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Changes in Depth and Time of Certain Chemical and Physical Conditions and of the Standing Crop of Asterionella Formosa Hass. In the North Basin of Windermere in 1947

J. W. G. Lund, F. J. H. Mackereth and C. H. Mortimer

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CHANGES IN DEPTH AND TIME OF CERTAIN CHEMICAL AND PHYSICAL CONDITIONS AND OF THE STANDING CROP OF *ASTERIONELLA FORMOSA* HASS. IN THE NORTH BASIN OF WINDERMERE IN 1947

By J. W. G. LUND, F. J. H. MACKERETH and C. H. MORTIMER, F.R.S.*

Freshwater Biological Association, Ambleside

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CONTENTS

The annual cycle of phytoplankton production in the North Basin of Windermere has been a major object of study by the Freshwater Biological Association for 30 years. The year 1947 provided the first opportunity for a combined attempt—concentrated on the water column near the deepest point—to describe in detail and to interpret the annual cycle of temperature, algal cell numbers, and selected chemical variables, with the aim of presenting an integrated picture of open-water conditions, to which other less detailed or more specialized studies may be referred.

Temperatures were measured and samples were taken for phytoplankton counts and for chemical analyses (dissolved and total silica, alkalinity, oxygen, nitrate, and phosphate) at weekly or sometimes more frequent intervals from 2 January 1947 to 12 January 1948 and at the following or sometimes more frequent depth intervals; every metre from the surface to 6 m, every 2 m to 12 m and every 5 m from 15 to 60 m.

Although marked by an abnormally cold winter and hot summer, the annual temperature cycle (figure 1) followed a normal course. After the ice had disappeared in mid-March isothermal conditions prevailed until the beginning of May. Thermal stratification became established by the end of that month; the main thermocline lay near 9 or 10 m during most of the summer, and occasional temporary thermoclines were formed and destroyed. With autumnal cooling and storms, thermocline depth increased until isothermal conditions were re-established in early December. A parallel study of changes in temperature distribution in the whole basin (the subject of another paper—Mortimer 1952) disclosed a picture of wind-induced displacements of isotherms, followed by internal seiche motion with a dominant uninodal period near 14 h. The influence of these movements on events in the selected water column is discussed. As the column lay near the seiche uninode, conditions in it did not diverge widely from average conditions in the open water.

The layer of greatest vertical density gradient (*pycnocline*) is shown stippled in figure 2. Identical stippling superimposed on later figures illustrates the strong correlation between density stratification and the development of chemical and biological discontinuities in the water column. Suppression of turbulent mixing and of associated friction gave the pycnocline the properties of a slippery interface; and the epilimnion, driven by wind or impelled by seiches, could therefore slide relatively freely without much mixing with layers below. As epilimnion depth coincided with

* Present address: Marine Station, Millport, Isle of Cumbrae, Scotland.

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that of the photic layer for much of the season, phytoplankton growth was largely confined to the epilimnion; and replenishment of nutrient salts from below was impeded. While turbulence in the epilimnion was sufficient to keep diatom cells in suspension, this was not so in the pycnocline, where they could sink passively through with little chance of return.

The diatom *Asterionella* is the dominant member of Windermere phytoplankton. A general account of the seasonal cycle in the North Basin is given for the period 1932–61. The cycle of events in 1947, which followed the normal course for the period 1932–61, is described in detail with the aid of diagrams showing the distribution of live cells (figure 3), total cells (figure 4), dead cells (figure 5), and number of cells per colony (figure 6) in depth and time. The crop was low in mid-winter, started to increase in early spring, and reached maximum numbers (over 5 million cells per litre in the 0 to 8 m water column) in early June. As the population increased there was a corresponding fall in concentration of silicate in the water (figure 7) to a level at which there was not enough remaining to support one more division of the standing crop. When, in early June, silicate supply could no longer meet the demands of diatom growth, there was a heavy mortality and a catastrophic decline in cell numbers in the epilimnion, until, by late August, there was less than one live cell per litre in the 0 to 5 m water column. Dead cells reached a maximum some weeks after the live cell maximum, but processes removing cells from the epilimnion eventually reduced total numbers (and total silica, figure 8) there to very low levels. Some silicate replenishment from inflows later occurred, but the main feature of the post-maximum phase was loss of cells through the pycnocline, because single dead cells, and colonies containing a high proportion of dead cells, sank relatively rapidly (figures 5, 9).

During this phase there was some increase of numbers in the upper layers of the hypolimnion. But this was only temporary, and there was no accumulation in the lowest layers of the water column, although a layer of dead and dying cells was found on the mud surface.

The relationships between the biological situation—in particular the changes in diatom population, already outlined—and the physico-chemical environment are discussed in the light of fluctuations in the chemical variables listed in the first paragraph of this summary.

Changes in the distribution of dissolved and total silica (figures 7, 8) were closely related to diatom growth, and are here used to infer the magnitude of total production of diatoms and rates of loss by sinking (figure 9).

Respirational consumption of oxygen in the hypolimnion occurred both at the mud surface and in the free water. The distribution of oxygen concentration in depth at the end of summer stratification (figures 11, 13, and tables 1 to 3) suggests, either that the rate of consumption at the mud surface measured in the laboratory is higher than that occurring in the lake, or that considerable downward migration of oxygen occurred within the hypolimnion.

Total respirational oxygen consumption is used, in conjunction with sedimentary and dissolved organic carbon estimates, to infer a rough carbon budget for the lake. It is concluded that the carbon fixed by phytoplanktonic photosynthesis was a small proportion of the total organic carbon entering the lake.

Changes in alkalinity (figure 10) and nitrate concentration (figure 14) in the epilimnion reflected seasonal changes in the inflowing water; and there was evidence (particularly from distribution of oxygen saturation, figure 12) of horizontal flow, out over the lake surface, of water warmed in shallow littoral areas.

The concentration of phosphate, always near the lower limit of reliable estimation, was generally less than 1 μg/l. in the epilimnion and about 2 μg/l. in the hypolimnion. These small concentrations were, however, sufficient to support the observed maximum diatom crop.

No significant contribution to the concentration of dissolved nutrients was derived from the deep sediments, the surface of which remained aerobic throughout the period observed.

I. Introduction

The founders of the Freshwater Biological Association recognized that a fuller understanding of the mechanisms controlling plankton production in lakes must be based on regular, quantitative observations extending over many seasons, not only of plankton

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populations, but also of the relevant physical and chemical variables. Numerous studies have therefore been made of the water and of the organisms in Windermere North Basin (reviewed in Pearsall, Mortimer, Lund & LeCren 1959), which is divided from a southern basin by shallow sills and islands (Mill 1895; Mortimer & Worthington 1942). The two basins, although qualitatively similar in chemistry and biology, show consistent quantitative differences and may be regarded as separate.

The year 1947 presented the first opportunity for a combined*, intensive investigation in the North Basin. Attention was almost entirely concentrated in the deep region, and the object was to describe and interpret the annual cycle of temperature, algal cell numbers, and chemical variables at Station B (Mortimer 1952), approximately 60 m deep at that point. At the same time a study of wind-induced water movement, which bears on the interpretation of events at Station B and which forms the subject of another paper (Mortimer 1952), developed from surveys of temperature distribution in the whole basin.

The annual cycle of events described here is repeated with relatively minor differences each year, judging from the less detailed and less complete observations made in almost every year for over a quarter of a century (*Annual Reports of the Freshwater Biological Association*; Pearsall *et al.* 1959). The distribution of the various features in depth and time at Station B is also closely similar to that of the open waters of the North Basin as a whole, making due allowance for the variations in depth. It is only in shallow water, or near inflows, or at the antinodes of internal seiches (see § III), or in sheltered bays or in the larger reed-beds, that conditions may be markedly different from the open water. For example, on 16 September 1947, the alkalinity of the epilimnion expressed as mg/l. of $CaCO_3$ varied in the open waters from 8·6 to 8·8 and in sheltered bays only from 8·6 to 9·2. At this time marked differences from the open water were found in the following localities only: in the reed-bed at the north end (Sandy Wyke) where a stream draining the Coniston Limestone passes into the lake (9·5 to 9·8 mg/l. $CaCO_3$); at the mouths of the inflow from Blelham Tarn (19·7 mg/l. $CaCO_3$); and at the main inflow—the Brathay–Rothay confluence (4·5 mg/l. $CaCO_3$). (For maps see Mill 1895; Godward 1937.) In all these areas the depth of water ranged from one-tenth to one-fifth of that of the epilimnion.

The findings reported here therefore permit a representative picture to be built up for the open water, to which more limited or specialized investigations may be referred. The main results, which are largely descriptive, are presented in depth–time diagrams, on which appropriate isopleths (lines of equal numbers or concentrations) have been drawn free-hand. The dots show the depths at which samples were taken for the estimations concerned. Depth–time diagrams may lack the precision of other graphical methods or tabular presentations, but what is more important here is that numerous data can be presented in one figure. The fair copies of the figures were made by Mrs J. Worthington, Mr A. E. Ramsbottom and Miss M. L. Wright.

* Dr B. M. Knudson (Mrs Kipling), Mr D. Gawen, Mr W. H. Moore, and at times Dr H. M. Canter (Mrs Lund) and various members of the Association's assistant staff under the direction of Mr G. J. Thompson gave valuable help.

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II. Methods

Estimation of Asterionella *cell numbers*

The samples used for quantitative work were collected with a rubber hose (Lund 1949; Lund, Le Cren & Kipling 1958) or with a Friedinger water sampler. Aliquots from these samples were used for chemical analysis. The rubber hose was used to sample the 0 to 5 m water column, which during the first 10 months was also covered by Friedinger samples at the surface and at intervals of 1 m. The size of the standing crop was determined from counts of one hundred or more colonies where possible. In January, February, late October to the end of 1947, and in January 1948, the number of colonies present was small so that twenty-five to seventy were usually counted. During August, September and early October so few colonies were present in the top 10 m of water that accurate counts were rarely possible. The errors in counting live cells are those statistically inherent in the method; human errors are insignificant (Lund *et al.* 1958). The potential error in counting dead cells is greater and variable. If the majority of the dead cells are still united in colonies the counts closely approach those of live cells in accuracy. On the other hand, isolated cells are easily overlooked, particularly if other particles are abundant. Moreover, there is a larger human error in deciding whether or not to count fragments of cells. Dead, empty cells often break, and pieces were only counted as 'cells' if the observer decided they were more than half the length of a whole cell. Even if almost all such decisions are correct, the number of dead cells recorded will be on the low side if, as often happens, the number of fragments shorter than half exceeds those longer than half a cell length. The counts for dead cells are, therefore, under-estimates, particularly during the catastrophic decline in numbers after the spring maximum, but they do reflect with reasonable accuracy the seasonal changes in abundance.

Chemical analysis of water samples

With the exception of those samples taken for the determination of dissolved oxygen and total silica, all samples were filtered through Whatman 541 papers which had been washed in distilled water before use.

Silicon

All concentrations of silicon are expressed in terms of silica (SiO_2) since the precise chemical structure of the various silicon compounds present in solution or in suspension is not known. That part of the dissolved silicon which reacts directly with molybdate is described as 'dissolved silicate', or sometimes as 'dissolved silica'. Silicon incorporated into diatom cells, and which is normally in suspension and does not react directly with molybdate, is referred to as 'silica'. The sum of these—'total silica'—is determined by the method described in the next paragraph.

Dissolved silicate was determined by the colorimetric method of Diénert & Wandenbulcke, as modified by Atkins (1923). Determination of total silica was made by heating 100 ml. samples of well-shaken and unfiltered water to 100 °C in 'Monel' metal beakers to which three pellets (about 0·5 g) of A.R. potassium hydroxide had been added. After approximately 30 min at 100 °C, the samples were neutralized in the 'Monel' beakers by dropwise addition of approximately 50 % HCl using phenolphthalein as indicator.

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After neutralization the samples were transferred to glass vessels, the volume re-adjusted to 100 ml. and the dissolved silicate (now comprising the whole of the silicon initially present both as silicate and suspended silica) determined in the usual manner. Blanks on the reagents were run simultaneously. The blank was normally small.

Oxygen

Dissolved oxygen was determined by the method of Winkler (1888) unmodified. The reagents were added to the samples in the field. No modification of the original method was thought to be necessary since the water under examination was substantially free from interfering substances.

Alkalinity

The 'alkalinity' was measured by titration of 100 ml. samples with 0·01 N HCl to an end-point in the vicinity of pH 4·5 using as indicator, either B.D.H. '4·5', or a mixture of methyl red and bromcresol green. This titration measured, in effect, the concentration of bicarbonate ion, but the result was expressed as the equivalent concentration of calcium carbonate. This facilitates comparison with other data, frequently expressed in the same units. The alkalinity was regarded as a conservative property which could be used in the identification of water masses.

Nitrate

Nitrate was determined colorimetrically by treating the residue remaining from the evaporation of 100 ml. of the sample with phenoldisulphonic acid and measuring the yellow coloration produced on dilution and neutralization against standards.

Phosphate

Phosphate was determined colorimetrically by reduction of the phosphomolybdate by means of stannous chloride and comparison of the blue colour resulting with standards after the manner of Denigès (1921). The concentration of phosphate phosphorus was, however, normally below the limit of accurate measurement, i.e. below 0·001 mg/l. P.

III. The distribution of temperature and density in 1947

The depth distribution of temperature, measured at weekly or more frequent intervals by a thermoelectric thermometer, reading to the nearest 0·05 °C and described in Mortimer (1952), is plotted in figure 1. The weather in 1947 was unusually cold in winter and warm in summer. The whole surface of the South Basin and almost all that of the North Basin was frozen during March. This was the only year that virtually the whole of the lake has been frozen since observations by the Freshwater Biological Association began in 1936 and, so far as can be ascertained, the second occasion in this century.

