere during January 1967. Method of plotting, as in Fig. 2. Temperature profiles are shown for each sampling date.

Other species in Crose Mere

The most abundant of the other blue-green algal species in Crose Mere was *Coelosphaerium naegelianum*, which had a similar periodicity to *Microcystis*. In 1966, 120 colonies/10 ml. were recorded at the end of July, with small numbers persisting until January 1967. It reappeared in June 1967 with 330 colonies/10 ml. in mid-July, persisting in superior numbers to *Microcystis* and disappeared a week later, in mid-August. Three colonies/10 ml. were recorded in July 1968.

Anabaena flos-aquae was present in the plankton of Crose Mere during June and July 1966 (maximum: 10 filaments/ml.) and in June 1968 (40/ml.). Small numbers of *A. spiroides* f. *spiroides* developed in June 1966 (maximum: 18/ml.). In 1967, a population of 1,400/ml. developed during June, following the decline of the *A. circinalis* maximum disappearing itself during early July.

A. spiroides f. *crassa* was present during June and July 1966 (maximum: 10/ml.), June 1967 (20/ml.) and July 1968 (4/ml.). *A. solitaria* f. *planctonica* was present in August 1967 (maximum 12/ml.) and again during June and July 1968. In the latter year, it increased rapidly between 10 and 27 June to a maximum of 860/ml., but had declined to less than 1/ml. by mid-July. In both years, its presence coincided with surface water temperatures in excess of 17 °C.

Periodicity in other meres

The periodicity of blue-green algae in Cole Mere, White Mere and Ellesmere are included in Table 2. Though based on fewer data, some general trends are evident. Either *Aphanizomenon* or *Anabaena circinalis* or both appeared regularly before other species, and at approximately the same times as they did in Crose Mere. *Microcystis* and *Coelosphaerium* increased in July or August, when the water was warmer.

Gloeotrichia echinulata was present in the plankton of White Mere in July of each year. *Microcystis wesenbergi* Komarek (=M. *flos-aquae* (Wittr.) Kirchn.) was present in Ellesmere simultaneously with *M. aeruginosa.*

In 1966 and 1967 the plankton of White Mere included several species of blue-green algae which persisted together through July, and surface blooms were multi-algal. The populations were smaller in 1968, when there was a much lower phosphorus content compared with the two previous years (40 μg/l. cf. 247 and 530 μg/l. respectively in August).

In Cole Mere, there were heavy growths of *Aphanizomenon* in May 1967, and of *Anabaena circinalis* in June 1968; *Microcystis aeruginosa* formed dense "blooms" in 1967 and in 1968, where August phosphate concentrations were respectively 151 and 50 μgP/l. In Ellesmere *Anabaena circinalis* and *Microcystis aeruginosa* were present in large numbers in both 1967 and 1968. The phosphate concentration in the lake was consistently above 400 μg/l.

Discussion

The appearance of blue-green algae in temperate lakes is generally acknowledged to occur in response to increased light and temperature at the end of spring, though other factors may also be operative (Pearsall, 1932).

In the meres, the succession described here is typically *Aphanizomenon* and *Anabaena circinalis* appearing during spring, and *Microcystis* and *Coelosphaerium* during the summer. Less extensive data suggest that *Anabaena flos-aquae* and *A. spiroides* f. *spiroides* may be classified with the "spring forms", whilst *A. solitaria, A. spiroides* f. *crassa* and *Gloeotrichia echinulata* belong with the "summer forms". Further, there is evidence to suggest that the time of appearance and sequence of bloom formation is influenced by water temperature, which is in accord with Hammer's (1964) general conclusions. In Crose Mere, *Anabaena circinalis* increased at lake temperatures between 6–10 °C., and maximal growth was recorded when temperatures ranged between 11–15 °C. *Aphanizomenon* increased very slowly at temperatures below 10 °C., but a more rapid increase occurred between 10° and 15 °C. *Microcystis aeruginosa* did not increase until epilimnion temperatures were greater than 15 °C., although colonies tolerated winter temperatures in 1966/1967. The apparent ability of *Anabaena circinalis* to increase more rapidly than *Aphanizomenon* at temperatures between 6° and 10 °C. was probably of selective advantage in years when the lake warmed up gradually in spring, as in 1967 and 1968, but the cold, wintry spring months of 1966, followed by a warm sunny spell resulting in an abrupt increase in water temperature, were more favourable to the growth requirements of *Aphanizomenon.*

Whilst temperature is undoubtedly an important factor in influencing the growth of planktonic blue-green algae, it must be borne in mind that temperature increase

is itself influenced by sunlight and by wind, whose importance in determining the succession should not be discounted. It is possible that increased wind-induced mixing suppresses the growth of *Aphanizomenon* by reducing the effect of insolation below a critical level; conversely, growth would be favoured by decreased circulation. Equally, *Anabaena circinalis* may have a greater tolerance of low light intensities than *Aphanizomenon*, and grows better when the depth of circulation is less satisfactory for the increase of *Aphanizomenon*.

In Ellesmere, the largest and deepest of the Shropshire meres, the epilimnion is consequently deeper, and *Aphanizomenon* was not seen in large numbers. That temperature alone is not the critical factor in the development of *Aphanizomenon* is apparently supported by the fact that the temperature optima for species in Crose Mere do not coincide with those quoted by Hammer (1964). In the lakes in southern Saskatchewan where he worked, large numbers of *Aphanizomenon flos-aquae* developed only after the water temperature had exceeded 20 °C. It would seem that light and temperature are both of critical importance, but at this stage it is speculative to attempt to distinguish their effects.

