A Study of the Spring Diatom Increase in Loch Striven.

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With 15 Figures in the Text.

THE spring diatom increase in the open sea and probably also in inshore waters is one of the most important annual biological events and information regarding it or its causes is likely to be of value. In an inshore area changes are not only more pronounced, but also take place more rapidly than in the open sea and, for this reason among others, the increase was studied in Loch Striven, a well-sheltered loch in the Clyde Sea Area. A general description of the weekly changes occurring in this loch has already been made (Marshall and Orr, 1927). The changes during the spring, however, are so rapid that an examination at even closer intervals during this period was thought advisable. Such an examination was made in 1927 and 1928, the interval between successive visits being generally two days. The methods used were the same as those described in the above-mentioned paper.

During the spring increase in Loch Striven in the years studied the sea was an almost pure culture of *Skeletonema costatum*. The other diatom species which occurred were few enough to be negligible and animal life was scarce. Before the increase began Skeletonema formed over 96% of the diatoms. On March 19th, 1928, of the first thousand cells counted, only five cells were not Skeletonema, on the 22nd less than 10, and on the 26th only 13. Thus the changes occurring were due almost entirely to one diatom species.

The spring increase of 1926 has been described in the paper referred to (Fig. 7). Visits were made only about once a week and the depths worked were 0, 5, 10, 20 and about 30 fathoms. The increase was regular in form, beginning at the surface and sinking gradually into

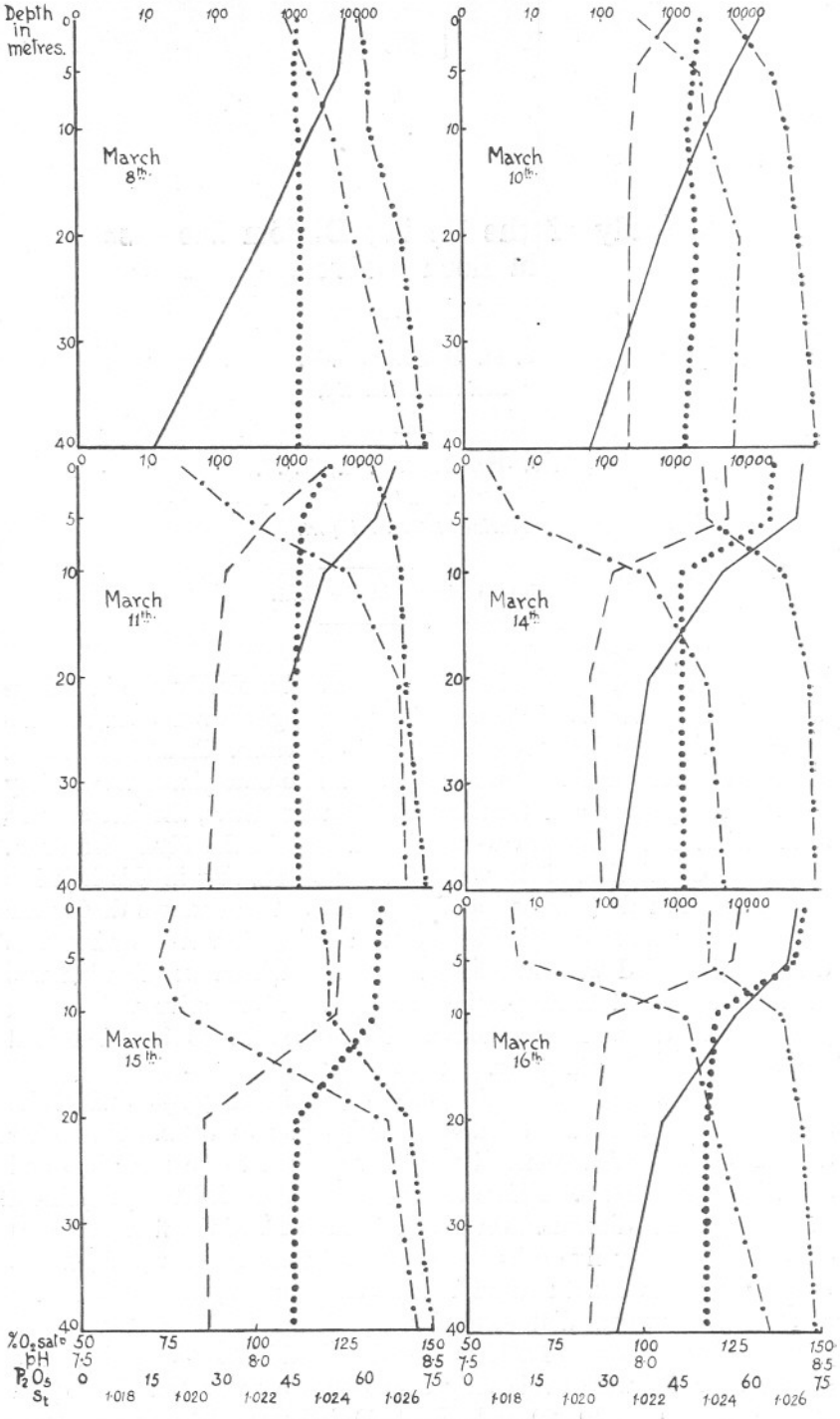

FIG. 1.—The spring increase in 1927.

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — . . — . . S_t.

deeper water, so that the maximum at 5 fathoms occurred the week after the maximum at the surface, and the maximum at 10 fathoms a week later. After this the fall was rapid, showing that the diatoms had sunk below the depth to which photosynthesis was possible. Three weeks after the beginning of the increase the diatoms had almost disappeared from the loch. The chemical factors showed a similar series of changes, the pH value and oxygen content rising and the phosphate falling with an increase in diatom numbers.

In 1927 (see Figs. 1, 2, 3 and 8, and Table 1) the loch was visited more frequently and the depths worked were 0, 5, 10, 20 and 40 metres. The increase had started before the first visit was made on March 8th and there were more than 5000 diatom chains per 20 c.c. in both surface and 5-metre samples. This is an unusually early increase when compared with previous years. The diatoms had increased again on the 10th, and between the 10th and the 11th the numbers were doubled at the surface (16,700 to 33,100) and 5 metres (6900 to 16,400). This very rapid change was accompanied by a sharp rise in oxygen saturation (110% to 121%), a slight rise in pH value and a marked fall in dissolved phosphate. In the deeper water, however, there was also a considerable change, the phosphate and dissolved oxygen saturation values being different from that for the 10th. This leads one to suppose that the change was not due entirely to diatom growth, but that the water examined was not the same as on the previous day. That such an increase can take place naturally, however, is shown by Gran (1927).

At this time the surface density was lower than that of the other layers so that no vertical mixing was going on. On the 14th a fall in density at surface and 5 metres stabilised the loch still further and the chemical changes were correspondingly more marked. The diatoms also reached their maximum for the increase and were almost as numerous at 5 metres (51,000) as at the surface (62,700), but this is probably due to the mixing of the waters between these depths.