After the ice disappeared in mid-March the basin remained isothermal, and therefore well mixed, while warming up to nearly 6 °C by the beginning of May. By the end of that month the lake was well stratified with a thermocline at 5 m depth and a surface temperature of 14 °C. The development of this thermal stratification was illustrated in Mortimer (1952, fig. 4), which also makes it clear that changes in the temperature structure of the water column at Station B could not be explained by vertical heat transfer alone,

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and that horizontal transport (advection) of water masses of differing temperature was taking place. The nature of this motion, in terms of wind-induced displacements followed by internal seiches, was inferred from detailed studies of changes in temperature distribution in the whole basin during May and June. The findings are the subject of other

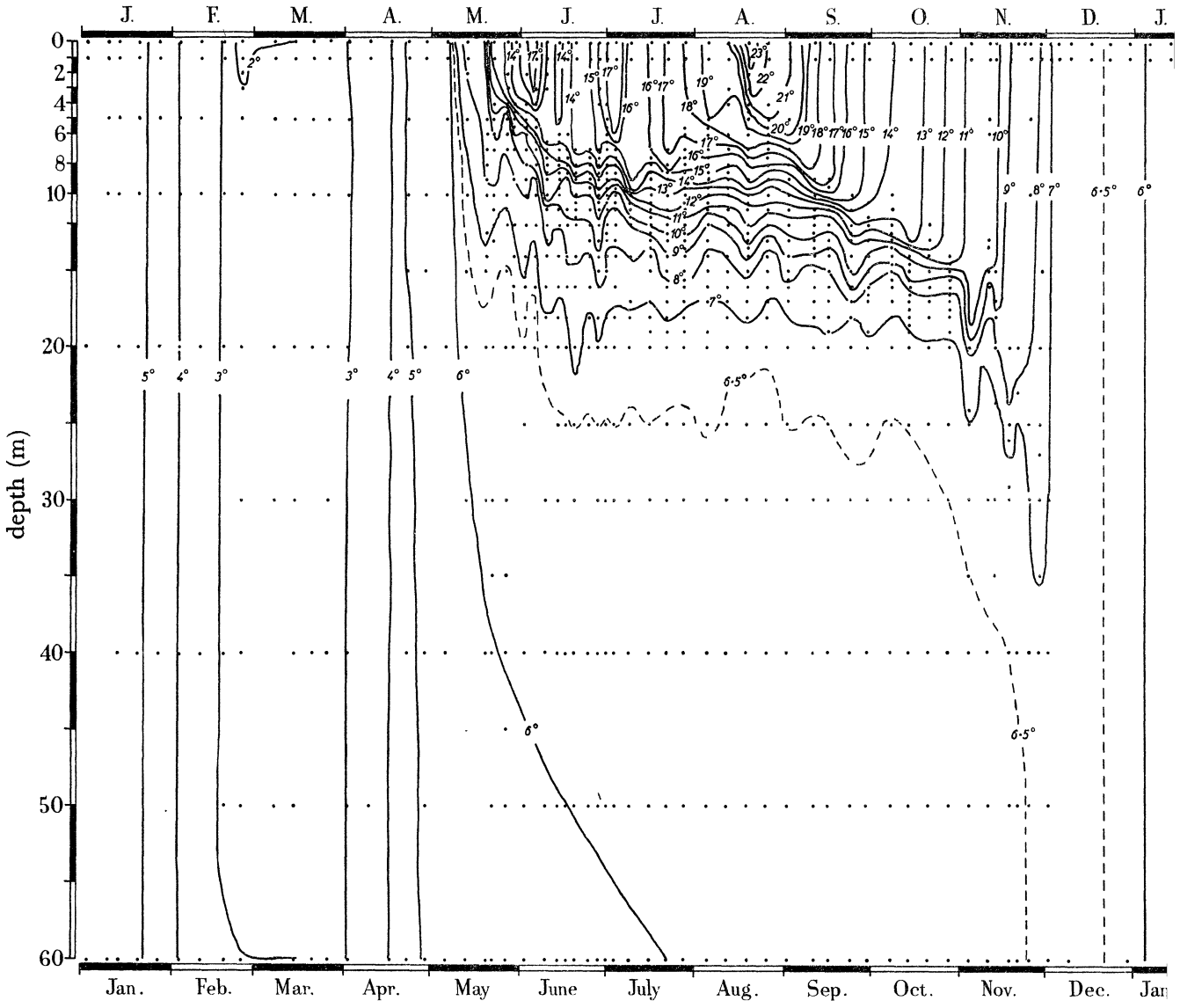

FIGURE 1. Temperature (°C). This and the following figures illustrate the distribution in depth and time of certain variables at Station B (60 m depth) in Windermere, North Basin, during 1947. The method by which these depth–time diagrams are prepared is explained at the end of the Introduction.

papers (Mortimer 1952, 1954), and only as far as they bear on the interpretation of figure 1 and on the distribution of other variables in the water column at Station B, need they be considered here.

A uninodal internal seiche with a period of about 14 h was the dominant feature of motion and, as Station B was not far removed from its node, vertical oscillations of the layers in the water column produced there by that seiche were small in comparison with

those observed near the extremities of the basin. The corresponding horizontal displacements, however, were near their maximum at B and took the form of to-and-fro excursions of the water layers with different phases at different levels and with horizontal amplitudes that frequently exceeded 1 km in the epilimnion. At the same time, wind displacements and seiches of higher nodality (particularly the binodal) sometimes produced oscillations in isotherm depth of several metres at B. Figure 1 (which presents temperature measurements made when water samples were taken for counting and analysis) provides evidence of such oscillations during May and June; and even larger oscillations came to light during the interval 26 May to 21 June, when the fequency of observation was increased to 40 profiles in 27 days (Mortimer 1952, fig. 6).

It may therefore be concluded that the vertical structure of the water column at B, both in respect of temperature and of chemical and cell concentrations, was influenced—on any one sampling occasion—not only by the previous history of such factors as cell growth and heat exchange through the lake surface, but also by the previous history of motion of one or more of the water strata. Horizontal motion was rarely absent at any depth, and the velocity and direction of motion varied with depth, the main component normally following the long axis of the basin. There was, however, evidence of transverse motion as well (Mortimer 1952, fig. 7).

While any particular set of samples may, therefore, have been unrepresentative of the mean conditions prevailing in the basin, the frequency of sampling during this investigation was sufficient to enable oscillations produced by wind action and seiche motion to be distinguished from long-term trends (cf. figure 1). Nevertheless, an attempt was made to determine the order of magnitude of the short-term deviations. On five occasions during the period 5 to 14 June estimates were made of the mean temperature distribution in the whole basin based on isotherm depths observed at four stations (including B) along the main axis. On no occasion did a thermocline isotherm at Station B (Mortimer 1952, fig. 6) differ in depth by more than 2 m from the corresponding whole lake 'mean'. On any one occasion the B isotherms lay, with minor exceptions, all above (+) or all below (−) the whole lake means; and the following average deviations of the B isotherms from the lake mean will indicate how far other conditions observed at B may be taken as representative of the lake as a whole: 5 June, −0·7 m; 9 June (p.m.), +0·6 m; 10 June, +0·3 m; 13 June (p.m.), −0·4 m; and 14 June, +0·5 m. These small deviations reflect the fact that Station B lay near the uninode of the internal seiche; much greater deviations were found at other stations.

The density stratification associated with the thermocline is illustrated in figure 2, which is a transformation of part of figure 1 in terms of density, neglecting the effect of chemical stratification. The region of greatest vertical density gradient (2×10^{-4} g ml.$^{-1}$ m^{-1} or more), here denoted as the *pycnocline*, is shown stippled; and identical stippling superimposed on later figures illustrates the correlation between the pycnocline and the development of chemical and biological discontinuities in the water column. From the point of view of this study, the density stratification in the pycnocline has two important consequences: (i) it tends to suppress turbulence and mixing; and (ii) it consequently reduces the friction opposed to shearing motions. This gives the pycnocline the properties of a slippery interface. The epilimnion, driven by the wind or impelled by seiches, can

therefore slide relatively freely without mixing much with the layers below. If epilimnion depth approximately coincides with that of the photic layer, plant growth is largely confined to this layer, and replenishment of nutrient salts from below is impeded. Equally, turbulent transport of diatom cells through the pycnocline is slowed down but, as a result, the passive sinking of the cells in this layer becomes important. In the epilimnion, turbulent transport rates are much higher than the sinking rate; and the cells are kept in suspension. In the pycnocline this is not so; and cells which arrive in this layer sink through it with little chance of returning to the surface.

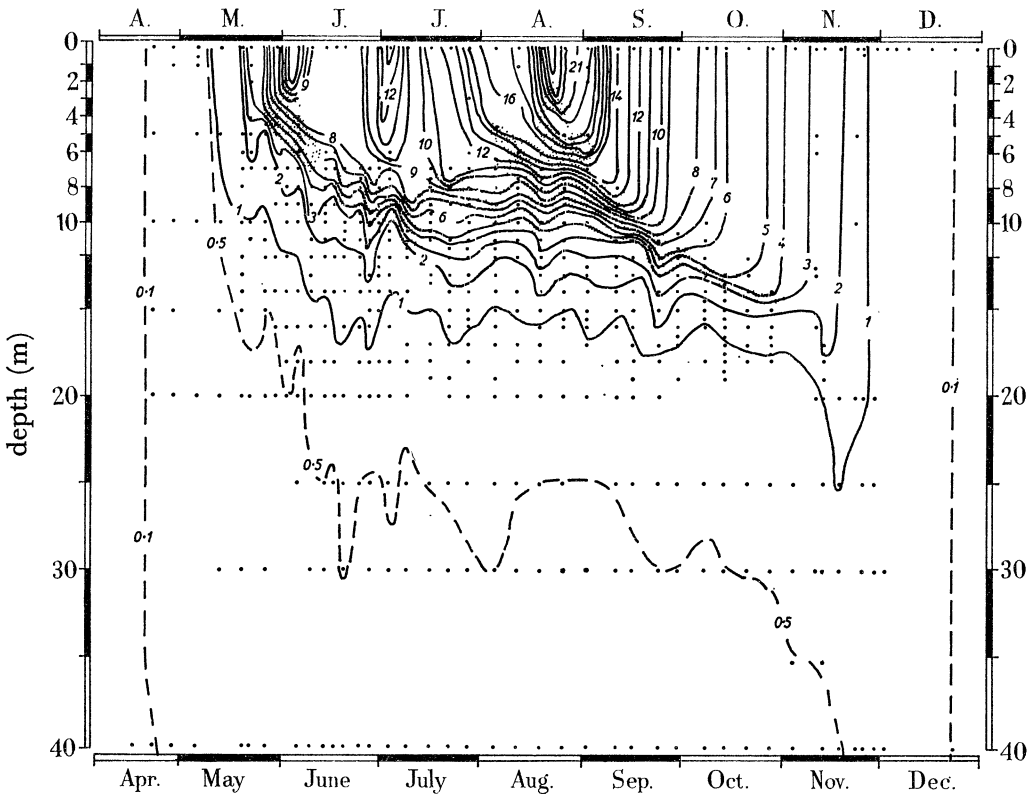

FIGURE 2. Density decrement ($d \times 10^4$), derived from figure 1, on the assumption that temperature is the sole density-determining factor; d is defined as the difference between unity and the density (g/ml.) of pure water at the temperature concerned. The stippled area, which is also reproduced on some later figures, shows the depth–time distribution of the greatest vertical density gradients (2×10^{-4} g ml.$^{-1}$ m^{-1} and above, viz. the pycnocline) associated with the thermocline.

The history of the 1947 thermocline (pycnocline) in Windermere followed a pattern common in temperate lakes. The main thermocline was well established at about 8 m by late spring and fluctuated between 9 and 10 m during the summer. Secondary thermoclines were formed during hot spells, for instance early July and late August, and later destroyed by wind mixing. In August, temperatures exceeding 23 °C were recorded in the uppermost layers, and over 20 °C to 5 m depth. In most years the maximum temperature in the central regions is either less than 20 °C or very little in excess of it. Since 1947, 20 °C has only been reached at 5 m depth in one other year.

Progressive loss of heat from the basin during the autumn, coupled with the mixing effects of storms, forced the thermocline to below 15 m and finally effected complete mixing of the basin at the beginning of December. It is interesting to note that, during the latter half of November, the vertical density gradient was less than 1×10^{-5} g ml.$^{-1}$ m^{-1}, and yet stratification persisted.

IV. The seasonal cycle of *Asterionella*

(i) *General account for the period* 1932–61

The biology of *Asterionella* in Windermere has been the subject of several investigations (Pearsall *et al.* 1959). The cycle of events is similar in most years, the chief variation being the size of the maximum standing crop. Such years may be considered as 'normal'; and 1947 was one of them. The normal cycle is outlined in the following paragraphs.

At the beginning of the year the numbers of *Asterionella* are low, either because the rate of loss of whole cells and of cellular material (respiration losses) exceeds growth, or loss and gain are roughly balanced. The factors limiting the crop are physical; nutrients are present in excess of needs, and the rate of growth is limited by low light and temperature. The main source of loss is by outflow; losses from sedimentation onto the deposits, ingestion by animals, and parasitism by fungi are of minor importance. That loss by sedimentation is small is shown by the close agreement between the decrease in dissolved silicate and increase in silica incorporated into the cells of *Asterionella* in years when the maximum is reached before thermal stratification sets in (unpublished data). The wetter and colder the winter the smaller the size of the crop by the end of it.

By about the middle of March increase by growth exceeds all sources of loss, and this enhanced rate of growth is caused by increased light intensity and length of day. The temperature of the water is still very low, indeed usually close to its minimum. In the succeeding period the crop roughly doubles itself each week and, once it exceeds a million cells per litre, a marked and accelerating fall in the amount of silicate dissolved in the water follows. The maximum crop is present when the silicate content, expressed as SiO_2, has fallen to about 0·5 mg/l., from a winter value in the range 1·5 to 2·5 mg/l. Thereafter, though dissolved silicate content continues to fall, the crop increases very slightly or often not at all, as more and more of the cells are dying or dead. The maximum is usually reached between the second half of May and the first week in June. Before this, however—commonly early in May—the water becomes thermally stratified. Growth is restricted to the photic zone, that is from the surface to about 8 to 10 m which coincides approximately with the depth of the epilimnion. Numerous experiments on cells in culture fluid or in lake water (in laboratory and lake experiments) show that, no matter how fast they grow when in the light, no detectable growth takes place on transfer to the dark. Below the thermocline light is insufficient for growth so that, in the hypolimnion, utilization of dissolved silicate ceases once the water is stratified. During the latter half of June and July the crop decreases with great rapidity in the epilimnion, and the proportion of dead to live cells rises sharply. There are now large numbers of colonies containing few live cells, and the number of single cells—mostly dead—is also considerable. A mass of bacteria grow attached to the dying cells and colonies. During the later part of the summer the crop may fall to very low levels in the epilimnion, usually to ten or less cells per litre

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as against five to ten million at the time of the maximum. The dissolved silicate concentration remains low, of the order of 0·1 to 0·2 mg SiO_2/l. In the hypolimnion the decrease in numbers is much slower, though by October only one or two hundred cells per litre may be present.

In the absence of sufficient diatoms to utilize new supplies of silicate from inflows during the summer, the silicate content of the epilimnion water rises at a rate which depends on how wet the year is. By late summer or autumn the concentration has reached 0·5 mg SiO_2/l. or more, and a new increase in the crop follows. However, this autumn maximum is small and rarely more than 200 cells/l. During this period the temperature of the water is falling and the epilimnion consequently deepens—a change mainly caused by the autumnal high winds. At the same time the decrease in numbers in the hypolimnion has continued, and the usual position from late October onwards is that the crop in the hypolimnion is less than that in the epilimnion. At the same time, daylength and light intensity are falling, and the rainfall is commonly high so that losses of cells by outflow increase. By the first week in December the lake is once more isothermal and winter conditions return.

The number of live cells per colony commonly reflects the environmental conditions (Gardiner 1940–41; Pearsall, Gardiner & Greenshields 1946), though it is not known which factors have the greatest effect. If a population is dying, the average must fall; but even when dead cells do not form a significant part of the population, the number per colony tends to be higher when conditions for growth are potentially most favourable. Thus they may be high even when the population is kept low by physical factors, for instance, loss from floods or short daylength. But if the amount of light is so low that the cells cannot multiply at all, then the number of live cells per colony slowly falls, a feature always seen when colonies in a favourable chemical environment—for instance, in a culture solution containing a small population—are kept in the dark. In nature a fall in the average number is commonly observed when the nutrient supply approaches minimal values which limit the rate of growth.

Many other planktonic algae have a less regular cycle. The major changes in the phytoplankton as a whole are described in the next section.