The succession of blue-green algae may also be influenced by the chemistry of the water. Pearsall's (1932) observation that the abundance of blue-green algae was related to the concentration of dissolved organic matter is now largely attributed to the extracellular products that these algae themselves produce during their active growth (e.g. Fogg, 1952; Whitton, 1965; Fogg, Nalewajko and Watt, 1965), and it remains disputed whether organic matter is an essential growth factor for these algae. If it is so, it is arguable that populations of *Microcystis* develop in the meres utilizing the organic products of the earlier *Anabaena* and *Aphanizomenon* maxima. The role of organic matter in promoting the growth of blue-green algae is uncertain, but if it acts merely as a chelating agent, as is suggested by the work of Gerloff, Fitzgerald and Skoog (1950), then it is unlikely than any such specific relationship exists. Gerloff *et al.* (1950) succeeded in culturing *Microcystis* in an inorganic medium, with only citrate added to maintain iron in an available form. Indeed most blue-green algae are thought to be obligate photoautotrophs (Kratz and Myers, 1955), though Hoare, Hoare and Moore (1967) have produced experimental conditions under which *Anabaena flos-aquae* assimilated carbon from acetate.

There seems little likelihood either that the appearance of the later species is influenced by the ability of earlier species to fix dissolved atmospheric nitrogen. Nitrogen fixation has been established for several planktonic species of *Anabaena* (see Lund, 1965), and the presence of a large population can contribute to an increase in combined nitrogen in the lake (Fogg and Stewart, 1965). For some time it was accepted that *Aphanizomenon* does not possess this ability, implying not only a selective advantage to *Anabaena*, but that *Anabaena* populations might herald greater numbers of other species at a later stage. However, more recent studies by Stewart, Fitzgerald and Burris (1967), using the acetylene-reduction technique, indicate that *Aphanizomenon* possesses the enzymes to fix nitrogen.

Analysis of Crose Mere water showed that, far from adding to the combined nitrogen of the lake, the main periods of increase of *Aphanizomenon* and *Anabaena* populations were accompanied by large reductions in nitrate level. Any contribution that they may have made was insufficient to avert considerable nitrate depletion over the period of their growth. It may be that nitrogen fixation only takes place when other nitrogen sources are in short supply (Fogg, 1942; Fogg and Stewart,

1965). Though nitrogen fixation may be important in some lakes, in the Shropshire meres at least it is an insignificant factor in the seasonal succession.

The failure of *Microcystis* to produce a maximum in Crose Mere during 1968, and its early decline in 1967 appear to have been due to nutrient limitation. In the summer of 1967, both nitrogen and phosphorus fell to very low concentrations whilst *Microcystis* was increasing (0·97 μgN/l.; 0·43 μgP/l.), and it failed to recover after the nitrogen concentration was increased during windy weather. In 1968, nitrate nitrogen never fell below 40 μgN/l., but phosphorus fell to 0·6 μgP/l. in June, and remained below this level until September. During the summer of 1966, when *Microcystis* was numerous, however, phosphorus levels remained above 25 μgP/l., and nitrate above 40 μgN/l. Thus the evidence is that the low phosphorus concentration prevented the growth of *Microcystis* in 1968, and limited growth during 1967, though nitrate concentration in that year may also have been close to limiting values.

Gerloff, Fitzgerald and Skoog (1952) considered that in many lakes, nitrogen was more likely to be a limiting factor to the growth of *Microcystis* than was phosphorus. In a series of experiments, Gerloff and Skoog (1954, 1957) substantiated this view, showing that the minimum requirements of *Microcystis* for nitrogen and phosphorus were in the ratio approximately 60 : 1. In the Shropshire meres, as in Wisconsin lakes, these elements are normally present in the ratio 10 : 1 or less, and it would appear inevitable that nitrogen becomes limiting before phosphorus. At the time when *Microcystis* appeared in Crose Mere in 1968, however, the ratio of N/P was already in excess of 60 : 1; on the basis of Gerloff and Skoog's data, it follows that in this instance phosphorus would become exhausted first.

In the other meres studied, *Microcystis* was abundant in both 1967 and 1968, and neither nitrogen nor phosphorus appeared to have been depleted to limiting concentrations. It is, however, true to say that there was a general correlation between abundance of *Microcystis* and the phosphate concentration in these lakes.

Different species probably have widely differing nutrient requirements. The development of the large *Anabaena solitaria* population in Crose Mere in June 1968, took place in a medium of low phosphorus content, and in the absence of severe competition from *Microcystis* or *Coelosphaerium*. *A. solitaria* may be a species which is normally excluded from the meres by faster growing blue-green algae, but is able to dominate when competition is reduced.

The distinct pattern of seasonal periodicity of blue-green algae in the North Shropshire meres, it is concluded, is largely due to the influence of light and temperature, and the environmental requirements of the species concerned; however, nutrient limitation may become important during the period of summer stagnation.

It is also important to stress that at no time during the three-year study was there any evidence of "explosive" development of populations. Many of the earlier explanations of the "sudden" appearance of water bloom suggested that a phase of rapid multiplication preceded bloom formation. There were plenty of "blooms" during this period, and alternative explanations are offered in the next section of this account.