On the 15th there was a hard S.E. wind and the effect of this was similar to that described by Murray for some Scottish lochs (1888) and by Gran and Gaarder (1918) for the Oslo fiord. The surface waters were piled up in the loch so that the values found the previous day at surface and 5 metres were now found at surface, 5 and 10 metres. Diatoms were not counted this day, but it is almost certain that the high figures would have been found at 10 metres also. On the 16th and 17th conditions had returned to normal and were very much the same as on the 14th. By the 18th diatoms were very much more numerous at 5 metres than at the surface in spite of the fact that the density at these depths was much the same. This shows that the diatoms have begun to sink and this process had gone still further by the 22nd when the maximum numbers

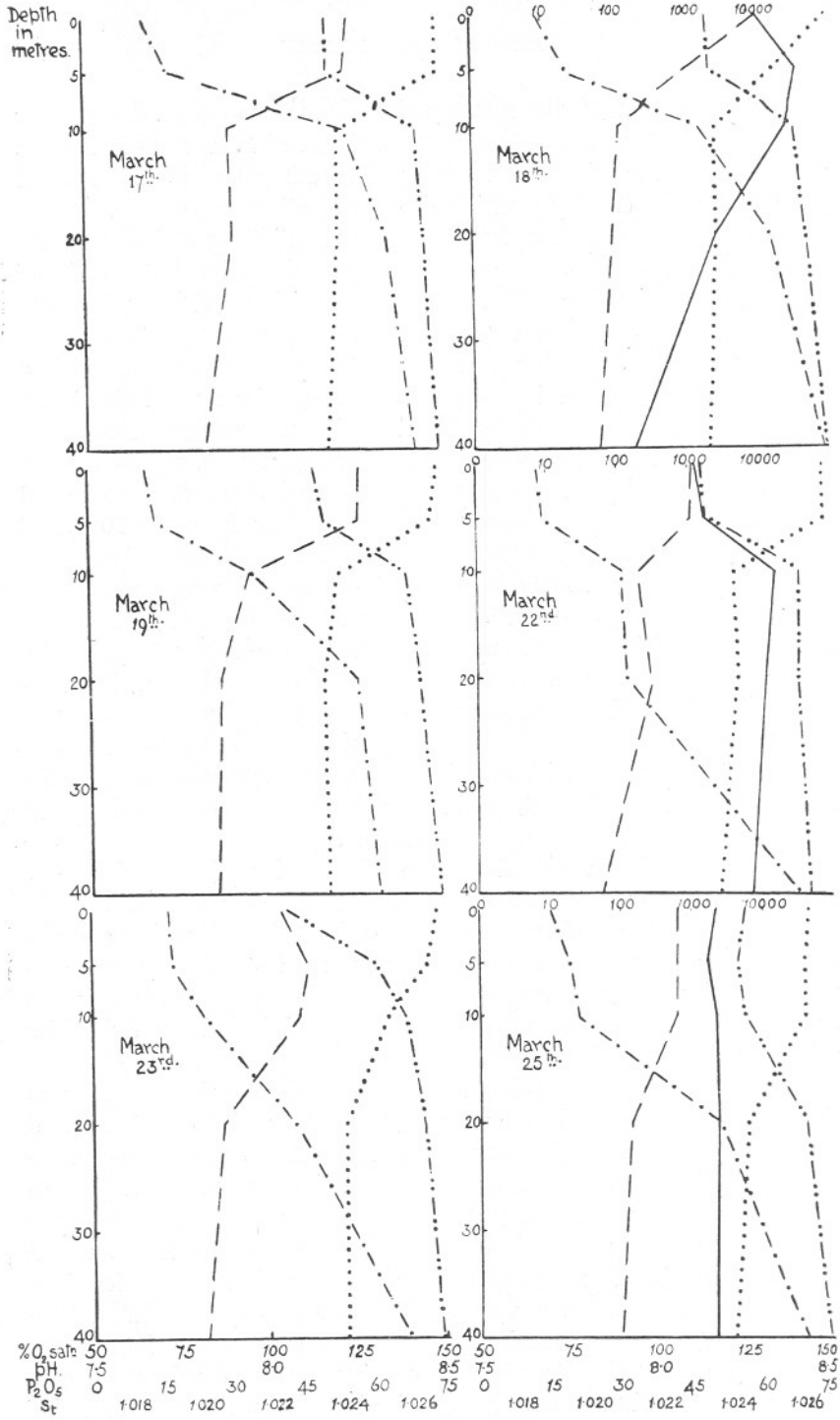

FIG. 2.—The spring increase in 1927 (contd.).

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

were found from 10 to 40 metres. By the 25th numbers at all depths had fallen and the increase was over. There are no chemical changes corresponding to the high diatom numbers at and below 20 metres, which indicates that the diatoms are sinking passively and that no photosynthesis is going on there.

An examination of the loch at intervals of about two days shows that the regularity of the increase is not so marked as when the examination is made only once a week. These irregularities are partly because in an enclosed area the effect of wind and tide is much more marked than in the open sea. Another point of interest is that the increase falls off before all

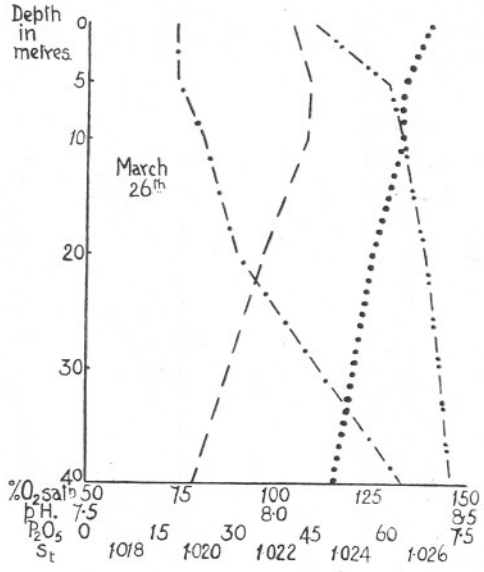

FIG. 3.—The spring increase in 1927 (contd.).
——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

the phosphate is utilised, which is at variance with the results obtained in the open sea (Atkins, 1926), but is in agreement with the results obtained during the spring increase in the same loch in 1926. No other essential nutrient salts were estimated, however, and it is possible that one of these may have been limiting. There is, nevertheless, a definite relationship between the chemical factors and the diatoms. Estimation of small quantities of phosphate is not very exact when diatoms are very numerous, for they then give the sample a brownish tinge which interferes somewhat with the blue colour given by the phosphate reagent.

In 1928 (see Figs. 4, 5, 6 and 9, and Table 2) the number of diatoms was estimated by counting the cells and not the chains. Several counts