(ii) *Detailed account for* 1947

The 1947 survey provides, for the first time, a detailed picture in time and depth of the seasonal cycle outlined above. From 2 January to 5 May the water was isothermal, except for those parts of the basin which were under ice in February and March. The amounts of dissolved and total silica (figures 7, 8) and the numbers of live and dead *Asterionella* cells (figures 3, 5) showed insignificant differences from the surface to the bottom, except under the frozen areas (see below). The concentrations of dissolved silicate showed some changes, but these depended on the amounts coming into the lake in solution. The standing crop rose from 2 to 200 cells/ml. but the amount of silica incorporated into 2×10^5 cells/l. is so small (*ca.* 30 μg SiO_2/l.) that it produced no significant change in the amount in solution. Loss of silica to outflow in the form of cells was approximately compensated by the gain of dissolved silica from the inflows. Had there been a substantial loss to or gain of cells from the deposits this would have been reflected in changes in the total silica in the water

column. The slight irregularities in the size of the standing crop in the upper half of the water column at the end of February and in March were caused by a partial covering of ice. A complete ice sheet was never present, and the parts covered varied in position and area during this period. As in the case of *Melosira italica* (Ehr.) Kütz. subsp. *subarctica*

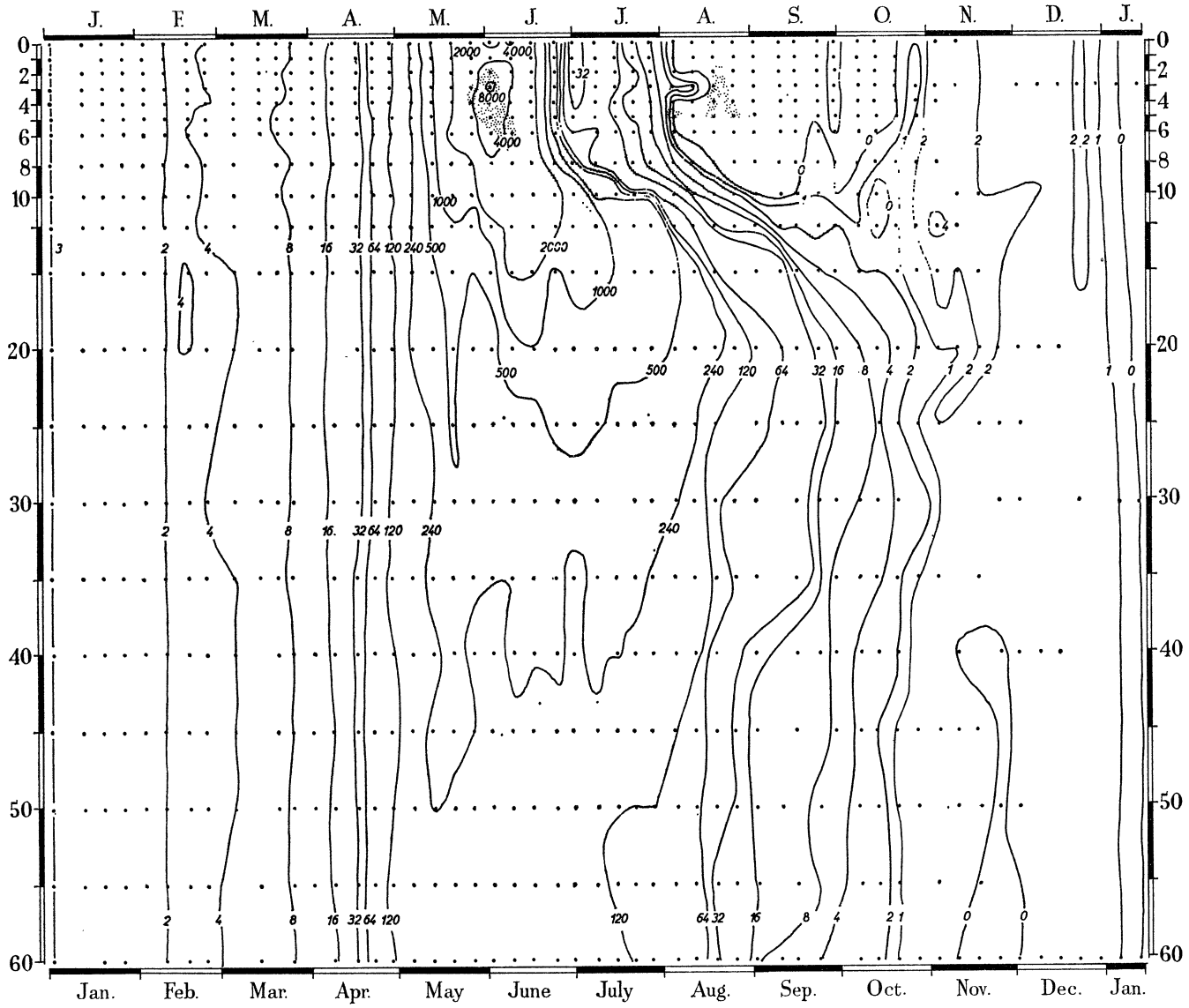

FIGURE 3. *Asterionella*, the number of live cells per ml. For further details see the legends of figures 1 and 2.

O. Müll (Lund 1954, 1955, 1959), the inverse stratification led to an uneven distribution of *Asterionella*. This effect was, however, slight; for apart from the incomplete ice-cover, the rate of sinking of *Asterionella* is far less than that of *Melosira* (Lund 1959). Indeed the early effects of ice-cover are a diminution in numbers just below the ice and an increase at depths between 2 and 5 m, because of aggregation there of the cells which have sunk from above and the growth of cells at these lower levels. The amount of growth under ice naturally varies with the thickness of the sheet and its texture; if snow is absent, light penetration is

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good. Table 2 in Lund (1959) illustrates the stratification in the north and south basins of the lake.

The number of live cells per colony was about 7 on the average (figure 6) during this period. After the beginning of the year, the average fell to under 6 at most depths (middle

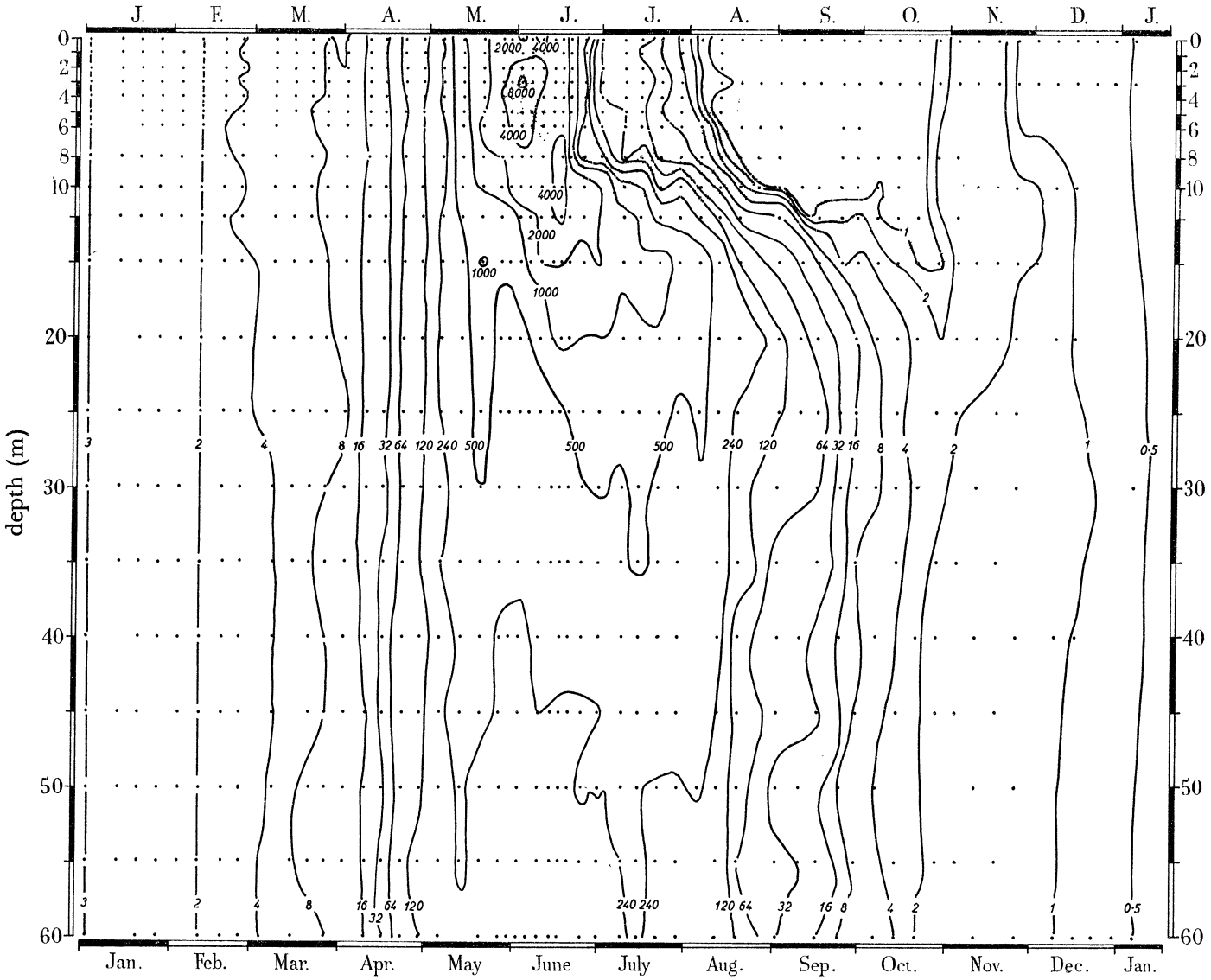

FIGURE 4. *Asterionella*, the total number of cells (live and dead) per ml. For further details see the legends of figures 1 and 2.

of January). It then rose again, and in February and early March was fairly commonly over 8 in the upper layers. This change was probably a reflexion of an increased rate of growth and of stratification under ice, which kept cells in the photic zone (except close to the ice sheet) for longer periods than under fully turbulent conditions, so that they received more light. The average next fell back to about 7 and showed a further rise at the very end of this period when the water was warming up, but before definite thermal stratification had set in.

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After 5 May thermal stratification began, and the distribution of *Asterionella* in depth at once altered (see also Lund 1949, fig. 6). The standing crop rose steadily in the upper third of the water column, especially in the top 10 m which covered most of the epilimnion and the photic zone; but below this the growth-rate decreased with depth. Below 30 m the

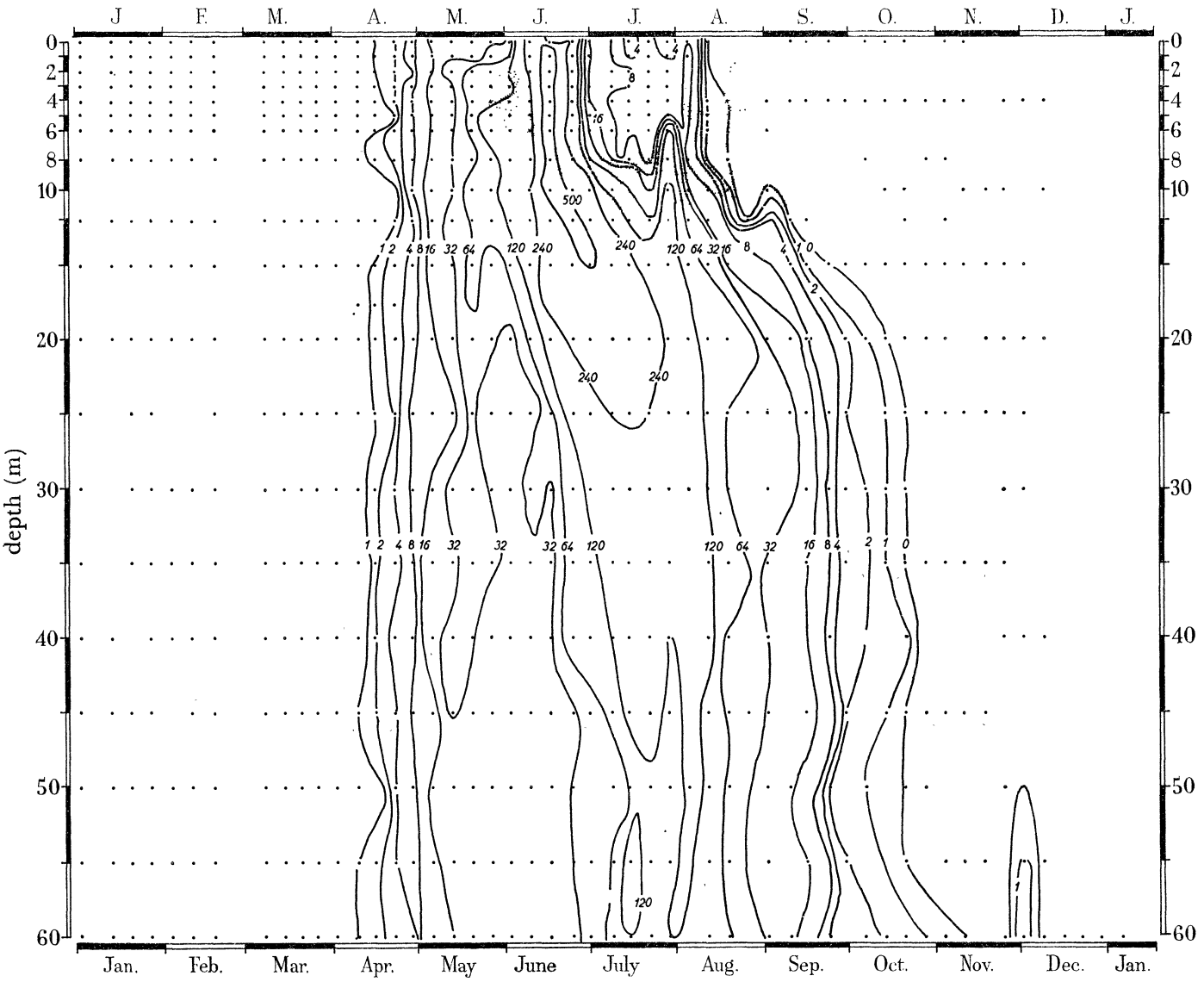

FIGURE 5. *Asterionella*, the number of dead cells per ml. For further details see the legends of figures 1 and 2.

increase was nowhere equivalent to more than one cell division per week, and below 50 m to much less than this. Since 30 m is well below the photic zone, any increase below this level must have been derived from cells passing from the epilimnion through the thermocline. In culture experiments in the lake extending over 6 complete years no detectable growth ever took place in any bottle suspended at a depth greater than 12 m or in control bottles kept in the laboratory in the dark during each weekly experiment (unpublished results, and see Lund 1949).

By early June the maximum crop was reached, with nearly 8 million cells per litre at 3 m depth and an average exceeding 5 million over the whole 0 to 8 m water column (figure 4). The absolute number of dead cells also rose during this period (figure 5) but proportionately there was no significant change; the ratio of live to dead in the 0 to 8 m water column remained at about 50 to 1.