The formation of surface blooms or "breaks"

The term "breaking" is drawn from the similarity of the appearance of surface scums of blue-green algae on the meres, to the rising, or "breaking", of the wort

or yeast, in the manufacture of beer (Sinker, 1962). It is essentially a local term, but it was equated with the early definitions of water bloom and Wasser-blüthe by Whipple (1899). The original use of the word "bloom" has been greatly abused, and has necessitated its redefinition by Smith (1950) as a "concentration of algae sufficient to discolour the water", and has been applied to large populations of other than blue-green algae. In the present account, "bloom" is applied only in the original sense, and is prefixed by the word "surface".

The planktonic species of blue-green algae are characterized by the possession of gas vacuoles, which impart to the algae the property of flotation. Moreover, when vegetative colonies were examined microscopically gas vacuoles have always been found to be present. In every sample of freshly collected plankton allowed to stand for half an hour or so, any blue-green algae present were seen to be floating on the surface, regardless of the time of year when the sample was collected. The only exceptions have been in *Anabaena* and *Aphanizomenon* cells immediately after germination from spores during the spring though vacuoles soon appeared in actively growing cells (cf. Smith and Peat, 1967a). If the ability to float is inherent in these algae between germination and death, and they are present in a water body, then there is a constant tendency for the algae to drift towards the surface, and that water body is potentially liable to surface blooms. However, because the algae are small, and only a little lighter than water, this tendency is normally countered by turbulence and diffusion currents within the lake. Only when there is a reduction in turbulence will the tendency to rise to the surface become manifest.

The Shropshire meres are small shallow lakes, and their situation in moraine hollows ensures that they are well sheltered from wind action; the occasional presence of mature alder or other woodland on their fringes increases this sheltering effect. During calm weather, vertical temperature profiles frequently show a differential of several degrees, even within the top 4 metres of the lake, indicating that turbulence diffusion currents rapidly weaken when the wind drops. Moss (1969) has shown that vertical heterogeneity in physical and chemical conditions is likely to influence the distribution of phytoplankton, and further examples have been given by Reynolds (1971).

Planktonic blue-green algae are most likely to be able to drift towards the surface when turbulence becomes insufficient to prevent vertical temperature disparity. Such conditions occur during calm weather, and these are precisely the conditions under which the meres have been observed to "break", not only during the present study, but also according to Phillips (1884) and Wilson (1966). Water becomes most still under continuous ice-cover, and a perfect bloom formed in Crose Mere, just beneath the ice, between 7 and 10 January 1967, when only a small population of *Coelosphaerium naegelianum* was present in the lake. Vertical distribution diagrams of *Microcystis aeruginosa* during summer 1966 are presented in Figure 2 and of *Coelosphaerium* in January 1967 in Figure 3. The diagrams demonstrate a constant tendency of the population to rise towards the surface; their vertical distribution is dependent upon the extent of wind-induced mixing, as indicated by the temperature profiles.

Given that a reasonable population of suitable algae is present in the lake, a surface bloom may be anticipated during the next spell of calm weather. Accordingly, it has been possible to predict the occurrence of a "break", and to be on the site to make a series of collections whilst a bloom was forming at the surface. One such

occasion was at Crose Mere on the night of 21/22 July 1966. The prior week had been fine and windy, but during the afternoon of 21 July, the wind dropped and a warm, still evening ensued. In the plankton, *Microcystis* was increasing in the lake, and a "break" of moderate intensity was anticipated. A series of four column samples, from the surface to depths of 100 mm., 200 mm., 1 m. and 5 m. respectively were collected each hour between 2200 and 0600 hours the next morning; the chlorophyll a content of each was determined subsequently. The results are presented in Figure 4. The shapes are constructed by superimposing rectangles whose width represent the chlorophyll concentration in each column sample at each hour. The first samples show that the organisms were still fairly well distributed within the 5 metre column; in the later samples, there was shown to have been a steady increase in the top metre throughout the night, and a more dramatic accumulation in the top 100 mm. towards dawn. By morning the entire surface was festooned with patches of blue-green algae; 87 per cent of the chlorophyll contained in the 5 m. column was located in the top metre, and 56 per cent in the top 100 mm. It is stressed that during the period of observation there was no significant change in the chlorophyll content in the samples taken with the 5 m. tube, and no real algal increase had taken place.