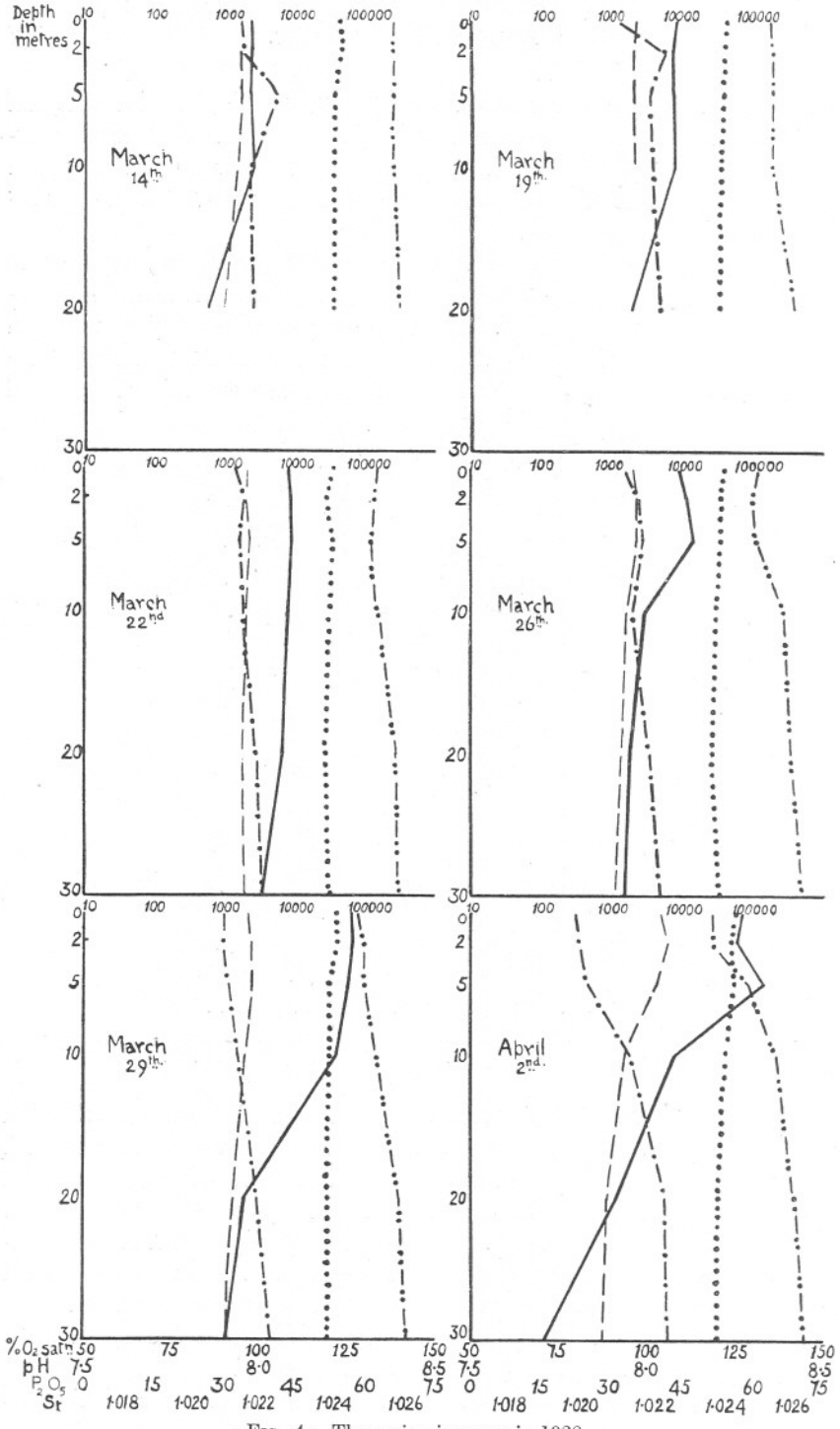

FIG. 4.—The spring increase in 1928.

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

gave an average of about 10 cells per chain and this figure held till the end of the increase when it fell somewhat. They were counted in this way to bring the work into line with that done elsewhere, and the comparison with 1926 and 1927 can be made by multiplying the figures for those years by 10. Gran (1929) estimates that the number of cells in a chain of *Skeletonema costatum* is 16 or more. The reason for the difference may be that our samples were centrifuged living and not after preserving. The depths worked were 0, 2, 5, 10 and 20 metres. The additional depth of 2 metres was chosen because the maximum amount of photosynthesis may not occur at the surface.

On March 14th there were already between two and three thousand cells per 20 c.c. down to a depth of 10 metres. This is higher than normal for winter, and a certain amount of growth must have been going on. The pH value was also higher than the normal winter value. By March 19th numbers had increased at all depths counted but were still much the same, 7000 to 8000 from 0 to 10 metres. Values for density, oxygen saturation, pH and phosphate show the same conditions. The temperature overturn had not yet taken place and the loch was therefore in an unstable condition in which vertical mixing was possible. Conditions were much the same on the 22nd, but mixing, and along with it, diatom numbers had spread deeper. The increase had progressed considerably by the 26th and diatoms were fairly rich (9000 cells at the surface, 11,300 at 2 metres, 13,500 at 5 metres). At the same time, however, density was almost uniform to 5 metres so that this distribution is apparently not due to a real sinking of the diatoms but to vertical mixing to this depth. The chemical changes also agreed with density. By the 29th the temperature had risen at the surface, the loch was in a more stable condition, and there was a great increase in the number of diatoms down to 10 metres. The values for the chemical factors, however, showed little alteration. On April 2nd the loch was supersaturated with oxygen down to 5 metres and the phosphate values had fallen as far as the same depth. The diatom distribution was irregular, rising as far as five metres, then falling sharply in the deeper water. Two days later, on April 4th, density had fallen again at the surface and there was a steep gradient from there down to 10 metres. Corresponding with this phosphate had fallen to zero at the surface, the oxygen saturation had risen to 115% and pH value had also risen, while the diatoms had multiplied still further and were richer in the 2-metre sample (248,000) than at the surface (180,000). Since the loch was now quite stable, this is probably a real sinking and not caused simply by mixing.

On April 6th the loch remained stable, the diatoms had fallen to 5 metres where they reached their maximum number for this increase (510,000 cells in 20 c.c.), the oxygen saturation had also reached its

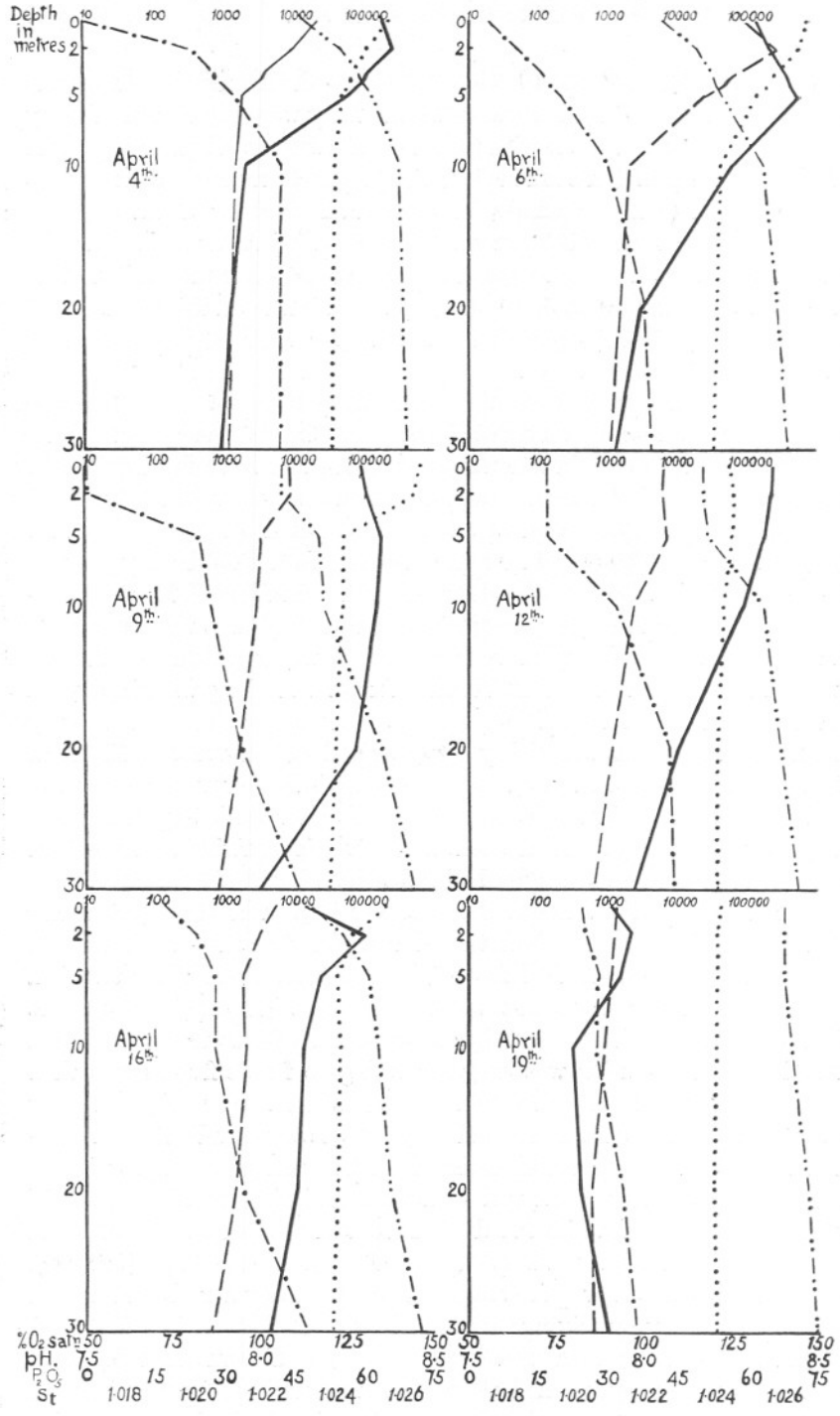

FIG. 5.—The spring increase in 1928 (contd.).