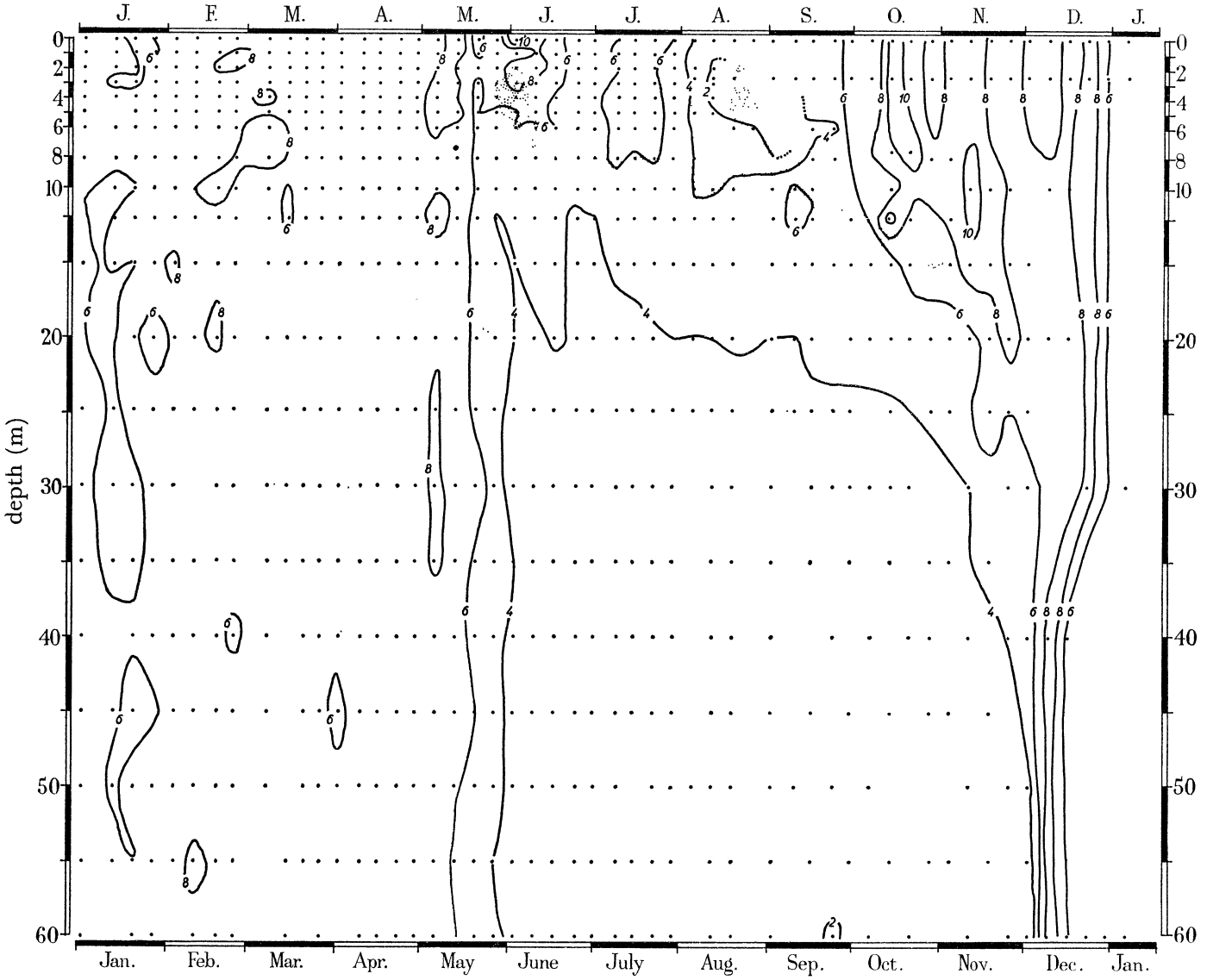

FIGURE 6. *Asterionella*, the number of cells per colony. For further details see the legends of figures 1 and 2.

The number of live cells per colony showed marked changes (figure 6). The average fell to about 6 between 5 and 12 May but showed little difference with depth. Thereafter large differences appeared between the upper and lower parts of the column. The closer to the surface, the higher the average rose until by the time of the maximum it exceeded 11 at the surface, while it was below 6 at 6 m and was 5 or less between 10 and 60 m. The highest values for the 0 to 5 m water column, 7·7 to 10·8, were attained between 1 and 12 June when the number of cells/l. varied between about $3\frac{1}{2}$ and $5\frac{1}{2}$ million. Even on

16 June, when the numbers had fallen to $2{\cdot}5 \times 10^6$/l., the number of cells per colony in the 0 to 5 m column was still over 7, while it ranged from 3 to less than 2·5 between 40 and 60 m. Since this was also the period when the dissolved silicate fell to a very low value in the 0 to 5 m water column (0·15 to 0·25 mg SiO_2/l. by 16 June) it may appear that the relation between the number of cells per colony and the environmental conditions is the reverse of that stated earlier. However, it has been pointed out (Lund 1950*b*, pp. 24–25; cf. also Talling 1957, p. 42) that limitation of growth by silicate shortage differs from some other types of limitation in that, in the light, the cells are apparently stimulated to continue growing even in the absence of sufficient supplies, and this is in consequence a self-destructive process. Therefore until the very end of the growth period the population continues to increase at a rate which is virtually unaffected by the ever-decreasing amount of silicate available. This relationship may be contrasted with others well known from experimental studies, particularly in large algal cultures, where reduction in the amount of light or carbon dioxide causes a diminution in the growth-rate well before, or in the absence of, any decrease in the size of the living population.

In addition, figure 6 shows that high average numbers of cells per colony were only attained in the top few metres; especially in the top metre. There can be little doubt that they are also a reflexion of the otherwise favourable conditions for growth early in June and that this in turn was related to the warm weather (figure 1). The relatively hot water flowing in from the rivers tended, particularly in the less windy periods, to flow over the surface of the lake as a 'skin' rich in nutrients. The synchronous rise in alkalinity (figure 9) bears out this view. Since the silicate in the inflows (see p. 276) remained relatively high, even this nutrient was being added in appreciable quantities to the uppermost layers. The values for dissolved silicate in the surface layers of the lake, however, showed no increase, because the population of *Asterionella* was so large that any addition was immediately utilized. This, then, was a period during which the rate of supply and uptake of silica were in delicate balance and, once the rate of supply no longer kept pace with the biological demand, the equilibrium was upset and the catastrophic decline in numbers of cells per unit volume and per colony followed.

After the first week in June, when the silicate concentration fell below the limiting value of approx. 0·5 mg SiO_2/l., a rapid reversal of the previous changes in the standing crop took place in the epilimnion until, by the second half of August, there was less than one live cell per litre in the 0 to 5 m water column. With the exception of a short period early in July discussed below, the dissolved silicate also lay close to or below 0·5 mg SiO_2/l. (figure 7). The rates of fall in the total cells and total silica lagged behind those of live cells and dissolved silica (compare changes in 0 to 10 m water column in figures 4 and 8, 3 and 7) because the maximum crop of dead cells (figure 5) was reached some 3 weeks later than that of live ones (figure 3). All these changes are understandable if the differences between total and dissolved silica are directly related to the rate of removal of cells from the epilimnion. There is clear proof of this relationship in the fact that the total silica did eventually fall to levels of concentration similar to those of dissolved silica. Moreover, if the cells in the epilimnion had been lost largely by outflow, there would have been a synchronous marked increase in the amount of dissolved silicate present through replacement from the inflows. It is true that silicate concentration in the inflows does

fall somewhat in summer, partly because of diatom growth, mainly non-planktonic, in the lakes (e.g. Grasmere, Rydal Water, Elterwater, Blelham Tarn, Loughrigg Tarn) and rivers in the drainage system (see map in Knudson 1954). However, it never fell to low levels; even in mid-July the main inflow, the Rothay–Brathay confluence, still contained 1·9 mg SiO_2/l. and by the beginning of September 1·2 mg/l.

It is clear from the changes in the rate of decline in the standing crop with depth (figures 3 to 5) that colonies containing a high percentage of dead cells or single dead cells sink relatively rapidly. The effect of the steep temperature (and therefore density) gradients in the water in the thermocline (figures 1, 2) can be seen in the displacement of the isopleths of the standing crop (figures 3, 4) after the onset of thermal stratification (5 May onwards). For dead cells this effect is delayed in time (figure 5) because no marked increase in the death rate took place until after the total crop began its catastrophic decline (first week in June). At first, when the thermocline was near the surface, the largest numbers were found in it and in the epilimnion. Later, as the thermocline came to lie at a lower level and stabilized its position (July to October), the largest standing crop was found first in this zone (10 to 15 m) and later in the hypolimnion, for then (September onwards) few cells were left which could be removed from the epilimnion and thermocline.

The variations in the number of live cells per colony are those to be expected if the above interpretation of the changes in the position of the maximum standing crop is correct. The number per colony remained relatively high in the epilimnion until mid-August, when it was nearly free of cells, and low in the thermocline and hypolimnion. From mid-June to August the average was about 6 in the epilimnion, 4 in the thermocline, and 3 in the hypolimnion. A relatively small amount of growth is possible in the upper part of the thermocline, particularly if the weather is fine.

The course of the isopleths of cell numbers during July (figures 3, 5), when cells were being rapidly lost from the epilimnion to lower layers, shows large vertical gradients in numbers near the upper part of the thermocline at about 10 m. This suggests that turbulence had been reduced in this layer to a level at which the sinking rate of the cells became important. While at higher levels, particularly during isothermal conditions, turbulence could maintain a relatively uniform depth distribution of cells (as when the whole lake was isothermal), any cells or colonies which approached the thermocline entered a zone of decreased turbulence, and had a high chance of sinking into and through the thermocline itself. Their chances thereafter of returning to the epilimnion, except occasionally— for instance, at the windward end of the lake when isotherms are displaced by storms (Mortimer 1952)— were extremely small.

The changes in the hypolimnion are those to be expected on physical grounds, in the absence of sufficient light for growth. Here the isopleths, after the *Asterionella* maximum in the epilimnion, approached the vertical (figures 3 to 5) except in the upper part where the population was, at first, augmented by a steady and increasing rain of cells from the epilimnion via the thermocline into a region of low turbulence. But before long this augmentation ceased, when the population in the epilimnion had become very small. There was no accumulation of the cells in the lowest part of the water column (figures 3, 4), which means that the cells reaching the bottom were mainly held on the surface of the

deposit. The mud surface in cores taken with a Jenkin surface mud corer at this time were found to be greyish and flocculent with the mass of dead and dying cells.

The thermocline therefore acts as a 'sink' with respect to the epilimnion. When thermal stratification starts, the 'bottom' of the lake rises, as far as growth of *Asterionella* is concerned, from the level of the true bottom to that of the upper limit of the thermocline. In the deepest part of Windermere North Basin this represents a depth change of about 50 m or over 80 % of the total depth.

During July an increased supply of silicate from inflows, reflected in 'total silica' (figure 8), led to a renewal of growth of *Asterionella* in the 0 to 6 m water column. The crop had decreased very rapidly in the preceding fortnight, from approximately 2·5 to $0{\cdot}03 \times 10^6$ cells/l. It then rose to about $0{\cdot}05 \times 10^6$/l. This renewal of growth is of particular interest in relation to the alleged physiological dormancy of the cells of *Asterionella* after the spring maximum (Storey 1942, 1944; Pearsall *et al.* 1946, pp. 19–20: see also the views of Chu 1943, 1945), a view with which Lund (1949, see especially pp. 402–5) disagreed. Lund's view, from observation and experiment, is that if any cells do pass into such a stage they form a very small minority of the population and that, in any period, the growth of the diatom is directly related to the physical and chemical conditions in the immediate environment of the cells. The catastrophic decline in numbers before July was clearly caused, not merely by the passive loss of cells from the epilimnion, but also by their death. This can be seen from the great increase of dead cells in this period (figure 5). By the end of June the ratio of live to dead cells in the 0 to 6 m water column was approximately 5:3, by July 8 it had risen to 25:4. If the live cells remaining at the end of June had been physiologically dormant, no such increase in numbers—exploiting additional supplies of silica or any other nutrient in their immediate environment—could have occurred. Yet, approximately one month after the maximum, this is what happened despite the previous rapid rate of decline. The distribution of the cells in depth and the marked stratification in this warm period (figures 1, 2) precluded any mixing from the lower layers. The synchronous increase in average number of live cells per colony in the 0 to 6 m water column (figure 6; below 6 per colony in the second half of June and above 6 from the second week in July), while the numbers remained low at lower levels, provides additional support for the views expressed here and in Lund (1949). It may be mentioned that similar increases after the post-maximal decline in the population have been observed in other years and lakes, but rarely so shortly after the decline.

The decrease in the amount of dissolved silica (from about 0·8 to 0·4 mg SiO_2/l., figure 7) in this period of renewed growth is equivalent to nearly 1·5 million cells per litre. This is greater than the observed increase in crop, even allowing for losses to the thermocline and for the growth of other plankton diatoms. It may well be that the explanation of this discrepancy is the same as that suggested for the high oxygen concentration (p. 279), namely, the movement of water from the littoral areas into the central regions. Since we are here concerned with growth taking place in the uppermost layers of the water, utilization of silicate by the free-living and attached diatoms in the marginal regions could lead to such a change. This would, of course, be the reverse of that in the case of oxygen, namely, a reduction in concentration from the incorporation of silica into the frustules of the littoral diatoms.

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The minimum standing crop in the epilimnion was reached in the middle of August, and in September the numbers were clearly increasing there while still decreasing in the hypolimnion (figure 3). The rise was relatively small, for the concentration of dissolved silicate fluctuated around 0·5 mg SiO_2/l. so that there was a precarious balance between supply and utilization. It was not until the end of October and early November that both the silicate concentration and the standing crop had markedly increased. However, by then the physical conditions were rapidly deteriorating. The epilimnion was deepening at the expense of the thermocline and hypolimnion (figure 1), as a result of falling temperatures and autumn storms. The numbers of *Asterionella* in the thermocline and hypolimnion were low so that their addition led to no significant increase in the population. Indeed, as time passed, the numbers in the hypolimnion fell to such low levels that progressive mixing led to the admixture of water containing fewer cells than were present in the epilimnion. Dilution from increasing rainfall also depleted the population. The average time which each cell spent in the photic zone was decreased as the epilimnion deepened, and this effect was reinforced by a progressive decrease in temperature, in length of day, and light intensity. The lake became completely isothermal early in December, when the numbers became the same throughout the water column and thereafter decreased during the winter.

The changes in the average number of cells per colony (figure 6) during this period are instructive. In October they rose to very high levels, even over 11 in the 0 to 6 m water column, and after the middle of November fluctuated between 7·5 and 8·5 until the end of the year. Even after the overturn there were for a time over 9·5 cells per colony at 60 m. Since the physical conditions were steadily becoming less favourable there seems little doubt that, provided the cells receive some light, it is the chemical environment that is the main controlling feature. That this was favourable was suggested by the fact that colonies grown in lake water at that time over 80 W lamps in the laboratory grew as rapidly as those in culture solution.