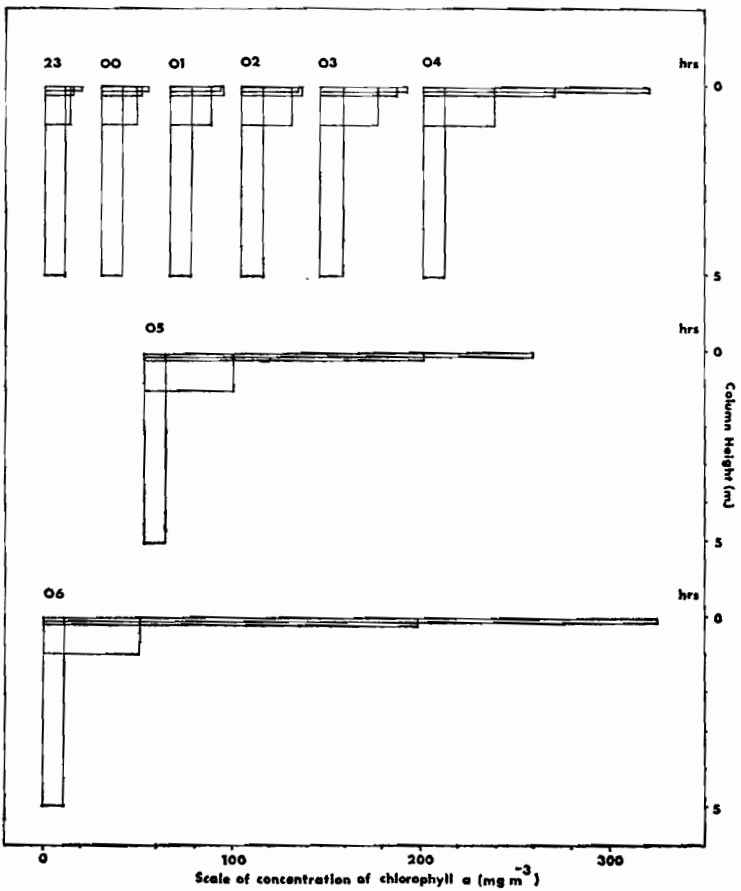


FIG. 4.
Hourly variations in the vertical distribution of chlorophyll a during the formation of a surface bloom, 21/22 July 1966. For method of construction, see text.

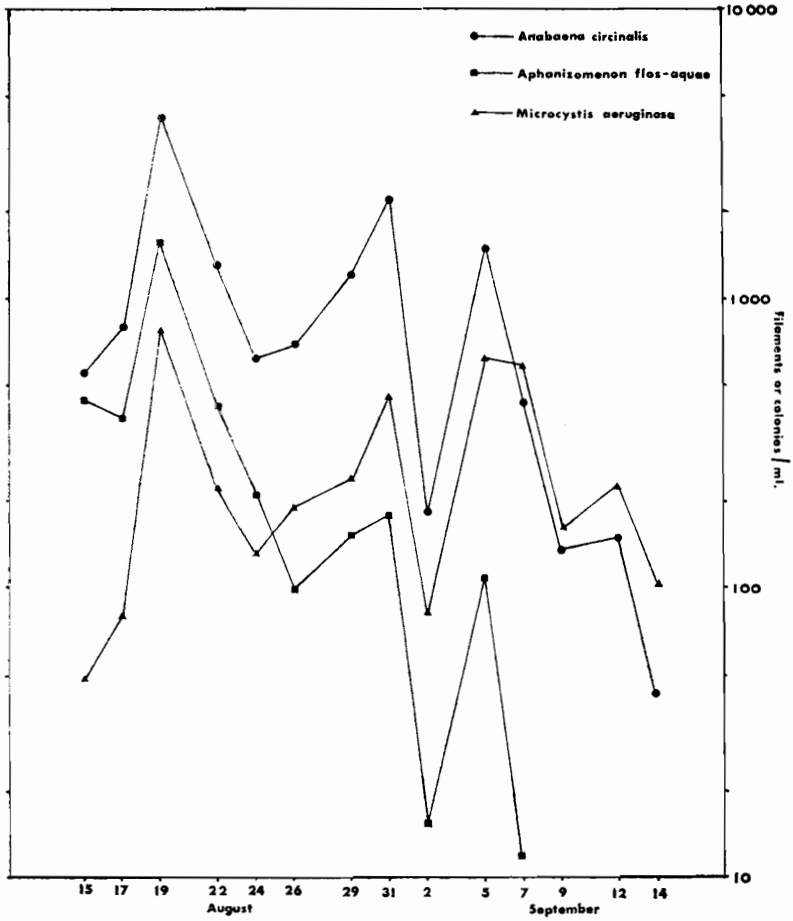


FIG. 5.
Variations in the number of blue-green algal colonies in a 200 mm. water column inserted at the surface of White Mere, summer, 1967.

If several species of blue-green algae are present, then all will presumably respond in a similar manner to changes in the physical medium, and multialgal blooms are probable. Figure 5 shows the numbers of three species of blue-green algae in the top 200 mm. of White Mere at two- to three-day intervals during the summer of 1967. The coincidence of the peaks implies that aggregation of organisms near the surface is determined by similar causes for each species. A surface bloom is a purely physical response to suitable environmental conditions, when the algae become telescoped from a layer several metres in depth into one of a few millimetres at the surface. The scum that forms is the accumulation, and to some extent aggregation, of blue-green algae present in the water at that time.

Laboratory experiments indicate that the role of surface tension is an important factor in maintaining a surface bloom. When a collection of blue-green algae was allowed partially to accumulate at the surface of water in a beaker, and then the entire sample stirred so that the surface was not broken, it could be seen that the suspended algae continued to circulate laterally well after the algae caught in the surface film had become stationary. In other samples placed in glass beakers

accumulation of blue-green algae was shown to be greatest at the glass/surface film interface, where surface forces are greatest. The relevance of the surface tension to a lake population becomes apparent when the wind develops after "blooming" conditions: a strong breeze may disrupt the lake surface into waves, and floating algae become resuspended in the medium, and recirculated in the wind-induced turbulence; a light breeze may simply ripple the surface, in which case algae are carried across the lake and deposited on the lee shores.

The algae involved in bloom formation have been shown to possess widely differing rates of flotation. This was at first apparent after comparing the vertical distributions of different species in the same lake and during the same period; Figure 6 shows an example, where the distributions of *Anabaena circinalis* and *Aphanizomenon flos-aquae* in Crose Mere between 21 May and 3 June 1968 are plotted against depth. It can be seen that *Anabaena* was consistently more buoyant than *Aphanizomenon.*

Further evidence has been derived by determining the apparent increase in numbers of each species between disturbed and calm conditions on successive days, and by comparing the relative abundance of the different species in a surface bloom with that in the suspended population at the same time. By expressing the apparent increases in each case as a ratio of the equivalent increase of the most frequent participant, *Aphanizomenon flos-aquae*, Table 3 has been constructed.