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

maximum (138% at 2 metres), pH value had risen to 8·47, and phosphate had fallen at 2 and 5 metres. There are slight discrepancies in the phosphate results at surface and 2 metres on the 4th, 6th and 9th. These are due in part at least to the increased difficulty in matching colours when diatoms are very numerous.

It is curious that on the 6th, although the diatom present was as before, *Skeletonema costatum*, the type of cell was quite different from that of previous days, the cells being both larger and longer. This new type was found at surface and 2 metres while in all other samples they

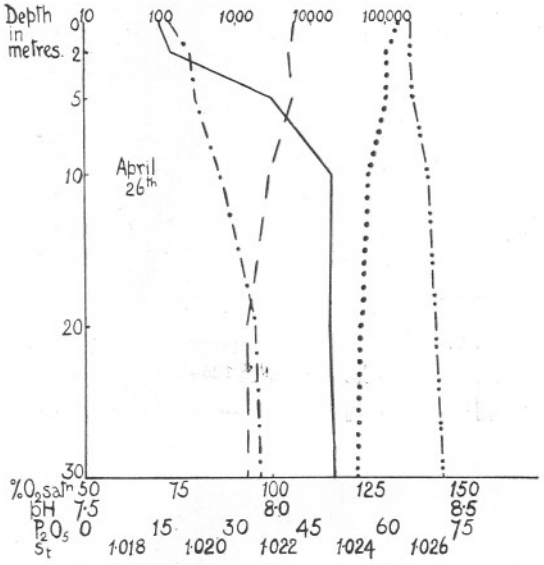

FIG. 6.—The spring increase in 1928 (contd.).
——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

were of the usual form. On April 9th the diatoms were sinking and numbers had fallen except in the deeper water. The new type of Skeletonema cell was predominant at surface and 2 metres, at 5 metres the types were mixed and below this a few chains of the new type were present at each depth. Density conditions had altered again, so that there was vertical mixing between 0 and 2 metres, and between 5 and 10 metres. The chemical factors were correspondingly altered. By April 12th mixing had gone on to 5 metres and had brought up a fresh supply of phosphate into the surface water, at the same time lowering pH and oxygen saturation values. With the introduction of phosphate the diatoms had increased slightly again at the surface and 2 metres.

The new type of cell had disappeared and all samples contained only the old type.

By April 16th the loch was stable once more and the diatoms were sinking, their numbers having decreased again except in deeper water.

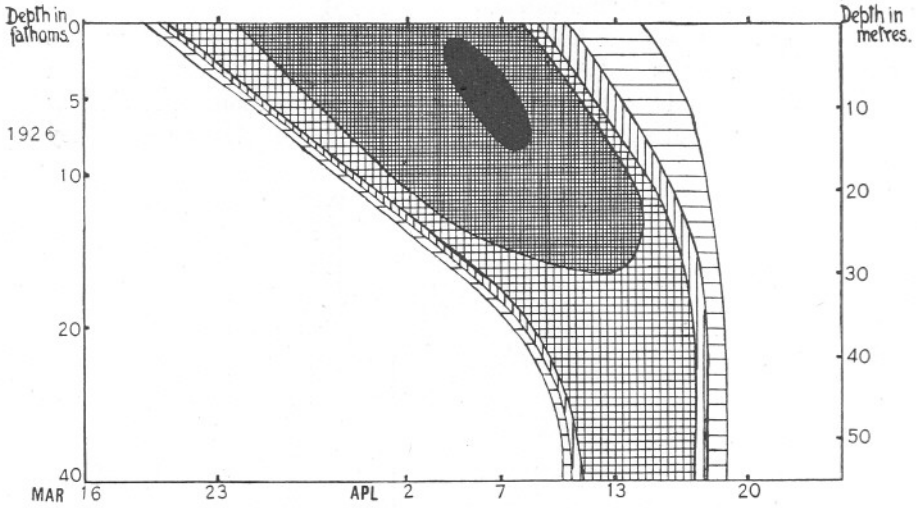

FIG. 7.—Diatom diagram. Spring increase of 1926.
□ under 50, ▭ 50–125, ▥ 125–250, ▦ 250–500,
▩ 500–1250, ■ over 1250 diatom chains per c.c.

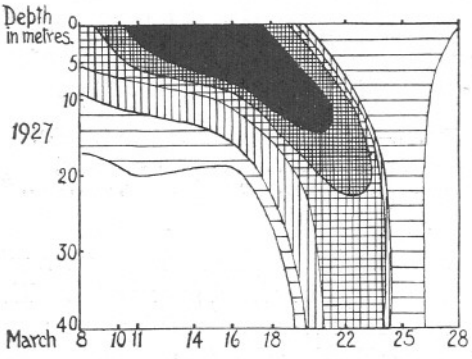

FIG. 8.—Diatom diagram. Spring increase of 1927.
□ under 50, ▭ 50–125, ▥ 125–250, ▦ 250–500,
▩ 500–1250, ■ over 1250 diatom chains per c.c.

There was still a fair amount of phosphate in the surface layers and it is difficult to understand why the diatoms stopped increasing at the surface. Diatom numbers were very low at all depths on the 19th and the distribution was irregular. The density gradient was only slight from top to

bottom and the loch appeared to be mixed. A week later it was visited again and there was evidence that another small increase of diatoms had taken place meanwhile, for the phosphate value had fallen a little, the pH value and oxygen saturation had risen and the diatoms increased in numbers down to 10 metres and then remained constant down to 30 metres.

The spring increase of 1928 was thus of a quite different type from that of 1926 and 1927, being much less regular. It began while vertical

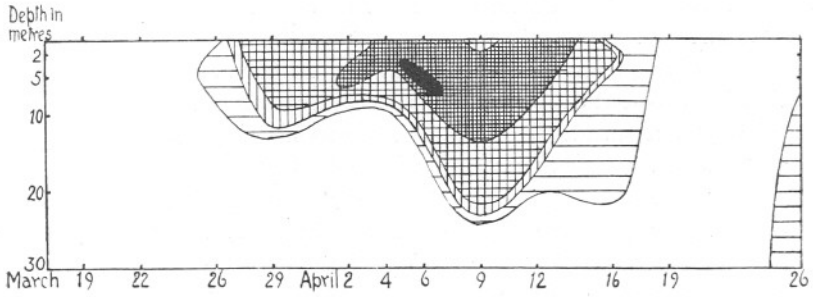

FIG 9.—Diatom diagram. Spring increase of 1928.
□ under 500, ▤ 500–1250, ||| 1250–2500,
▦ 2500–5000, ▩ 5000–12,500, ■ over 12,500 diatom cells per c.c.
The scales have been adjusted so that Figures 7, 8 and 9 are directly comparable.