V. Chemical data for 1947

(i) *Silica* (figures 7, 8 and 9)

During the winter, when the lake was completely mixed and the inflow rate was high, the concentration of dissolved silicate in the lake was similar to that found in the major inflowing rivers (about 2·2 mg SiO_2/l.). No significant difference was found in this period (in the absence of diatom cells) between the concentration of dissolved silicate reacting directly with molybdic acid and the total concentration of silica found by treating the samples with potassium hydroxide before making the determination of silicate. While the lake remained unstratified, the concentration was uniform in depth. The onset of thermal stratification, coincident with the start of substantial growth of *Asterionella*, marked also the beginning of non-uniformity in the distribution of dissolved silicate. Thereafter the fall in the concentration of dissolved silicate in the epilimnion was markedly correlated with the rise in the diatom population. From our own observations which agreed well with those made earlier (Lund 1950*b*, table 3) the amount of silica contained in *Asterionella* was relatively invariable and amounted to some 0·14 mg $SiO_2/10^6$ cells. From the fall in the concentration of dissolved silicate it was therefore possible to calculate the actual

production of *Asterionella* in the epilimnion during any chosen interval regardless of losses by sinking which reduced the standing crop. This calculation could be applied over a limited time interval only, since dissolved silicate was continually added to the epilimnion by inflowing waters relatively rich in this substance. During the 12-day period (29 May to 9 June), which coincided with the most rapid fall in silicate, the concentration fell from

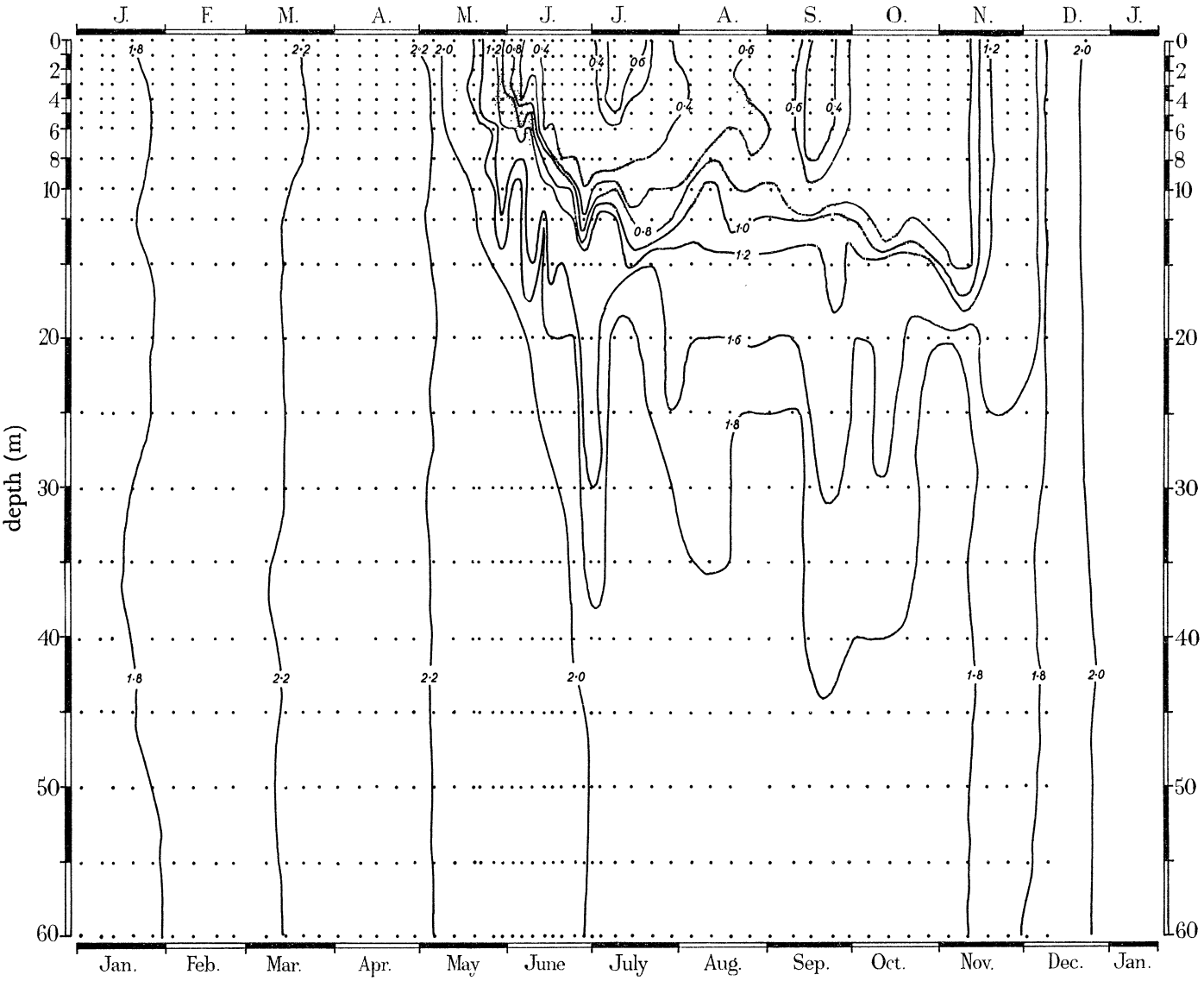

FIGURE 7. Dissolved silica (or 'dissolved silicate'), expressed as mg SiO_2/l. For further details see the legends of figures 1 and 2.

1·4 to 0·5 mg SiO_2/l. in the uppermost 7 m of the lake. This rate of fall corresponded to a production of $6{\cdot}4 \times 10^6$ cells/l. during this period. Since the content of carbon in *Asterionella* cells is 20% of the dry weight, and the dry weight is 0·3 mg/10^6 cells, the rate of fixation of carbon by the diatoms in this period in the upper 7 m of the lake can be calculated to have been 0·2 g C m^{-2} day^{-1}. An approximate correction for the effect of additional silicate derived from inflow would increase this rate of fixation to some extent.

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Assuming an average inflow rate of $0{\cdot}5 \times 10^6$ m^3/day (derived from Mortimer 1938) and an average silicate concentration in the inflow of 2·0 mg SiO_2/l., the amount of SiO_2 added to the epilimnion in this 12-day period would have been 12 metric tons which, when mixed into the epilimnion of approximately 70×10^6 m^3 volume, would have raised the SiO_2 concentration by 0·17 mg/l. This additional quantity must have been consumed by

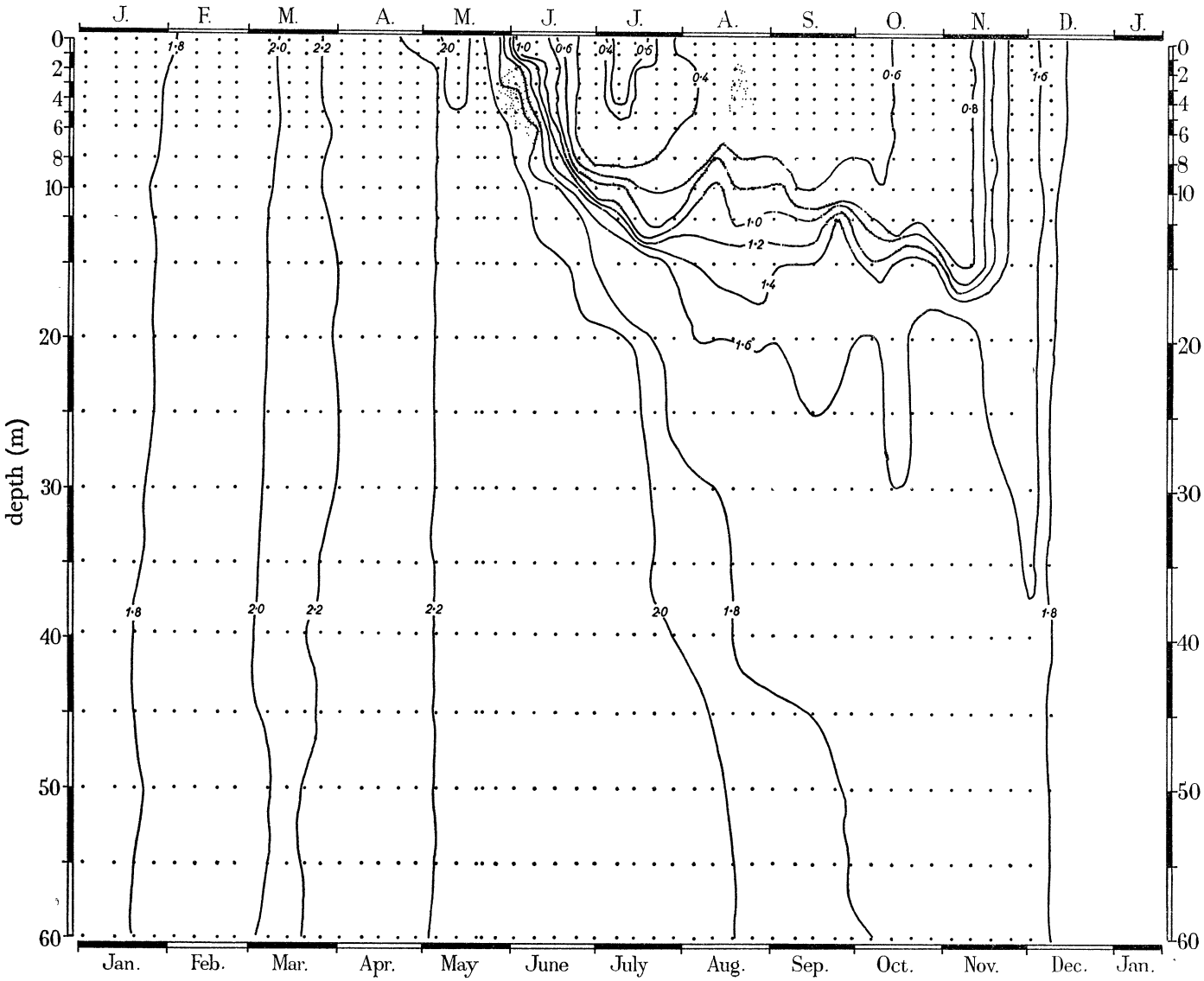

FIGURE 8. Total silica, mg SiO_2/l. For further details see the legends of figures 1 and 2.

the algae in the period under consideration and would be equivalent to an additional 10^6 cells/l. The probable real production in this period was therefore approximately $7{\cdot}4 \times 10^6$ cells/l. and the carbon fixation rate was nearer 0·24 than 0·20 g C m^{-2} day^{-1}.

Similarly the rate of loss of cells from the epilimnion by sinking may be calculated, independently of growth, from the rate of loss of total silica. A correction may be made on the above basis for the amount of silicate added by inflow. Thus over the period 6 to 26 June, the total silica concentration fell from 1·8 to 0·4 mg/l. in the uppermost 8 m of the

lake. To this loss of 1·4 mg SiO_2/l. must be added a further 0·2 mg/l. derived from inflows during this period. The total loss was therefore approximately 1·6 mg SiO_2/l. corresponding to a loss of some 10^7 cells/l. from the epilimnion to the hypolimnion. Therefore 8×10^{10} cells passed through 1 m^2 of the thermocline in 20 days or about 4×10^9 cells m^{-2} day^{-1}. It seems likely from this that the rate of loss of cells per unit of population must have

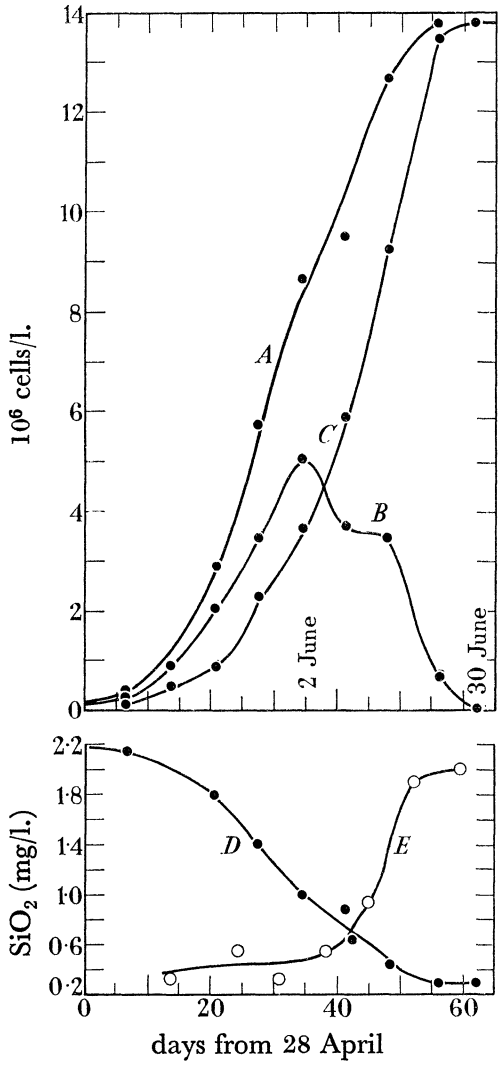

FIGURE 9. *Asterionella* production and loss, 28 April to 30 June 1947. The epilimnion is assumed to occupy the top 8 m and the curves represent: *A*, the cumulative total of cell production computed from silicate uptake; *B*, the mean concentration of cells in the epilimnion (standing crop); *C*, the cumulative loss of cells from the epilimnion (*A* minus *B*); *D*, epilimnetic silicate concentration; *E*, relative rates of loss of cells from unit epilimnetic population (arbitrary scale).

been considerably greater at the end of the phase of growth, when many cells were dead, than it was during the period of maximum growth-rate, since the average rate of loss of cells calculated above is of the same order as the rate of production of cells already calculated for the period of maximum growth (29 May to 9 June). Such a rate of loss at the time of maximum growth-rate would, therefore, have prevented the build-up of population

density actually observed in the epilimnion. That dead or moribund cells were lost more rapidly by sinking than actively growing cells appears to be demonstrated in figure 13. In this figure the epilimnion is considered to occupy the upper 8 m and the following quantities are plotted against time: *A*, the cumulative total production of *Asterionella* in the epilimnion, derived from the observed fall in silicate concentration, taking 0·14 mg of SiO_2 as being equivalent to 10^6 cells; *B*, the observed standing population (crop) in the epilimnion (mean population density); *C*, the cumulative total loss of *Asterionella* cells from the epilimnion, derived from the total production *A* minus the observed standing crop *B*; *D*, the observed concentration of dissolved silicate; and *E*, the rate of loss of cells per unit of population density. The curve *E* was obtained by assessing, for each week, the total of cells lost from the epilimnion, derived from the slope of the curve *C*. This rate of loss was then divided by the mean population density of that week to obtain a figure representing the rate of loss of cells per unit of population density. It will be seen that this quantity *E* was reasonably constant and independent of population density in the weeks up to and including the time of maximum observed population, but that the end of active growth coincided with a sharp rise in the rate of cell loss per unit of population density to approximately five times the previous rate, and that this higher rate of loss was maintained until only a very small population remained in the epilimnion. In constructing these curves no correction has been made for the dissolved silicate added to the epilimnion by inflowing water over the period under consideration. This would increase the calculated total cell production by some 30 %. On the other hand, if the epilimnion is subjected to much horizontal movement resulting in circulation of epilimnetic water over littoral regions containing significant attached diatom populations (and later consideration of the distribution of dissolved oxygen makes such movements appear likely), then losses of silicate from the epilimnion to littoral algae may be significant. These losses would require a negative correction in calculated *Asterionella* production. It is expected that the above gains from inflows and losses to littoral algae will tend to cancel each other but, since no estimate can be made of the losses, the conclusions derived from figure 9 are to some extent uncertain.