Table 3. *Relative buoyancy of some planktonic blue-green algae, determined from distributional data; the left hand column is derived from the apparent increase in numerical density of each species at the mere surface between disturbed and calm conditions; the right hand column is derived from the density of each species at the surface relative to the suspended population in a 5 m. water column, under calm conditions. The ratios are expressed relative to the corresponding ratio for* Aphanizomenon

Species	Disturbed : Calm surface ratio	Surface : Suspended ratio
Aphanizomenon flos-aquae	1·00	1·00
Anabaena spiroides f. *spiroides*	1·05	1·06
Anabaena flos-aquae	1·21	1·34
Anabaena circinalis	1·58	2·30
Coelosphaerium naegelianum	2·41	4·24
Microcystis aeruginosa	7·62	10·70
Gloeotrichia echinulata	8·40	—

In the laboratory some progress was made in determining *in vitro* flotation rates of blue-green algae. Freshly collected algae were introduced into Utermohl counting chambers (Lund, Le Cren, and Kipling, 1958) containing filtered lake water. The height of the water column in the chamber was measured before each tube was thoroughly shaken to randomize the population. The time taken for the water to clear in each case was recorded, and from these data the speeds at which the mean distance (that is half the depth of water) was traversed by the algae were extrapolated. In cases where several species were present together in one collection it proved possible to separate the species by progressive fractionation, by repeating this method several times. Frequently, rates of flotation were so different that this method of separation was very efficient. The ranges of results for each species are presented in Table 4.

Table 4. In vitro *flotation rates of some planktonic blue-green algae*

	In vitro rates of flotation	
	No. of expts.	Rate (μm/sec)
Aphanizomenon flos-aquae	10	1·95– 16·10
Anabaena solitaria f. *planctonica*	1	4·18
Anabaena spiroides f. *spiroides*	1	30·06
Anabaena circinalis	14	8·00– 33·60
Coelosphaerium naegelianum	4	28·50– 41·60
Microcystis aeruginosa	6	19·90– 71·70
Gloeotrichia echinulata	6	115·00–227·00

It is evident that when the results given in Table 4 are arranged in ascending order of flotation rate, the order is similar to that presented in Table 3. The difference in flotation potential of lake populations of blue-green algae means that a surface bloom of *Gloeotrichia* or *Microcystis* is liable to form far more rapidly than one of *Aphanizomenon.*

In another series of experiments designed originally to show that the property of flotation was imparted by the presence of gas-vacuoles, freshly collected algae were centrifuged under water columns at pressures equivalent to 6–9 atmospheres. When redispersed in filtered lake water, the algae no longer floated, but sank to the bottom. By redispersing in a Utermohl counting chamber, and making frequent counts along a diameter of the chamber, it was possible to obtain comparative data on the sinking rates of different species. Again, these rates were expressed as a ratio of *Aphanizomenon*, and are presented in Table 5.

Table 5. In vitro *sinking rates of some planktonic blue-green algae, after suppression of the gas-vacuoles. The rates are expressed relative to the corresponding rate for* Aphanizomenon

	Relative rate of sinking after suppression of gas vacuoles
Anabaena flos-aquae	0·74
Aphanizomenon flos-aquae	1·00
Anabaena circinalis	1·67
Coelosphaerium naegelianum	7·72
Microcystis aeruginosa	8·65

It is striking that the species which float most rapidly are also the ones which sink the fastest when the vacuoles have been collapsed. The relative rates of sinking appear to conform with Stokes' Law, those in which the surface : volume ratios are the greatest being slowest to fall. Since the rates of flotation are in similar order, Stokes' Law may be applied equally to rates of negative fall; the vast differences in flotation potential between the various species studied is probably more a function of frictional resistance than of vacuolation. This view is supported by Smith and Peat (1967a) and Walsby (1969) whose determinations of the percentage of cell volume occupied by gas-vacuoles in vegetative cells of various species of blue-green algae suggest that variations are within a limited range (typically between 4 and 8 per cent).

The ranges of observed rates of flotation presented in Table 4 are appreciable, particularly in the case of the filamentous forms *Aphanizomenon* and *Anabaena circinalis.*

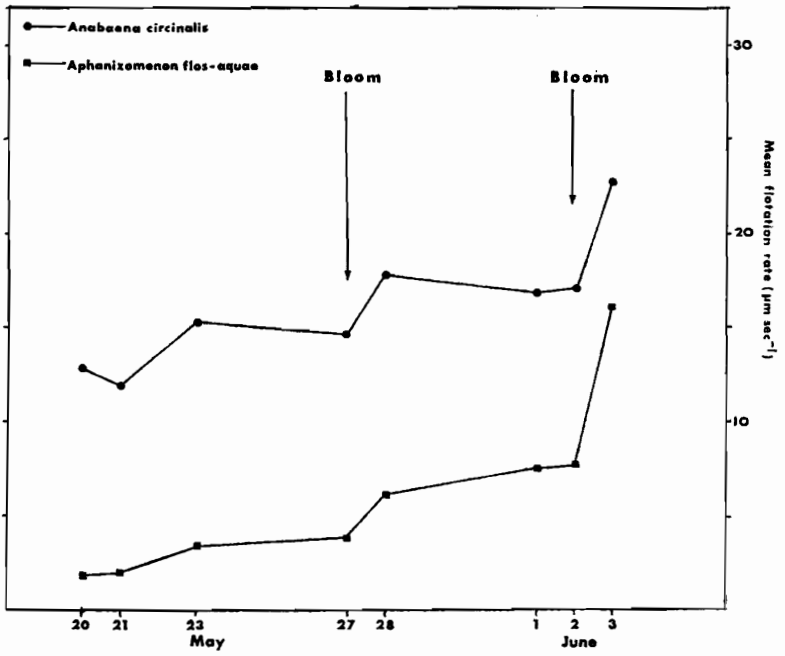


FIG. 7.
In vitro flotation rates of *Anabaena circinalis* and *Aphanizomenon flos-aquae*, collected from Crose Mere, during spring, 1968; surface blooms had formed on 27 May and on 2 June.