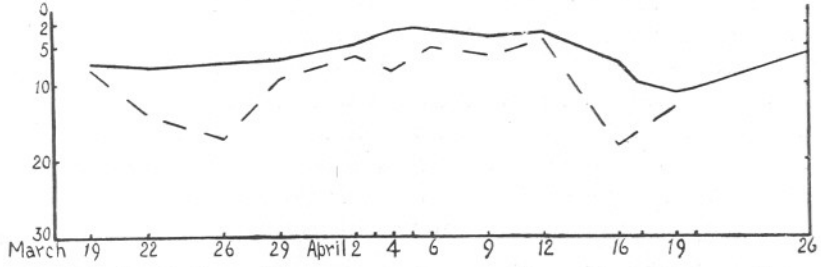

FIG. 10.—Secchi disc readings ———, and compensation-points for diatom cultures — — —, during the spring increase of 1928.

mixing was still going on and the diatoms increased in numbers simultaneously down to a considerable depth instead of only at the surface as usual. Since in deeper water there was not enough light for growth, the diatoms there sank as soon as mixing stopped and there was a great fluctuation in numbers at depths of 10 and 20 metres. When the temperature rose and stabilisation took place, the increase progressed much as in previous years, increasing rapidly at the surface and then sinking downwards. This process was interrupted, however, by further mixing, this time due to wind as well as temperature, and diatom numbers rose at the surface once more.

There are thus two factors responsible for the vertical distribution of the diatoms. First, there is the sinking of the diatoms which is strongly marked in the years 1926 and 1927 and is particularly clear in the late autumn of 1926 (Marshall and Orr, 1927). Second, there is the mixing of the diatoms which occurs when the sea-water itself is mixed by wind or temperature. This is recognisable by a uniform density at the depths mixed. This second factor was of considerable importance in 1928, but was found only on one occasion in 1927 (see p. 855). Another unusual event in the increase of 1928 was the change of diatom type for a short period, although the species remained unaltered. There was no apparent cause for either its arrival or its departure. Finally, as in the years 1926 and 1927, the end of the spring increase was not marked by a total lack of phosphate in the surface layers, but there was sufficient still in solution to supply another increase which in all probability followed after a short interval.

The spring increase starts at a time of year when the light for photosynthesis is comparatively poor, except at the surface, and the enormous number of diatoms present must decrease the light available still further. The figures for oxygen content are to some extent a measure of the amount of photosynthesis going on, but they are not reliable, partly because during the increase the water was often supersaturated and so gave too low an estimate of the oxygen produced, and partly because during the windy weather there was probably a good deal of movement among the different water layers. It was therefore thought of interest to estimate the amount of photosynthesis possible by sinking diatom cultures to different depths in the sea and measuring the amount of oxygen produced. Since the sea at that time was an almost pure culture of *Skeletonema costatum*, some samples of sea-water were tested in the same way. A culture of *Coscinosira polychorda* was used, while the sea-water samples used were taken from various depths (see Marshall and Orr, 1928). The most important external factor was, as might be expected, the number of diatoms present in the sea, and during the increase the total photosynthesis decreased from day to day as the cloud of diatoms in the water grew denser. Figure 11 and Tables 4 and 5 show two curves for diatom culture photosynthesis in the sea, the first taken before and the second during the spring increase of 1928. In the curve for March 22nd–23rd the oxygen production at 5 metres was considerable and the compensation-point lay between 10 and 20 metres. In the curve for April 6th–7th a steep fall occurred between $\frac{1}{2}$ and 2 metres and another between 2 and 5 metres, while the compensation-point lay between 2 and 5 metres. Since there was more sunshine on April 6th than on March 22nd, the smaller amount of photosynthesis going on at and below 2 metres must be ascribed to the effect of a thick screen of diatoms

in the surface water. The same type of result is seen in Figure 12 of which the curve for March 18th–19th was taken during, and that for March 28th–29th after the spring increase of 1927. After the diatoms had disappeared the photosynthesis at 5 metres increased again considerably. There was more sunshine on March 28th–29th than on March 18th–19th and the

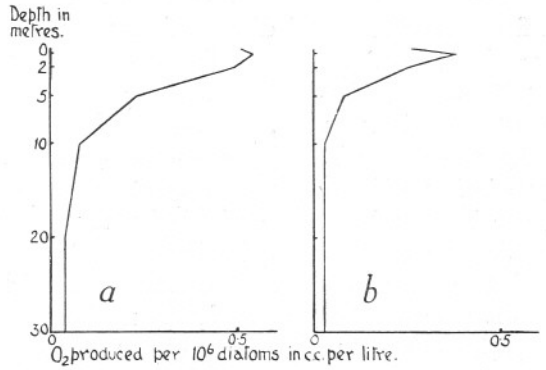

FIG. 11.—Oxygen production per 10^6 diatoms in Loch Striven, (*a*) 22–23/3/28 (0·41 hours sunshine), (*b*) 6–7/4/28 (4·25 hours sunshine).

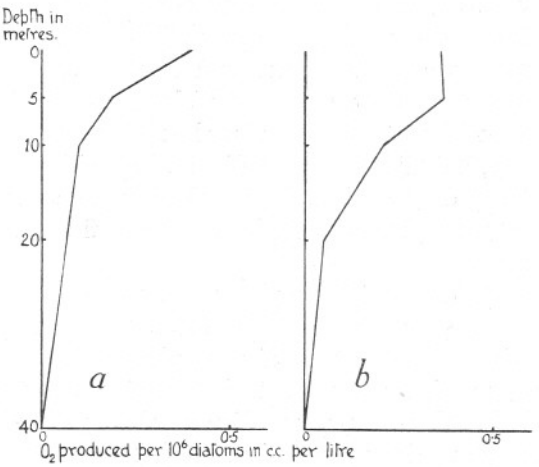

FIG. 12.—Oxygen production per 10^6 diatoms in Loch Striven, (*a*) 18–19/3/27 (no sunshine), (*b*) 28–29/3/27 (5 hours 50 minutes sunshine).

greater amount of photosynthesis at 5 metres may be due in part to this, but, as shown below, it is probable that it was also caused partly by the disappearance of the diatoms from the surface waters.

There is thus a relation between the type of curve and the number of diatoms present in the water. This is shown clearly in Figure 10 and Table 3,

where the compensation-points of eleven culture experiments carried out during the increase are plotted under the diatom increase diagram. The actual figures for compensation-points were arrived at by interpolation and are therefore only approximate. Before the increase began it was as deep as 17 metres, during the increase it rose as near the surface as 4 metres, and after the increase it sank again to 18 metres. This result is further confirmed by the Secchi disc readings which are plotted on the same figure. Before the increase the disc was seen to 7 metres and it disappeared at $2\frac{1}{2}$ metres during the height of the increase on April 5th. Diatoms were not counted on this day, but were at their recorded maximum on the 6th when the Secchi disc disappeared at 3 metres. After the increase was over, the reading was as deep as 11 metres. Confirmatory results were obtained with compensation-point figures in 1927, but Secchi disc readings were not taken. If allowance is made for the fact that the Secchi disc is not always seen as deep as the richest layer of diatoms, the correspondence becomes still more marked.

Poole and Atkins (1929) have found evidence of a decrease in the intensity of illumination due to the zoo-plankton, but did not find any effect produced by a diatom increase. While no data concerning the effect of the zoo-plankton are available for Loch Striven, the evidence quoted above seems to us conclusive concerning the obscuring effect of the phytoplankton. The results are not explicable either by rainfall or wind, the former by carrying down land detritus and the latter by agitation of the water. The much greater abundance of diatoms in the loch as compared with the open sea offers the most probable explanation of the discrepancy. The diatoms gave a distinct brownish tinge in columns of sea-water 15 cm. deep at the height of the increase and the quantity of detritus in centrifuged water samples was insignificant in comparison with the diatoms.