The growth of *Asterionella* in and loss from the epilimnion reduced the dissolved and total silica therein to some 0·3 mg SiO_2/l. by mid-June to early July. Later in July, however, the concentration of silicate rose in the surface waters to 0·9 mg SiO_2/l. This body of water richer in silicate than the epilimnion as a whole corresponded to a warm-water mass at 18 °C which was almost certainly derived from inflowing river water entering and spreading at the surface to be mixed to a depth of approximately 5 m. The main inflow to the lake possessed at this time a silicate concentration of 1·8 mg SiO_2/l. This additional dissolved silicate was utilized by a renewed small growth of *Asterionella* which reduced the concentration once more to 0·4 mg/l. In September the concentration of dissolved silicate rose rather slowly throughout the epilimnion. In November increasing inflow of silicate-rich water, and deeper mixing with the hypolimnion, produced a steeper rise in concentration, soon followed by complete mixing of the lake and a return to winter concentrations throughout.

No appreciable gain in silicate content was observed in the hypolimnion, although this was in contact with the lake sediment and with dead diatom cells sinking through it.

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Gains and losses of silicate were confined to the epilimnion where they could be respectively attributed to inflowing silica-rich water and to consumption by diatom growth. This is in contrast to the situation in lakes in which the hypolimnion (unlike that of Windermere) becomes devoid of oxygen during summer stratification. Under anaerobic conditions significant amounts of silicate are liberated into the water from the sediments (Mortimer 1941–42).

It is also clear that the major losses of *Asterionella* from the epilimnion must be attributed to sinking of the cells through the thermocline and eventually to the sediment, rather than by displacement of the epilimnion by inflowing water with loss of *Asterionella* to the outflow. As the inflowing waters were always rich in silicate, displacement of the epilimnion on a large scale could not lead to the loss of total silica observed.

(ii) *Alkalinity, oxygen, and carbon* (figures 10, 11 and 12)

The alkalinity of Windermere winter water closely approached that of the average winter inflowing water (6·8 to 7·0 mg $CaCO_3$/l.). The alkalinity of the lake was uniform throughout the water column until the onset of thermal stratification in early May. When stratification was established, a steady rise in alkalinity was observed in the epilimnion which was attributed to the addition of inflowing water to the epilimnion only. The alkalinity of the inflowing rivers is known to increase during the summer months, most noticeably in periods of hot dry weather. This increase is thought to derive from two major influences: (1) decreased rainfall and increased evaporation from the soils of the drainage basin, which leads to increased concentration of dissolved constituents; (2) decreased rainfall which diminishes the proportion of the drainage water derived from surface run-off and increases the proportion derived from a slower percolation through the soils. This increases the average contact time, and more efficient leaching of the soils takes place. It is possible that the higher temperature of the soil in summer also assists in producing more effective leaching.

The epilimnetic alkalinity reached a maximum in early September (9·6 mg $CaCO_3$/l.) followed by a steady decline as the inflowing water once more approached the winter concentration. The decline in epilimnetic alkalinity was hastened by the deepening of the thermocline, with consequent admixture of water from the hypolimnion which had risen little above the initial winter concentration throughout the summer. Uniformity of concentration with depth was produced by the final destruction of the thermocline. A minor increase in alkalinity was observed in the bottom water of the lake in September, when the alkalinity of the bottom 5 m of water had risen by some 1·0 mg $CaCO_3$/l. compared with the bulk of the hypolimnion. This increase in alkalinity was small compared with the total decrease in oxygen concentration at this level (*ca.* 3·5 mg O_2/l.), so that the alkalinity change did not bear the relationship to oxygen decrement observed by Mortimer & Mackereth (1958) in Torneträsk. In the bottom water of Torneträsk after 100 days of ice-cover, a rise in alkalinity of 1·5 mg $CaCO_3$/l. was accompanied by an oxygen decrement of 1 mg O_2/l. which was consistent with the assumption that the oxygen had been consumed in the conversion of organic matter to carbon dioxide with the production of hydrogen ions, which then exchanged with adsorbed cations on the mud surface liberating them as bicarbonate to produce the observed rise in alkalinity. It seems likely from this and from

later considerations that the proportion of the hypolimnetic oxygen decrement in Windermere actually attributable to consumption at the mud surface is smaller than was the proportion in Torneträsk. Though quantitatively insignificant when compared with the changes in the epilimnion, the rise in alkalinity close to the mud surface—which must be caused by diffusion from the sediment—does suggest a third mechanism which could play

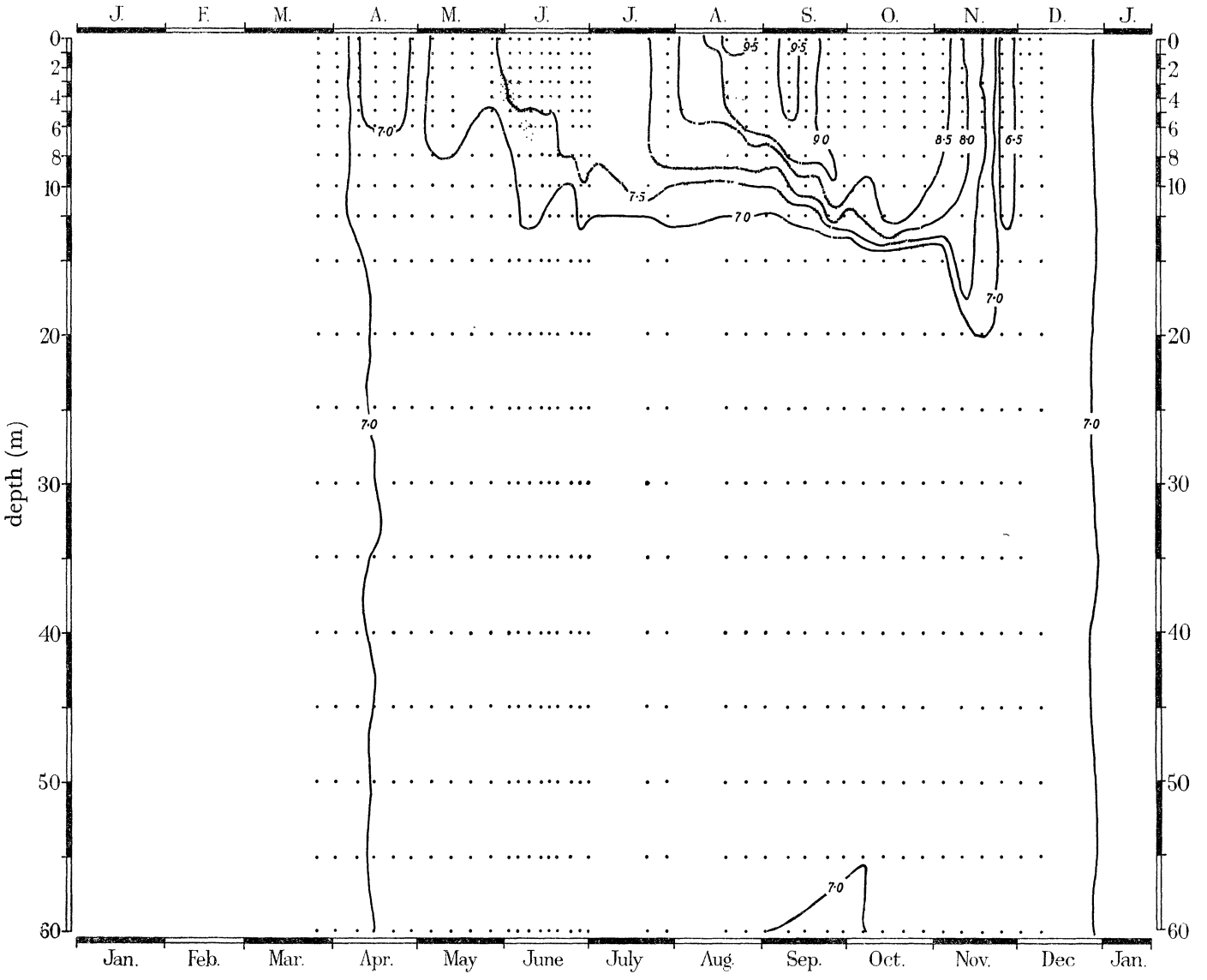

FIGURE 10. Alkalinity, expressed as mg $CaCO_3$/l. For further details see the legends of figures 1 and 2.

a part in the observed epilimnetic increase in alkalinity. It seems possible that water warmed on the shallows of the lake to a temperature above the average surface temperature, and containing additional bicarbonate derived from the littoral sediments, could by virtue of its reduced density migrate horizontally out over the lake surface, subsequently to be mixed into the epilimnion. Some support for the idea of such a movement may be obtained from a consideration of the distribution of oxygen saturation. Figure 12 shows that a state of super-saturation with oxygen persisted in the surface water in July and

August. This super-saturation cannot be explained by the photosynthetic activity of planktonic algae, since only small populations were present at the time. It is difficult also to postulate that the super-saturation resulted from a state of non-equilibrium between the water and the atmosphere in a period of rapid temperature rise in the water, accompanied by a relatively slow rate of loss of oxygen across the air–water interface. If such a

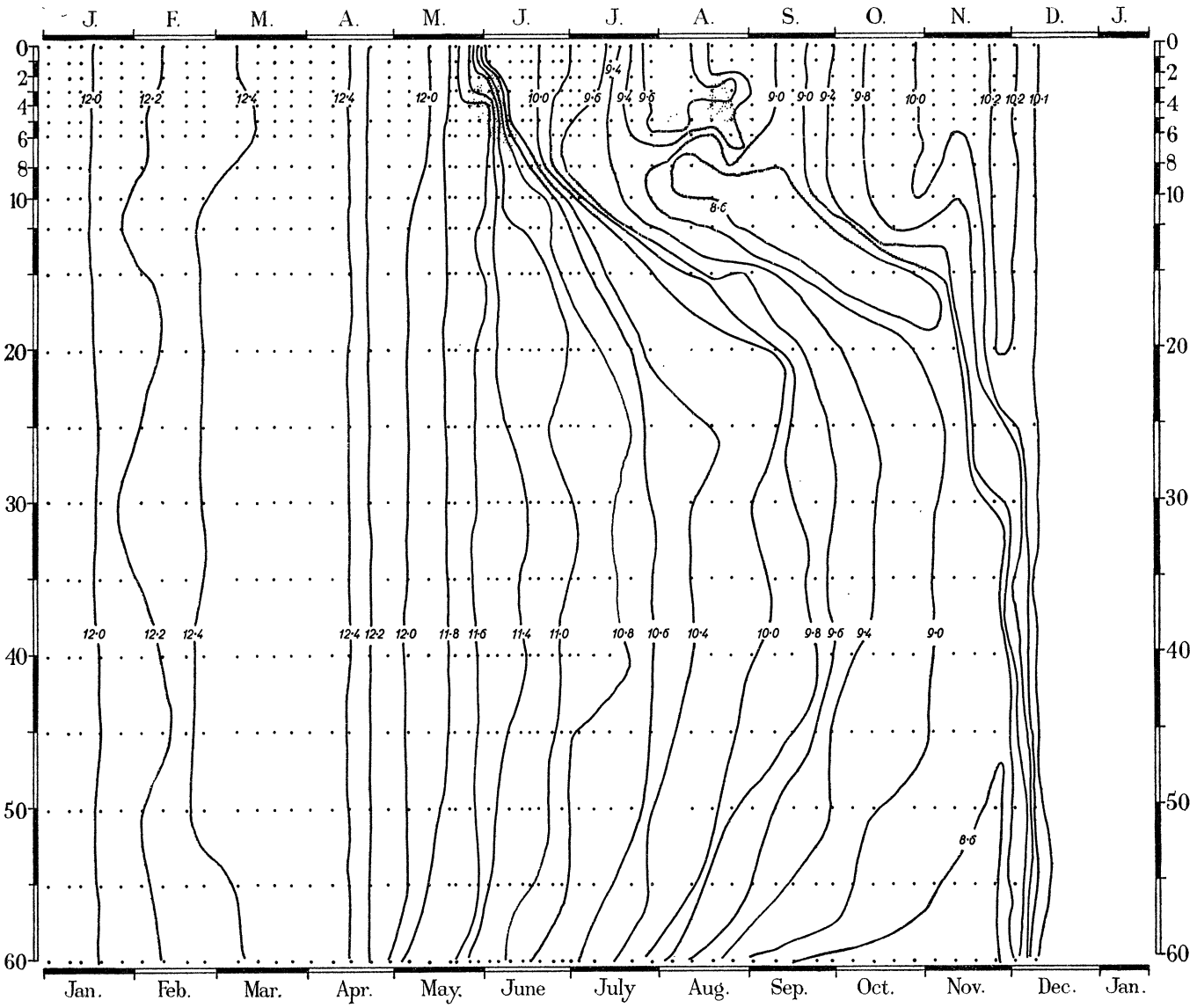

FIGURE 11. Dissolved oxygen, mg O_2/l. For further details see the legends of figures 1 and 2.

lack of equilibrium did in fact exist, the actual concentration of oxygen must nevertheless show a progressive fall in the surface water over this period; in fact no significant fall in concentration took place, despite the continuing state of super-saturation. A persistent, apparently unsupported state of super-saturation of this kind could, however, be explained by movement of littoral warmed water, super-saturated by the photosynthetic activity of attached littoral vegetation, into the open water of the lake followed by mixing of this water mass into the epilimnion. In considering a rather similar state of

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super-saturation observed by Riley (unpublished), Hutchinson (1957) supposed that a similar movement of littoral water must be invoked to explain the observation. It seems possible therefore that such movements do take place and that they may in fact be common during periods of calm sunny weather in stratified lakes. If such horizontal movements take place on a significant scale, no attempt can be made to calculate exit and entrance