The lower values in either range were derived from algae collected during a period of active increase, the higher values from rather older populations. The progressive increase of the flotation potential with age of the population was investigated during 1968, by determining the *in vitro* flotation rates of different species in fresh material collected at frequent intervals over several days. The results are presented in Figure 7. The increases in flotation rate were not gradual but occurred suddenly in collections made on days following the appearance of surface bloom. Thus the algae collected on the morning of 2 June, after an overnight "break", were found to have specific flotation rates similar to those collected the previous day. But by 3 June, after the bloom had been largely dissipated by a breeze, the rates had increased sharply implying that flotation potential had been increased only after the algae had been exposed at the surface for some 24 hours or more. Microscopic examination of algae collected from the surface revealed an apparent increase in vacuolation, compared with those collected from the freely suspended population, and it was also apparent that the greatest density of vacuoles occurred at the periphery of the cells. When the vacuoles were suppressed in algae subsampled from each collection the sinking rates were very similar; thus, the changes in flotation potential were not due to disfigurement or other alteration in frictional resistance of the cells but, apparently, to a change in percentage vacuolation.

One possible explanation for the observed change in vacuolation is that there is a reduction in pressure on the cell wall as the alga floats upward, and the vacuoles simply expand. Recent evidence, however, suggests that vacuole-membranes are considerably more rigid than was once supposed: vacuoles consist of clusters of minute cyclinders (Bowen and Jensen, 1965), which are sufficiently stable to be

isolated from the cell intact, without changing their shape (Walsby and Buckland, 1969). Walsby and Eichelburger (1968) have also demonstrated that the cylinder walls are kept distended by the presence of particulate hoop-like structures, spaced at 5 nm. intervals; this observation has been confirmed by Smith, Peat and Bailey (1969), who have also shown that the particles are proteinaceous. Walsby (1969) concluded that vacuoles are erected mechanically, for the membranes are fully permeable to gases. In the present study it has been shown that fixation in formalin does not destroy the vacuoles nor, consequently, the capacity to float. The rigidity of the membranes imparts considerable resistance to slight changes of pressure, and although an alga traversing a vertical distance of 4 to 5 metres may experience a decrease of external pressure of about 1/6 atmosphere, the change in percentage vacuolation is insignificant. Moreover, were external pressure the only factor determining vacuole-size, one would expect algae collected from surface bloom and from the lake to behave more similarly under replicate conditions of pressure in the laboratory.

Other possible explanations for increase in vacuolation at the surface are related to exposure of the algae to light. This may be as a direct effect of strong illumination; the peripheral distribution of vacuoles within the cells could be interpreted as a protective reaction (but see Walsby, 1969). Indirect effects might include increased vacuolation arising during photosynthetic activity as a result of high local concentrations of metabolic gases inflating membranous envelopes as was suggested by Buell (1938). Analysis of the gas contained in the vacuoles renders this theory unlikely, though not impossible (Walsby and Eichelburger, 1968). They concluded that the gas, mainly nitrogen with argon and occasionally oxygen, was not a specific product of metabolism. Waaland and Branton (1969) have demonstrated that *de novo* vacuolation can be induced in *Nostoc muscorum*; vacuoles developed without evident connection with photosynthetic membranes. If vacuoles are self-erecting structures it may be that increased vacuolation results when the rate of cell division is slowed down, and gas vacuole development catches up with mitosis.

To investigate the effect of light further, an experiment was carried out where freshly collected algae were enclosed in 100 ml. "Pyrex" bottles containing Crose Mere water which were then suspended from a buoy in the lake at 0·5, 1, 4 and 6 metres depth. After 72 hours the bottles were removed and the rates of flotation of algae in each sample were determined. The results are set out in Table 6. Though far from conclusive, they show that in both species examined, vacuolation tended to increase most in brightly or very poorly illuminated bottles. The pressure on the algae would have been similar in each case.

The possibility that vacuolation was artificially increased by a reduction in the rate of growth in the cultures kept in strong light and in dim light seems plausible. Increase in vacuolation due to increased rate of photosynthesis would not apply to the 6·0 m. cultures. In strong illumination the rate of photosynthesis in many algae is reduced, and it would appear that blue-green algae are no exception. Figure 8 shows the rate of oxygen production during a "break" on 2 June, 1967 as assessed by the light and dark bottle method. The curious curve is the result of most of the algae, located near the surface, having a slow rate of photosynthesis, whilst the optimal rate occurs at 1 m. where only a few algae are present. When the figures are expressed as rates of oxygen production per unit of chlorophyll, a more meaningful curve is produced (Figure 9): if persistent, an inhibited anabolic

Table 6. *Changes in* in vitro *flotation rates of* Anabaena circinalis *and* Aphanizomenon flos-aquae *after enclosure in 100 ml. bottles for 72 hours at different depths in Crose Mere, during June 1968*