The experiments done with samples of sea-water taken during the course of the increase gave small and irregular results. The production was usually much less than that of a diatom culture and was often within, or very near to, experimental error. This is largely because the diatoms are so much smaller than the culture diatoms that twenty-four hours is hardly long enough to show production. Gaarder and Gran (1927) left samples of sea-water in flasks in the sea for periods of three days and got a considerable amount of oxygen produced. In our experiments the compensation-point was always found nearer the surface than in the case of culture diatoms. On an average the compensation-point for diatom cultures during the increase (7 experiments) was 8 metres, while that for sea-water experiments giving positive results (13 experiments) on the same dates as the above culture experiments was 3 metres. Since the sea diatoms do not produce so much as culture diatoms, it might be thought

that the illumination before the spring increase, although good enough for the latter (see Fig. 11a), was not good enough for the former to multiply. Proof that there is, at the surface at any rate, sufficient light for the growth of sea diatoms, was obtained in another way. Some weeks before the spring increase in 1928, a sample of sea-water was taken into the laboratory, filtered through a sterile sintered glass filter (see p. 868) and allowed to stand in an unheated room. After some days a good mixed culture of Skeletonema, Thalassiosira, Nitzschia and a few other small forms appeared. Similar results were obtained in December 1929 with both

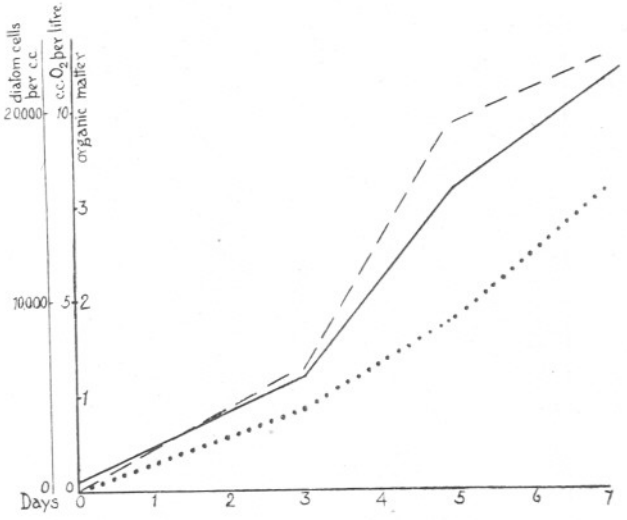

FIG. 13.—Curves showing relationship between ——— diatom numbers, — — — oxygen production, ... organic matter oxidisable by permanganate in a diatom culture in mg.O_2 per litre.

filtered and unfiltered water. It is apparent then that the sea diatoms themselves, as well as cultures, can grow in the ordinary illumination of the surface water before the date of the spring increase.

In view of the enormous production of diatoms during the spring increase, an attempt was made in 1928 to test whether there was a relationship between the organic matter oxidisable by permanganate in the sea (Ruppin, 1904) and diatom numbers. Because of the time required to complete the other work, the analyses for organic matter were not completed till two or three days after taking the samples. A disturbing factor is the inflow of water comparatively rich in dissolved organic matter from a burn at the head of the loch. This source of error was partially avoided by estimating the difference in organic matter between filtered and unfiltered samples. The filter used was a Jena sintered glass filter which

was found to be sufficiently fine in grain to stop practically all diatoms, although a few small forms were usually found on centrifuging the filtrate. The results were small but showed generally an increase with increasing diatom content. There was no good evidence that the organic matter in the filtered samples increased when the diatoms became richer, as would have been expected from the results obtained by Pütter (1924). He states that a large part of the organic matter produced by diatoms diffuses directly into the sea. Support was given to this work of Pütter's by Gran and Gaarder (1927), Gran and Ruud (1926), and Föyn and Gran

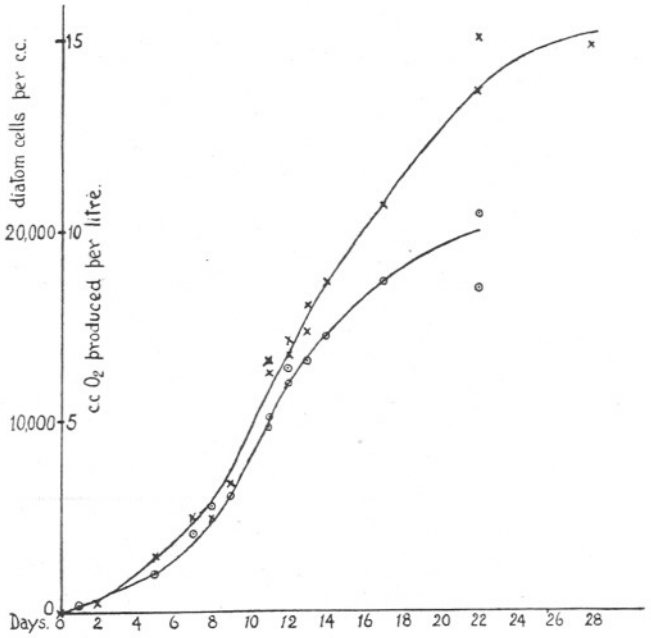

FIG. 14.—Diatom numbers (o) and oxygen production (x) in a diatom culture.

(1928) from results obtained in the Oslo fiord and later in the open sea. They used a biological method of estimating organic matter.

Since the results in sea-water are liable to error, some experiments were carried out with diatom culture, *Coscinosira polychorda* again being used. A few preliminary tests showed that while the total oxidisable organic matter was variable, the dissolved organic matter was higher in cultures old enough to have a fair number of dead cells. A culture was then started off by inoculating several litres of Miquel with a considerable amount of rich culture so that there were about 500 cells per c.c. This was then transferred to a large number of sterile stoppered bottles of about 120 c.c. capacity of which three were used for estimation of dissolved

oxygen content, diatom numbers and dissolved organic matter, filtered and unfiltered. The results obtained are shown in Figure 13 and Table 6. The difference in organic matter in the filtrate is negligible, showing that the dissolved organic matter does not increase along with the growth of diatoms but probably only when a number of the cells have died. The organic matter in the whole culture increases with the diatoms. At the end of the experiment the diatoms were very rich (21,300 cells per c.c.), so that, had diffusion of the organic matter taken place, the filtrate would have shown this clearly. Alkaline permanganate will, of course, only oxidise a portion of the organic matter present. In addition, though the analyses were made as described by Ruppin, it was found that, with diatom cultures, if the time of heating was increased the oxidation was also increased. It seems improbable, however, that any organic matter diffusing from the diatoms and so present in the filtered culture should have been entirely unaffected by it. While the above is true of a young culture, an old culture does show an increase in soluble organic matter, but this is more probably because the dead cells which are present are being attacked by bacteria.

The dissolved oxygen was estimated in the hope that it might be possible to find a factor by which the organic matter oxidisable by permanganate must be multiplied to give total organic matter. The increase of oxygen was so rapid and the degree of supersaturation so high that such a figure would be of doubtful significance. By the end of the experiment all the bottles had developed bubbles. The same type of growth was found in a similar experiment (Fig. 14) in which the slower rate of growth was probably due to the smaller amount of light in February than in May.

Discussion.

Of the many factors which might influence the beginning of the spring increase, there are several which can be excluded at once. The nutrient salts are probably present in abundance. Only one of these, phosphate, was actually estimated, but it does not seem likely that the mixing which led to the presence of phosphate did not bring up the other food salts also. Temperature also affects the spring increase only indirectly, since we find that on several occasions it started before the spring temperature overturn took place. We know, too, that Skeletonema can, and does, grow in waters both considerably warmer and considerably colder. It flourished at a temperature of 2–3° C. on the Norwegian coast in 1922 (Föyn, 1929), and at a temperature of 8–9° C. in Loch Striven in May, 1926 (Marshall and Orr, 1927), while it appears occasionally in the tropics (Karsten, 1907).