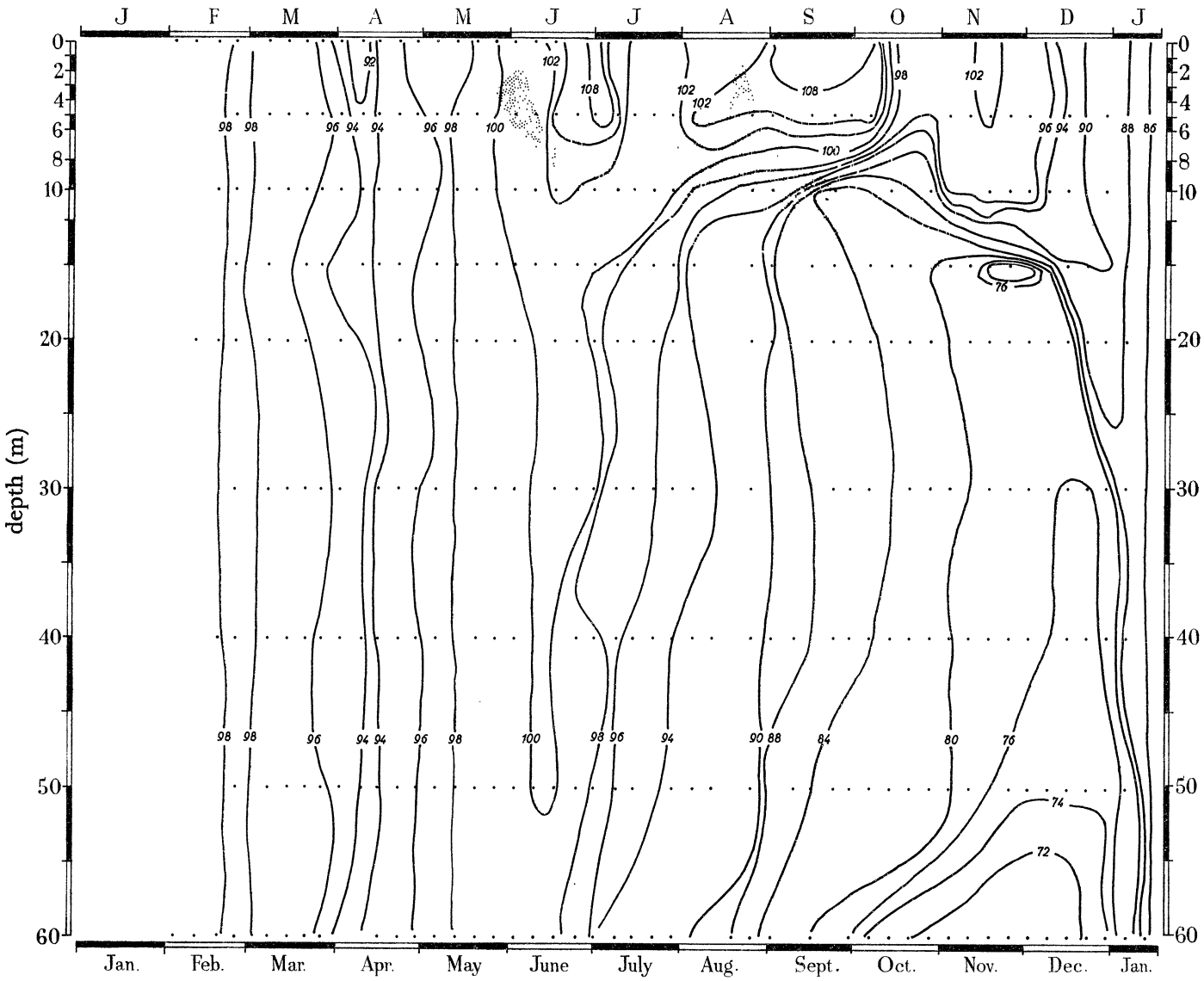

FIGURE 12. Oxygen, percentage saturation. For further details see the legends of figures 1 and 2.

coefficients for the open water of lakes during periods of stratification, by observing the changes in oxygen concentration with time.

It is also clear that such movements would supply a further reason (see also Mortimer 1952, pp. 394–6) for doubting the validity of the concept of a central water column as an isolated system in a lake, except perhaps for quite short periods of time.

The period of super-saturation which occurred in May to June may well have been associated with planktonic photosynthesis, since this period corresponded reasonably well

with that of maximum *Asterionella* production, but even here temperature conditions were such that horizontal migration of littorally super-saturated water could not be ruled out. It would be difficult to distinguish quantitatively between the two effects. The area of the epilimnion in contact with littoral sediments to a depth of 10 m (i.e. the area of the lake at the surface minus the area at the 10 m level) is 2·66 km^2, compared with the lake surface area of 8·16 km^2 (Mortimer & Worthington 1942). This is a minimum estimate because of the irregularities of the bottom, and the influence of this littoral area is not negligible if it

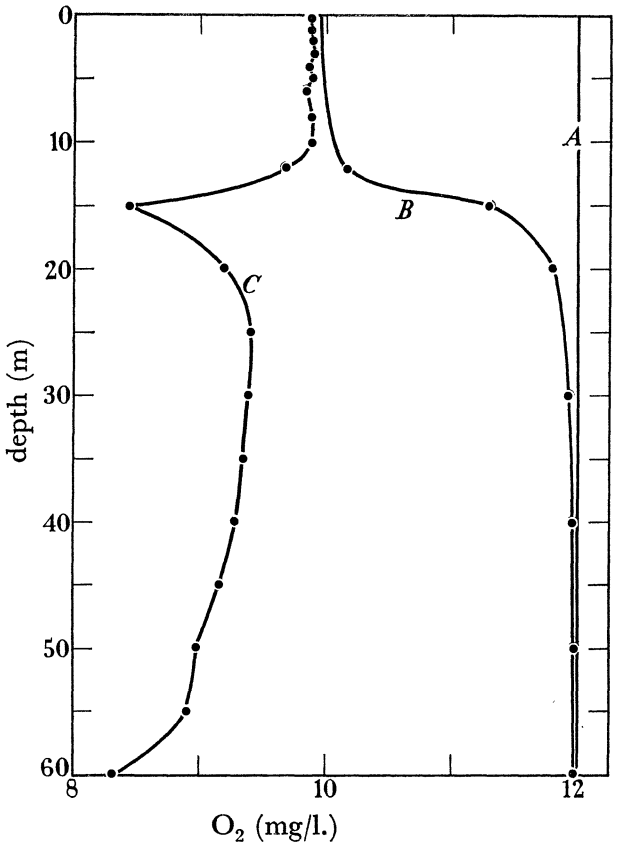

FIGURE 13. Hypolimnetic oxygen depletion 1947. The curves represent: *A*, 100 % saturation throughout the water column, corresponding to the isothermal condition on 5 May; *B*, a hypothetical curve representing 100 % saturation throughout the water column, corresponding to the temperature distribution observed on 13 October; *C*, the observed distribution of oxygen on 13 October.

can be brought into contact with the whole of the epilimnion by the mechanism suggested. Photosynthesis by attached vegetation would therefore bring about significant changes in epilimnetic oxygen distribution.

A steady decline in oxygen saturation was observed in the hypolimnion throughout the period of stratification, which produced in late October a body of water extending almost 10 m above the mud surface in which the oxygen saturation had been reduced to approximately 70 % of the fully saturated concentration at the temperature *in situ*. The oxygen saturation at this time was also reduced though to a somewhat lesser extent throughout the hypolimnion. The extent of oxygen consumption in the hypolimnion during the period of

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stratification between 5 May and 13 October (160 days) is presented in the curves of figure 13 in which curve *A* represents the concentration of dissolved oxygen plotted against depth immediately before stratification, when the lake was approximately saturated at atmospheric pressure throughout its depth. Curves *B* and *C* refer to the conditions in the lake on 13 October shortly before the stratification broke down. Curve *B* represents the theoretical concentration of oxygen to produce saturation with respect to one atmosphere at the *in situ* temperatures, and curve *C* the observed oxygen concentration distribution with depth on 13 October. In the hypolimnion below 20 m, the theoretical saturation curve on 13 October followed closely the observed distribution of concentration on 5 May (curve *A*) reflecting the insignificance of temperature change below 20 m in the intervening 160 days. The observed distribution of oxygen concentration on 13 October (curve *C*) diverged widely, however, from the theoretical saturation curve and from the distribution observed on 5 May.

This divergence represents, of course, the oxygen lost from or consumed in the hypolimnion in the interval. There seems to be no obvious mechanism for transferring oxygen from the hypolimnion to the epilimnion, and thence to the atmosphere, and the observed decrements are here assumed to be solely attributable to the consumption of oxygen by respiration either in the free water or at the water-sediment interface. The area between the curves *B* and *C* below 15 m in figure 13 represents the total consumption of oxygen in 160 days in the central column of water. If this consumption is referred to unit area of sediment in contact with a central water column (as was done for purposes of rough calculation by Mortimer 1941–42), the apparent rate of consumption at the mud surface must be a serious over-estimate, because the depth of water at Station B is considerably greater than the mean depth of the lake. In the present case such a procedure would lead to an apparent rate of uptake of 12·5 mg/cm^2 in the period of 160 days or 0·078 mg O_2 cm^{-2} day^{-1} compared with the figure of 0·052 similarly derived in Mortimer (1941–42). If the hypolimnion below 15 m is divided into 5 m depth zones, then using the morphometric data of Mortimer & Worthington (1942), the volumes of the zones and the total area of sediment in contact with the zones may be calculated. From the volumes of the zones and the mean oxygen decrement at the relevant depths, the total mass of oxygen consumed in each zone is derived (table 1). A summation of these zonal totals gives the total mass of oxygen consumed in the hypolimnion in 160 days. If this mass is then divided by the total area of sediment in contact with the hypolimnion, a mean apparent rate of consumption at the mud surface is obtained, assuming for the moment that the whole consumption takes place at that surface. This calculation produces a figure, comparable to Strøm's hypolimnetic areal deficit (Strøm 1931), of 0·041 mg O_2 cm^{-2} day^{-1}, which agrees closely with an earlier estimate of 0·04 mg cm^{-2} day^{-1} quoted in Mortimer (1941–42) as having been computed for Windermere North Basin by P. M. Jenkin (unpublished).

But this mean apparent rate of oxygen uptake of 0·041 mg cm^{-2} day^{-1} represents in fact the sum of the rates of consumption at the mud surface and in the free water. Laboratory measurements of oxygen uptake by undisturbed surface sediment cores and overlying water, obtained by means of the Jenkin surface mud sampler described in Mortimer (1941–42), led to the conclusion that the rate of uptake at the mud surface lies between 0·02 and 0·03 mg cm^{-2} day^{-1} at 4 °C. Since the degree of turbulence during the experimental

measurement was maintained (by stirring) at a higher level than that which probably exists in the hypolimnion of the lake, and as additional bacterial respiration must have taken place on the walls of the container, it seems likely that this measured rate was higher than the effective rate of consumption would have been at the mud surface *in situ*. The lower limit of the measured range (0·02 m cm^{-2} day^{-1}) is probably, therefore, closer to the rate occurring in the lake itself.

TABLE 1. TOTAL HYPOLIMNETIC OXYGEN CONSUMPTION (DEFICIT) IN WINDERMERE NORTH BASIN 1947, APPORTIONED TO DEPTH ZONES AND EXPRESSED PER UNIT AREA OF MUD SURFACE

Morphometric data from Mortimer & Worthington (1942)*.

depth zone (m)	zonal area in contact with bottom (km^2)	zonal volume (10^6 m^3)	zonal oxygen deficit after 160 days (10^6 g O_2)	apparent rate of O_2 consumption at unit area of bottom (mg O_2 cm^{-2} day^{-1})
15–20	0·50	23·5	66·0	0·083
20–25	0·57	20·8	52·0	0·057
25–30	0·48	18·2	45·5	0·060
30–35	0·40	16·0	41·0	0·064
35–40	0·40	14·0	37·0	0·058
40–45	0·68	11·3	30·5	0·028
45–50	0·69	7·9	22·9	0·020
50–55	0·38	5·2	15·6	0·026
55–60	0·40	3·3	10·7	0·017
	total area = 4·50 km^2	total volume = 120·2 × 10^6 m^3*	total consumption = 321 × 10^6 g O_2 in 160 days	mean apparent rate of O_2 consumption at mud surface = 0·041 mg cm^{-2} day^{-1}

* Neglecting Mortimer & Worthington's entries for 60 to 65 m. These were small, and their neglect takes into partial account the later discovery (unpublished, C.H.M.), confirmed by wire soundings, that the depths derived from the echo-records were approximately 4 % too great.

In table 1 the apparent rate of oxygen uptake at the mud surface has been calculated for each depth zone. It will be seen that, on an area basis (last column), the upper zones apparently consumed oxygen at three or four times the rate of the lower zones. Three different mechanisms may be suggested to explain this disparity: (1) the actual rates of consumption at the mud surface, or in the free water or both, were in fact higher in the upper hypolimnion than in the lower; (2) considerable transference of oxygen had taken place from the upper hypolimnion to the lower during the 160-day period; (3) the rates of consumption in the free water and at the mud surface were such that mechanism (2) need not be invoked. It will be demonstrated below that, since consumption at the mud surface is area dependent and consumption in the free water is volume dependent, a suitable allotment of rates at the mud surface and in the free water can be made to eliminate the necessity for oxygen transfer. This does not, of course, mean that such transfer did not occur. Mechanism (1) may also have made a contribution to the observed situation. The low concentration of oxygen at 15 m in curve *C* was probably associated with the decomposition of the quite large population of the alga *Paulschulzia tenera* (Korsh.) Lund (*ca.* 10^6 cells/l.) which had developed in the weeks preceding the observations of 13 October. Such a decomposition at or immediately below the thermocline must lead to an increased oxygen consumption in the free water of the upper hypolimnion. On the assumption that

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this effect is largely confined to the depth zone (15 to 20 m) immediately below the thermocline, and making the further assumptions (i) that oxygen consumption per unit volume of free water was substantially uniform in the whole basin below 20 m, and (ii) that consumption at the mud surface was everywhere constant (at the 'laboratory' rate of 0·02 mg cm^{-2} day^{-1}), it is possible to assess the quantitative significance of mechanism (2)—viz. oxygen transfer within the hypolimnion—by the following method.

TABLE 2. INTERPRETATION OF THE HYPOLIMNETIC OXYGEN CONSUMPTION, FOR DETAILS SEE TEXT

depth zone (m)	*a* zonal deficit after 160 days (*observed*) (10^6 g O_2)	*b* portion of *a* attributable to mud surface consumption, *assuming* a rate of 0·02 mg cm^{-2} day^{-1} (10^6 g O_2)	*c* final distribution of the free-water consumption after 160 days, *derived* from (*a* − *b*) (10^6 g O_2)	*d* total water consumption occurring in each zone, if a mean rate of 1·47 mg $l.^{-1}$ (160 days)$^{-1}$ is *assumed* (10^6 g O_2)	*e* difference *c* − *d* (10^6 g)
15–20	66·0	16·0	50·0	35	15
20–25	52·0	18·2	33·8	31	3
25–30	45·5	15·4	30·1	27	3
30–35	41·0	12·8	28·2	24	4
35–40	37·0	12·8	24·2	21	3
40–45	30·5	21·8	8·7	17	−8
45–50	22·9	22·1	0·8	12	−11
50–55	15·6	12·2	3·4	8	−5
55–60	10·7	12·8	−2·1	5	−7
totals	321	144	177	180	−3

The difference between the zonal oxygen consumption (i.e. zonal deficits in col. *a*, table 2, transferred from table 1) and the assumed zonal mud surface consumption (col. *b*, viz. the zonal contact area consuming at the 'laboratory' rate of 0·02 mg cm^{-2} day^{-1} for 160 days) provides an estimate of the 'final' distribution of that part of the deficit arising from free-water consumption. This represents only the distribution at the end of the 160-day period (col. *c*); it gives no precise information on when or where the free-water consumption took place.

One assumption which can be made is that, despite the distribution shown in col. *c*, the rate of respirational consumption of oxygen per unit volume in the free water was substantially uniform in depth—although not necessarily constant in time—throughout the basin below 15 m. Using table 2, a mean value for this rate can be estimated for the 160-day period by subtracting the total of col. *b* from the total of col. *a*, and dividing the difference (177×10^6 g O_2) by the hypolimnetic volume ($120{\cdot}2 \times 10^6$ m^3). This gives a mean rate of 1·47 mg/l. for the 160-day period, assumed to be independent of depth and retaining the assumption that the mud surface was 0·02 mg cm^{-2} day^{-1}. This rate of 1·47 mg $l.^{-1}$ (160 days)$^{-1}$, multiplied by the volume of each zone, provides an estimate of the respirational consumption which actually occurred in the free water in each zone (col. *d*), and this can be compared with the 'observed final' distribution of that part of the deficit (in col. *c*) attributed to free-water consumption, assuming a mud surface uptake rate of 0·02 mg cm^{-2} day^{-1}. The comparison is made in col. *e*, in which positive values of

(*c*−*d*) represent—on these assumptions—oxygen losses in addition to total respiration, while negative values represent net gains of oxygen. It will be noted that the values are all positive above the 40 m depth plane and all negative below it. The conclusion is that 31×10^6 g of oxygen has been transferred downward through the 40 m plane.