Species	Depth m.	Initial flotation rate	Flotation rate + 72 hrs.			Mean % change
			A	B	Mean	
Anabaena circinalis	0·5	12·2	15·20	16·70	15·95	+30·8
	1·0		12·20	11·40	11·60	— 4·9
	4·0		12·50	10·90	11·60	— 4·9
	6·0		12·50	12·90	12·70	+ 4·1
Aphanizomenon flos-aquae	0·5	1·95	3·40	2·90	3·15	+61·5
	1·0		2·00	2·80	2·40	+23·0
	4·0		1·65	2·35	2·00	+ 2·5
	6·0		2·60	2·90	2·75	+41·0

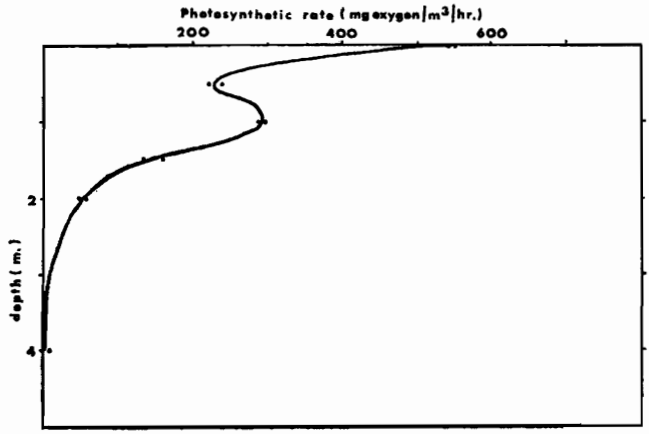


FIG. 8.
The rate of gross photosynthetic oxygen production in Crose Mere during a surface bloom, 2 June 1967.

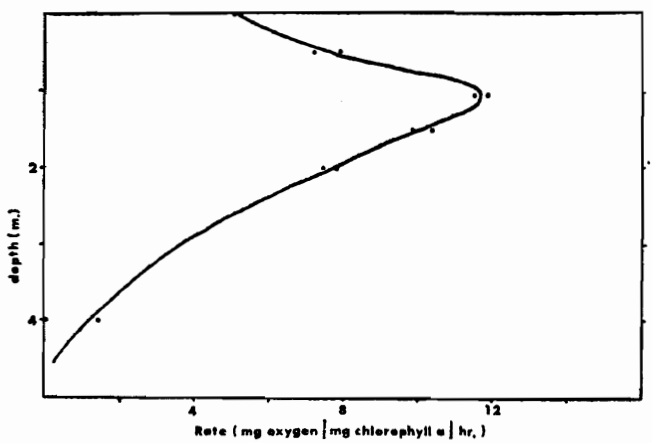


FIG. 9.
The rates of photosynthetic oxygen production in the same experiment expressed per unit chlorophyll a present at each depth.

rate may well lead to a reduced rate of cellular growth and division. Reduced rate of growth remains a reasonable explanation for the increase in vacuolation and in flotation potential. The careful observations made by Smith and Peat (1967b) of gas vacuoles in *Anabaena flos-aquae* in culture, where the density of gas vacuoles increased during the declining phase of growth, are in accord with this view.

Whatever the explanation, the fact remains that participation in a bloom apparently increases the flotation potential of that population. Thus, the next time physical conditions permit, the same blue-green algae may form a second bloom much more rapidly. This view has been verified during successive blooms on Crose Mere during May/June 1968, on White Mere during August 1967 and on Cole Mere during August/September 1967.

The results of a single experiment carried out in White Mere in September 1967 may also be mentioned. Floating blue-green algae, mainly *Microcystis aeruginosa* with a little *Aphanizomenon flos-aquae*, were collected from Cole Mere, and were centrifuged to collapse the gas vacuoles, removing the capacity to float. The algae were then apportioned into six 3 in. by 1 in. specimen tubes containing Cole Mere water, half of which were darkened by tightly wrapping them with aluminium foil; on the same day, the tubes were suspended from an old iron-hurdle fence which runs into the water on the eastern shore at White Mere, so that the samples were a few centimetres below the lake surface. An additional uncentrifuged sample of the Cole Mere algae, undarkened, was included as a control. The aim of the experiment was to ascertain the rate of vacuole regeneration in illuminated and darkened condition, by removing lit and darkened pairs at recorded intervals during the next three days. The results are summarized in Table 7.

Table 7. *The progressive regeneration of gas vacuoles in* Aphanizomenon flos-aquae *and* Microcystis aeruginosa *in darkened (D) and undarkened (L) bottles suspended in White Mere, September 1967*

L or D	Time of examination	Evidence of flotation	Gas vacuolation
L	+17 hrs.	None	None
D	+17 hrs.	None	Trace
L	+25 hrs.	Slight	Pinkish structures evident in *Aphanizomenon* only
D	+25 hrs.	V. slight	Trace in *Aphanizomenon*
L	+41 hrs.	Surface scum formed about 25% of algae floating	Vacuoles abundant in *Aphanizomenon* and present in *Microcystis*
D	+41 hrs.	Considerable surface film formed *c.* 15% of algae floating	Vacuoles present in most cells and abundant in *Aphanizomenon*

The experiment confirms that the collapse of the gas vacuoles is reversible (Bowen and Jensen, 1965), although vacuoles regenerated more rapidly in their experiment. Under the conditions of the present experiment, regeneration proceeded more or less equally between illuminated and darkened cultures, but specific differences were marked: the vacuoles of *Aphanizomenon* regenerated faster than those of *Microcystis*.