When we come to the question of light intensity the facts are more

complex. Diatom cultures grow well in winter, not only in the laboratory but also in the sea. The rate of growth is, of course, much slower than in summer and the growth in the sea shows that at the surface this effect is due chiefly to the shorter day. Below the surface the light intensity is suboptimal and growth is affected by both these factors. The result is that the compensation-point rises closer to the surface than in summer, to a depth of about 4 to 6 metres at midwinter (Marshall and Orr, 1928).

If we consider now the conditions for the sea diatoms themselves, we see that there is not only a sufficiency of food salts present in the sea throughout the winter, but the diatoms can grow in sea-water some time before the date of the spring increase if they are kept in a light approximately equal to that at the surface (see p. 867). Small diatom increases have been recorded after the autumnal temperature overturn has taken place. For example, in Loch Striven in November, 1926, there was a small increase of Skeletonema, and Atkins (1927*a*) has recorded an increase of Rhizosolenia in late autumn 1925 at Plymouth. In these cases food salts were present in sufficient quantity to have caused quite a large increase but did not do so. A probable explanation of this seems to be that the diatoms did not remain long enough in a sufficiently well-illuminated zone. In other words, the vertical mixing which takes place probably carries the diatoms below their compensation-point. Since the compensation-point in winter lies at 4 to 6 metres for culture diatoms and even nearer the surface for sea diatoms, it would need only a small vertical movement to bring the diatoms below their compensation-point. Such movements do occur in Loch Striven even in summer when the water is comparatively stable if there is a hard up-loch or down-loch wind and will be frequent in winter, during which time the loch is unstable. With the increasing light of the advancing spring, the compensation-point goes deeper and finally the diatoms will no longer be carried below it. Even after the increase has started, however, further mixing may modify its course considerably.

Gran (1929) has shown that on the Norwegian coast the spring increase near land is independent of the increase which occurs off the continental shelf. The former comes earlier and depends on the date of the melting of the snows. This fresh water lowers the salinity and adds large quantities of nutrient salts. In the Gulf of Maine also Bigelow (1924) believes that the spring increase depends on the nutrient salts added by the melting snows. This explanation will not hold for any area which has not a permanent covering of snow in winter, for the salts brought down by land drainage are being added all through the winter and are not held up to be added in a comparatively short time during the spring thaw.

On the other hand, Atkins (1928), among others, considers that the most important factor is the amount of spring sunshine. Figure 15 shows

the amount of sunshine daily during the spring months 1924–29, along with the date on which the number of diatom chains reached 20 per c.c. (or 200 in the case of diatom cells).* This is, of course, a purely arbitrary figure, but since the numbers usually increase very rapidly within a few days, the actual figure chosen makes little difference. It will be seen that the date of the spring increase is approximately constant, on about March 20th. In 1924 it was a little later and in 1927 a little earlier than usual, and it is interesting to notice that off the Norwegian coast in 1927

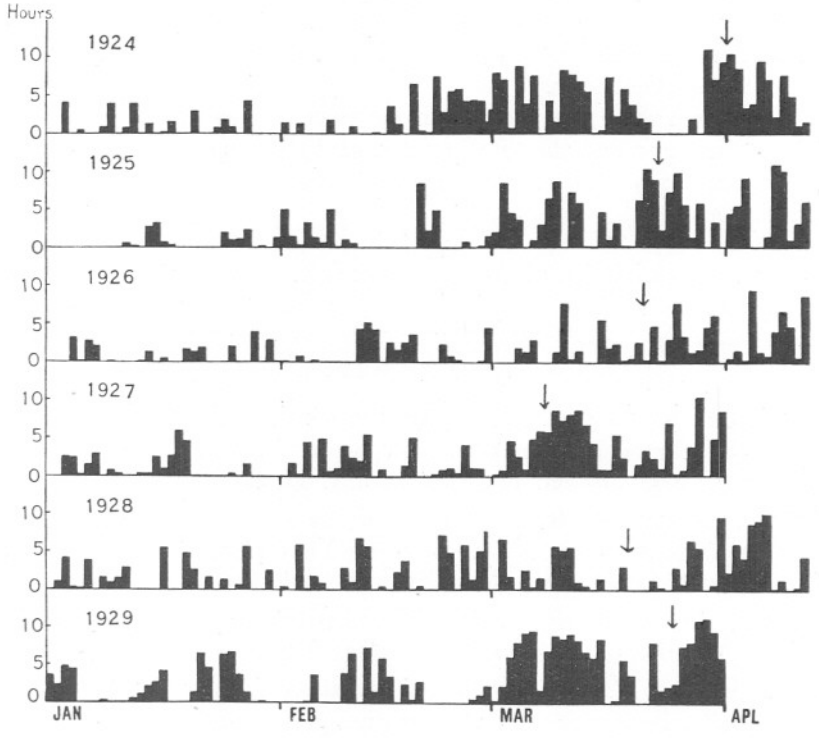

FIG. 15.—Daily sunshine during spring months of 1924–1929. The arrows show the beginning of the spring diatom increase.

it began exceptionally early too (Föyn, 1929). This was not a year with much early sunshine. At Plymouth the spring increase began earlier in 1924 than in 1925 (Atkins, 1927*b*), whereas the reverse was the case in the Clyde.

In Loch Striven, then, it appears that the date of the spring increase is decided chiefly by the total light which depends both on length of day and brightness. Only such a comparatively constant external factor could account for the narrow limits of time within which the increase

* The observations on diatoms in 1929 were made by Mr. Elmhirst.

begins. Vertical mixing may alter this date a little, but the increasing light gradually overcomes this factor and allows the spring increase to begin. As soon as the loch becomes stabilised the increase runs its normal course.

SUMMARY AND CONCLUSIONS.

1. The spring increase in Loch Striven is described in detail for three consecutive years. Contemporaneous experiments with diatom cultures and sea-water samples helped to elucidate the changes which occurred. Vertical mixing of the water layers was found to have an important effect on the form of the increase.

2. Although there is a relationship between organic matter oxidisable by permanganate and the total number of diatoms present, there is no relationship between *dissolved* organic matter oxidisable by permanganate and diatoms.

We wish to thank Mr. Elmhirst and members of the staff for their help throughout the work.

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TABLE 1.

1927.

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom chains in 20 c.c.
8–3–27.								
0	6·79	31·97	1·0251			8·13	45	6,400
5	6·87	32·11	1·0253			8·12	50	5,400
10	7·18	32·30	1·0253			8·13	55	2,280
20	7·30	34·01	1·0262			8·14	59	423
40	7·38	34·43	1·0269			8·13	70	12
10–3–27.								
0	7·09	31·54	1·0247	7·60	109·6	8·18	38	16,700
5	7·22	33·02	1·0258	6·72	99·5	8·16	50	6,900
10	7·21	33·39	1·0262	6·33	98·4	8·14	52	2,800
20	7·30	33·78	1·0265	5·97	97·4	8·17	59	670
40	7·39	34·49	1·0270	5·85	97·1	8·13	58	65
11–3–27.								
0	7·11	32·41	1·0254	8·35	120·7	8·22	22	33,100
5	7·25	33·09	1·0259	7·16	104·2	8·14	36	16,400
10	7·21	33·39	1·0262	6·33	92·1	8·13	58	3,200
20	7·26	33·56	1·0263	6·12	89·5	8·12	69	1,050
40	7·29	34·39	1·0269	5·92	87·2	8·13	70	.....
14–3–27.								
0	6·27	30·21	1·0238	8·99	124·4	8·38	5	62,700
5	6·28	30·34	1·0239	8·98	125·2	8·37	13	51,000
10	7·22	33·30	1·0261	6·35	92·3	8·12	39	4,350
20	7·35	34·21	1·0268	5·89	85·9	8·12	52	402
40	7·38	34·39	1·0269	6·04	88·8	8·12	55	141
15–3–27.								
0	6·12	30·34	1·0239	8·96	124·5	8·36	20	
5	6·12	30·58	1·0241	8·92	123·9	8·35	17	
10	6·12	30·60	1·0241	8·88	123·3	8·35	22	
20	7·30	33·74	1·0264	5·82	85·2	8·12	66	
40	7·38	34·47	1·0270	5·88	86·7	8·10	72	
16–3–27.								
0	6·24	30·41	1·0239	9·18	127·6	8·46	10	47,500
5	7·17	30·55	1·0239	8·82	125·7	8·43	13	36,300
10	7·19	33·26	1·0260	6·23	90·6	8·21	47	6,300
20	7·28	33·82	1·0265	5·97	87·4	8·18	52	600
40	7·37	34·41	1·0269	5·81	85·6	8·18	64	138
17–3–27.								
0	6·18	30·33	1·0239	8·98	125·1	8·50	12	
5	6·14	30·31	1·0239	8·91	123·8	8·50	18	
10	7·19	33·73	1·0264	6·25	91·2	8·22	55	
20	7·13	33·88	1·0266	6·29	91·8	8·22	64	
40	7·38	34·46	1·0270	5·77	85·1	8·19	70	
18–3–27.								
0	6·49	30·07	1·0236	9·44	131·0	8·51	14	11,000
5	6·48	30·16	1·0237	7·91	110·6	8·35	20	39,600
10	7·11	33·30	1·0261	6·37	92·5	8·19	48	26,400
20	7·21	33·72	1·0264	6·17	90·1	8·19	63	2,740
40	7·35	34·48	1·0270	5·83	86·0	8·17	74	212