If on the other hand it is assumed, as a limiting case, that no vertical transfer of oxygen took place in the hypolimnion, and further that the rates of consumption in unit volume of free water and at unit area of mud surface were essentially constant, then the observed distribution of zonal oxygen losses can be explained only by postulating a smaller rate of

TABLE 3. INTERPRETATION OF THE HYPOLIMNETIC OXYGEN CONSUMPTION, CONTINUED

Columns (*b*) list the rates of free-water consumption in mg $l.^{-1}$ (160 days)$^{-1}$ required to account for the observed total deficit in each depth zone, when various rates (*a*) of mud surface consumption (mg cm^{-2} day^{-1}) are assumed.

depth zone (m)	(*a*) = 0·02 (*b*)	(*a*) = 0·015 (*b*)	(*a*) = 0·010 (*b*)	(*a*) = 0·005 (*b*)
15–20	2·1	2·3	2·5	2·6
20–25	1·6	1·8	2·1	2·3
25–30	1·7	1·9	2·1	2·3
30–35	1·8	2·0	2·2	2·4
35–40	1·7	2·0	2·2	2·4
40–45	0·8	1·3	1·7	2·2
45–50	0·1	0·8	1·5	2·2
50–55	0·6	1·3	1·8	2·4
55–60	−0·6	0·3	1·3	2·3

oxygen uptake at the mud surface and a rate for the free water correspondingly increased to arrive at the same total consumption. By this means—as illustrated in table 3—the observed oxygen losses in the various depth zones can be explained without recourse to oxygen transport. The table shows that, in the absence of oxygen transport, a mud surface uptake rate of 0·02 mg cm^{-2} day^{-1} would require the free-water uptake (mg/l./160 days) to fall from 2·1 mg/l. in the 15 to 20 m zone to less than zero in the 45 to 50 m zone and below. On the other hand, if a value for the surface uptake rate of 0·005 mg cm^{-2} day^{-1} is assumed, then the free-water rate per 160 days varies only from 2·6 mg/l. in the 15 to 20 m zone to 2·3 mg/l. in the 55 to 60 m zone, and is essentially constant at intermediate depths. It is clear, therefore, that the amount of oxygen computed to have been transported within the hypolimnion is markedly dependent on the rates of consumption of oxygen assigned to the free water and to the mud surface, respectively. It is unlikely that the effective rate of mud surface uptake in the lake was as low as 0·005 mg cm^{-2} day^{-1}—in view of the laboratory measurement of the rate at 0·02 mg cm^{-2} day^{-1}—though the *effective* rate in the lake may well have been less than the laboratory rate if lake turbulence was less than that in the experiment. The final conclusion must be that the data are insufficient to decide whether the rates of free-water consumption were in fact distributed non-uniformly with depth (i.e. higher in the upper part of the hypolimnion), or whether considerable vertical transport of oxygen had occurred during the 160-day period, or whether the contribution to total consumption made by respiration at the mud surface was considerably less than that measured in the laboratory. It seems likely that each possibility must be invoked to account for the combined result.

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From the total decrease in oxygen content of the hypolimnion during the 160 days of stratification (321×10^6 g O_2) the total amount of carbon consumed can be estimated. Assuming that most of the organic material involved in the respirational oxygen deficit was carbohydrate, so that the relationship $C + O_2 \rightarrow CO_2$ was approximately true, then this deficit corresponds to a total carbon consumption of 122×10^6 g. For convenience this may be referred to unit area of sediment, irrespective of whether the respiration occurred in the free water or at the mud surface. The respiration of carbon at unit area was therefore equivalent to 2·47 mg C/cm^2 in 160 days. In addition to this carbon loss by respiration, carbon is continuously incorporated into the sediments and permanently lost from the metabolism of the lake. The sediment contains a substantially constant percentage of carbon in depth, so that once incorporated into the sediment, this carbon is protected from further oxidation. The average concentration is approximately 30 mg C/ml. of wet sediment. Since 5 m of this material have accumulated in about 10000 years, and if a constant rate of sedimentation is assumed as a first approximation, the amount of carbon precipitated on each square centimetre is approximately 1·5 mg C cm^{-2} year^{-1} or 0·65 mg/cm^2 in 160 days.

This added to the carbon respired, already estimated at 2·47 mg/cm^2 in 160 days, yields a total amount consumed and sedimented in 160 days of 3·1 mg C/cm^2. The carbon contained in the whole of the *Asterionella* crop (12×10^6 cells/cm^2) amounted to 0·72 mg C/cm^2 and, as it is unlikely that the total algal crop produced during stratification exceeded twice the *Asterionella* crop, a reasonable figure for carbon fixation by algae would appear to be about 1·4 mg C/cm^2 in 160 days. Algal photosynthesis then provided less than half of the total carbon respired or lost to the sediments during stratification, and the proportion is even less if the whole of the year is considered. For the 160 days of stratification contained approximately the whole of the year's algal production, while oxidation and sedimentation are presumably more nearly constant throughout the year. The greater part of the carbon metabolized or sedimented in the lake must therefore reach the lake from the drainage basin in dissolved or particulate form (for instance, the annual influx of plant debris, including fallen leaves).

Much of the dissolved organic matter carried into the lake by inflows is apparently stable; it remains in solution, and eventually leaves the lake at the outflow. The carbon carried in solution in this way, and apparently playing little part in the lake metabolism, amounts on average to some 1·3 mg C/l. which is equivalent in the hypolimnion to a total of 157×10^6 g of carbon or approximately 3·2 mg C/cm^2. Since the water is replaced by inflows in approximately 9 months, the carbon brought into the lake in this way in 160 days is about 90×10^6 g or 1·9 mg C/cm^2. It takes little part in lake metabolism, but must be added to the carbon respired and sedimented, in order to assess the total amount brought into the lake. If this is done, the proportion contributed by algal photosynthesis to the annual carbon budget is relatively reduced. On an annual basis, carbon brought into the lake in the form of dissolved organic material amounted to about 4·3 mg cm^{-2} year^{-1}, that reaching the sediment to about 1·5 mg cm^{-2} year^{-1}, that burnt in respiration 5·5 mg cm^{-2} year^{-1}, totalling 11·3 mg cm^{-2} year^{-1}. To this total, phytoplanktonic photosynthetic activity contributed 1·4 mg C cm^{-2} year^{-1}, assuming that the bulk of this photosynthesis took place during the 160-day period of stratification. This figure should be increased to take

account of photosynthesis continuing on a smaller scale throughout the year and photosynthesis taking place in marginal shallow areas, but it seems unlikely that this addition could raise the total of carbon fixation by phytoplankton above some 2·0 mg C cm^{-2} $year^{-1}$. Even with this hypothetical addition, the carbon fixed in the lake by photosynthesis remains a small proportion of the total carbon budget.

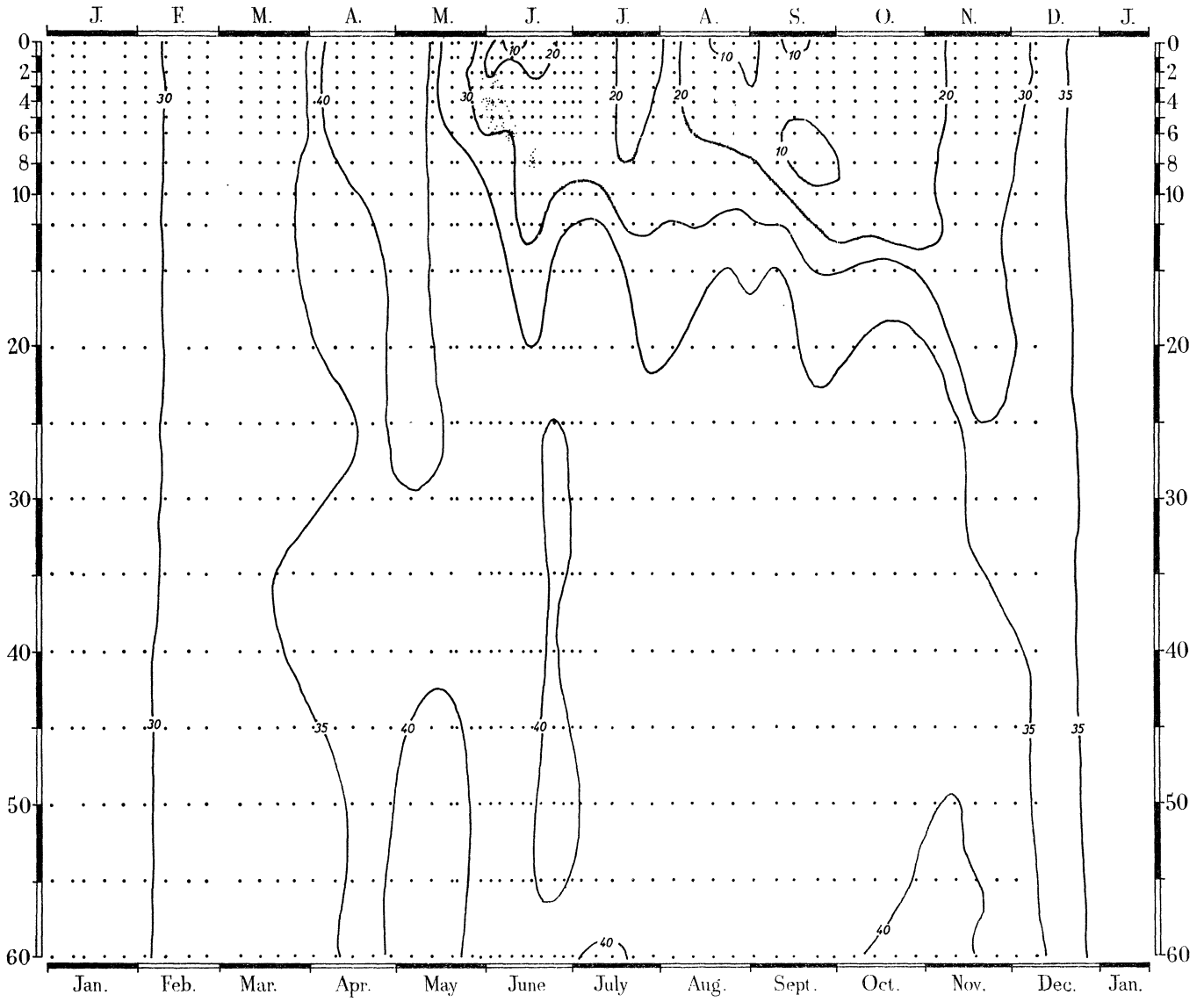

FIGURE 14. Nitrate nitrogen, mg NO_3.N/l. × 100. For further details see the legends of figures 1 and 2.

(iii) *Nitrate* (figure 14)

Nitrate supplies the major source of inorganic fixed nitrogen available for algal growth in Windermere. Ammonium and nitrite ions are present only in quite minor and negligible concentrations. The nitrate concentration in the whole lake rose steadily in the period from early January to early May, starting in January at some 0·25 mg N/l., and reached a maximum in April and May of approximately 0·40 mg N/l. (see figure 14). After the

establishment of stratification, the concentration in the epilimnion fell quite rapidly reaching approximately 0·25 mg N/l. by the end of May. In early June a surface layer of water 2 m thick had a nitrate content of as little as 0·008 mg N/l., but by mid-June this nitrate-poor layer had disappeared, presumably as a result of mixing with deeper epilimnion water. The concentration in the epilimnion as a whole continued to fall until mid-October when the concentration in a water mass extending to a depth of 12 m had been reduced to below 0·20 mg N/l. Thereafter deepening of the thermocline and mixing of the epilimnion with hypolimnetic water (in which the nitrate concentration had remained virtually unchanged throughout the summer) led to a steady rise in epilimnetic nitrate concentration throughout November. At the end of November uniformity of concentration with depth was practically established and the distribution approached that of winter conditions.

The nitrogen content of *Asterionella* is approximately 2 % of the dry weight, so that the consumption of nitrogen involved in the production of 15×10^6 cells/l. would be about 0·09 mg N/l. This consumption can clearly account for some part of the fall in nitrate concentration observed in the epilimnion as a whole in May and June, but it does not explain the low concentration occurring in the surface 2 m of the lake in mid-May, when a concentration of less than 0·1 mg N/l. was observed, corresponding to a loss of some 0·3 mg N/l. The consumption by planktonic algae is unlikely to account for the steady decline in the whole epilimnion throughout the summer, which reduced the epilimnetic concentration to about 0·15 mg N/l. in early September. Since the nitrate concentration of the inflowing rivers is known to fall in the spring and summer (1947 observations and those of Mortimer 1938) to as little as 0·08 mg N/l., it is reasonable to attribute some part of the observed epilimnetic summer decline to the admixture into the epilimnion of warm nitrate-poor river water. It is also possible, in view of the horizontal exchange between shallow littoral areas and the open water postulated earlier, that some part of the observed fall in concentration could be attributed to nitrate uptake by attached vegetation, for which no quantitative estimate can be made.

(iv) *Phosphate*

The concentration of phosphate phosphorus was normally too low to be measured with certainty by the colorimetric method employed (generally less than 0·001 mg P/l.) so that little reliance can be placed on apparent changes in concentration in the epilimnion. In general it can be said that the concentration of phosphorus in the epilimnion was lower than that in the hypolimnion (less than 0·001 mg P/l. and about 0·002 mg P/l., respectively), and that the concentration in the hypolimnion remained comparable with that initially present throughout the lake before stratification. No significant release of phosphate from the sediments was observed throughout the period of stratification, in contrast with the events associated with an anaerobic hypolimnion (cf. Mortimer 1941–42). The concentration in the epilimnion remained below the level of reliable measurement throughout stratification, in spite of the generally higher concentration in the inflowing rivers, which in July and August reached 0·018 mg P/l. and 0·06 mg P/l., respectively. The concentration in the rivers was much lower than this in winter, seldom exceeding 0·002 mg P/l. The removal of phosphate from solution in the epilimnion must therefore

have been rapid and effective throughout the period of stratification. That the lake sediment is the ultimate sink for this phosphorus is demonstrated by the very high concentrations found in the upper layers of the mud—some 500 mg P/kg of wet material in Windermere. Assuming a sedimentation rate of 0·5 mm/year, this mud concentration must mean that roughly 0·03 mg of phosphorus is deposited annually on each cm^2 of lake bottom. With a mean depth of 26 m (Mortimer & Worthington 1942), the phosphorus lost annually to the sediment in Windermere North Basin is equivalent to a water concentration of approximately 0·01 mg P/l. The much lower concentrations found in the water represent, therefore, only a small part of the total phosphorus brought into the lake. These small concentrations were, however, competent to support the spring crop of *Asterionella* without approaching the lower limit of cell phosphorus required for growth (Mackereth 1953).

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