The precise function of the gas vacuoles is still a matter of considerable debate. Certainly, vacuoles provide the alga with buoyancy, as has been demonstrated in

this and many other studies. Walsby (1969) noticed that vacuoles were produced in *Anabaena flos-aquae* more abundantly when the alga was grown at low light intensities. His suggestion that filaments growing near the bottom of the lake might respond to poor illumination by producing additional vacuoles and so rising to the surface is supported by evidence in the present account. However, some planktonic blue-green algae which produce vacuoles do not continue to float to the surface, but tend to occupy discreet layers of the lake: *Oscillatoria rubescens* (Findenegg, 1947) and *O. agardhii* v. *isothrix* (Lund, 1959) have both been reported to occupy a region close to the summer thermocline. Walsby (1969) suggests that this ability is conferred through a delicate balance between production of vacuoles in low light intensities and their dilution by growth under higher illuminations. In other blue-green algae, no such property has been demonstrated. Lund (1959) also shows the distribution of *Anabaena circinalis* in the same lake, during the same period of strong thermal stratification, when most of the population was located between the surface and a depth of 2 m. It is clear that the effect of light must be different in the two species. All the species of blue-green algae studied in the Shropshire meres evidently belong to the same category as Lund's (1959) *Anabaena*. For these algae, at least, the possession of gas vacuoles appears to represent a morphological adaptation to the planktonic habit (cf. Ruttner, 1963). The cells are marginally lighter than the water and are extremely effective in preventing sinking from the upper, illuminated layers of the lake. It is only turbulence which stops them from forming a scum on the surface.

However, the incidence of gas vacuoles in blue-green algae is not confined to planktonic forms. They occur in species of *Nostoc*, *Phormidium* and *Lyngbya*, especially when exposed to strong light (Lemmermann, 1910, in West and Fritsch, 1924). Further, Cannabeus (1929) induced gas vacuole formation in species which occur naturally without them. In reviewing this and other work, which variously suggested gas vacuoles as light shields, metabolic residues and bubbles of gas produced by fermentation in anaerobic conditions, Fogg (1941) concluded that flotation seemed to be incidental.

Wesenberg-Lund (1904) believed that planktonic blue-green algae developed in oxygen deficient conditions near the lake bottom, and rose to the surface when vacuoles were produced by fermentation. As Fogg (1941) pointed out, there has been no demonstration that any of the planktonic species first inhabit mud. Examinations of the surface deposits of Crose Mere have never revealed vegetative blue-green algae, though akinetes of *Aphanizomenon* and *Anabaena* have been identified. Mud samples, containing akinetes, have been bottled in March and allowed to deoxygenate in the dark at 15 °C. but no germination was evident. On the other hand it has been demonstrated that germination takes place in open, illuminated and oxygenated water, and that populations develop under similar conditions. It would appear, therefore, that the vacuoles which develop owe nothing to the alga first inhabiting deoxygenated conditions.

Fortuitous or not, the presence of gas vacuoles in the cells of planktonic blue-green algae would appear to be of considerable ecological advantage to the planktonic habit in the normal conditions of the lake, although it becomes a liability during long calm periods.

The question as to what becomes of the algae lodged at the surface is an interesting one. Phillips (1884) and Griffiths (1925) both referred to "breaks" persisting for

several weeks but it is difficult to imagine the same organisms being viable throughout. In the laboratory, *Aphanizomenon* and *Anabaena* die within two days, falling to the bottom and discharging their pigments into the water. *Gloeotrichia* survived only a day at the surface of White Mere in a "break" on 22 July 1966, before death, discharge and considerable disfiguration. In the lake, and in the laboratory, *Microcystis* and *Coelosphaerium* have been considerably more durable. Samples of both have been kept in the laboratory for over fourteen days before any shrinkage or discharge was evident.

The end of the "break" could conceivably result from the death of the constituent algae, but normally, the bloom is terminated by the return of wind. Depending upon its intensity, and the current flotation potential of the species concerned, floating algae may either be simply recirculated or they may be carried across to the lee shore in the surface tension. Several days of gentle breezes during June 1968 resulted in the progressive removal of *Anabaena circinalis* towards the lee shore, but *Aphanizomenon* which was less buoyant was removed less rapidly. After seven days the composition of deposit on the lee shores was estimated to be 85 per cent *Anabaena*, while the lake population was almost wholly *Aphanizomenon*. Thus, the difference in the flotation potential of the two species was sufficient for one alga to have been selected by the breeze in favour of the other.

SUMMARY

The studies on the "breaking" of the meres so far carried out revealed that surface blooms occurred only during quiet weather; that the bloom was caused by a redistribution of a population of blue-green algae whose gas vacuoles permitted them to accumulate in the superficial layers of the water; that blooms were not the result of explosive increases in numbers; that vacuoles are always present in vegetative cells, and that the vacuoles may be reversibly collapsed; that the capacity to float is increased by an increase in percentage vacuolation within the cells; and that the flotation potential is influenced by the frictional resistance of the colony. These conclusions, and those of workers elsewhere, support the view of Fogg (1941) who emphasized that it was the properties of the membranes rather than those of the gas itself that were relevant to studies on the vacuoles of blue-green algae. The present observations also confirm those of Phillips (1884); the additional factors described here, that the occurrence of blooms are also influenced by the size and species composition of the population, and by its recent history in the lake, may help to explain why the meres do not "break" simultaneously.

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