TABLE 1 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom chains in 20 c.c
19–3–27.								
0	6·79	29·83	1·0234	9·00	127·0	8·49	12	
5	6·51	30·21	1·0237	9·07	126·9	8·47	14	
10	6·99	33·12	1·0260	6·66	96·5	8·21	35	
20	7·25	33·72	1·0264	6·00	88·1	8·17	57	
40	7·35	34·49	1·0270	5·87	86·6	8·18	62	
22–3–27.								
0	7·50	29·87	1·0233	7·75	110·7	8·48	13	1,280
5	7·53	30·05	1·0235	7·75	110·7	8·48	14	1,700
10	7·00	33·26	1·0261	6·61	95·7	8·23	31	16,100
20	6·92	33·24	1·0261	6·91	100·2	8·24	32	12,000
40	7·25	33·72	1·0264	5·91	86·4	8·19	68	7,400
23–3–27.								
0	7·57	28·79	1·0225	7·33	104·4	8·48	16	
5	7·47	31·92	1·0250	7·76	112·3	8·45	17	
10	7·12	32·99	1·0259	7·51	108·9	8·34	24	
20	7·17	33·70	1·0264	5·95	86·9	8·22	43	
40	7·33	34·41	1·0269	5·61	82·5	8·22	67	
25–3–27.								
0	7·20	31·24	1·0245	7·42	106·4	8·43	15	2,200
5	7·21	30·98	1·0243	7·42	105·9	8·42	19	1,700
10	7·20	31·24	1·0245	7.39	105·7	8·42	21	2,200
20	7·03	33·37	1·0262	6·40	92·6	8·26	51	2,300
40	7·32	34·26	1·0268	6·15	90·3	8·22	69	2,200
26–3–27.								
0	7·17	29·32	1·0230	7·38	104·2	8·41	18	1,090
5	7·20	31·97	1·0250	7·55	108·6	8·34	18	67
10	7·18	32·40	1·0254	7·51	108·3	8·34	23	143
20	7.02	33·14	1·0260	6·70	97·0	8·26	30	688
40	7·30	34·10	1·0267	5·36	78·6	8·16	63	192

TABLE 2.

1928.

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
14–3–28.								
0	5·56	32·66	1·0258	6·75	94·5	8·22	33	2,182
2	5·50	32·65	1·0258	6·75	94·1	8·22	34	2,246
5	5·50	32·65	1·0258	6·79	94·6	8·21	41	2,191
10	5·52	32·65	1·0258	6·76	94·3	8·21	35	2,607
20	6·24	33·02	1·0260	6·31	89·5	8·21	36	579
19–3–28.								
0	5·55	32·38	1·0255	6·95	96·9	8·23	32	8,100
2	5·51	32·38	1·0256	6·92	96·3	8·22	42	7,300
5	5·50	32·34	1·0255	6·90	96·0	8·22	38	7,300
10	5·50	32·38	1·0256	6·91	96·2	8·21	39	7,600
20	6·17	33·30	1·0262	....	....	8·21	40	1,900

TABLE 2 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
22–3–28.								
0	5·63	32·01	1·0253	6·91	96·2	8·21	32	7,600
2	5·50	32·01	1·0253	6·90	95·7	8·19	34	8,300
5	5·58	31·87	1·0252	6·95	96·5	8·21	33	8,800
10	5·67	32·25	1·0254	6·87	95·9	8·20	34	7,800
20	5·94	32·89	1·0259	6·77	95·4	8·19	37	6,800
30	5·99	33·04	1·0260	6·78	95·9	8·20	38	3,400
26–3–28.								
0	5·93	31·85	1·0251	6·85	95·7	8·22	33	9,000
2	5·97	31·75	1·0250	6·92	97·0	8·21	36	11,300
5	5·85	31·87	1·0251	6·93	96·8	8·21	37	13,500
10	5·90	32·83	1·0259	6·64	93·5	8·20	35	2,900
20	6·02	33·15	1·0261	6·55	92·8	8·19	38	1,800
30	6·19	33·49	1·0264	6·37	90·7	8·21	40	1,500
29–3–28.								
0	5·95	31·52	1·0248	6·95	97·2	8·22	30	64,000
2	5·95	31·70	1·0250	7·01	98·1	8·22	30	68,000
5	5·97	31·75	1·0250	7·00	98·0	8·20	31	57,000
10	5·95	32·21	1·0254	6·83	96·0	8·20	33	41,000
20	6·02	33·02	1·0260	6·57	93·0	8·20	37	2,000
30	6·09	33·27	1·0262	6·42	91·2	8·20	40	1,050
2–4–28.								
0	6·62	30·36	1·0239	7·43	104·2	8·25	23	73,000
2	6·50	30·44	1·0239	7·53	105·6	8·24	24	61,000
5	6·09	31·62	1·0249	7·32	102·7	8·25	26	133,000
10	6·08	32·63	1·0257	6·65	93·9	8·22	34	8,000
20	6·22	33·34	1·0262	6·25	89·0	8·20	41	1,200
30	6·36	33·68	1·0265	6·18	88·4	8·20	42	115
4–4–28.								
0	6·55	29·54	1·0232	8·37	117·1	8·37	0	180,000
2	6·48	30·98	1·0243	7·79	109·7	8·31	22	248,000
5	6·18	31·99	1·0252	6·73	94·8	8·24	32	60,000
10	6·12	33·02	1·0260	6·56	93·1	8·22	42	2,100
20	6·12	33·15	1·0261	6·53	92·7	8·21	42	1,250
30	6·15	33·25	1·0262	6·37	90·6	8·21	42	890
6–4–28.								
0	6·49	28·56	1·0225	9·33	129·2	8·47	5	128,000
2	6·96	29·93	1·0235	9·77	138·0	8·44	10	199,000
5	6·56	30·76	1·0242	8·28	116·6	8·32	19	510,000
10	6·19	32·24	1·0254	6·81	96·1	8·22	30	56,000
20	6·11	32·81	1·0258	6·55	92·8	8·21	37	3,100
30	6·11	33·19	1·0261	6·41	91·2	8·20	39	1,280
9–4–28.								
0	7·00	28·83	1·0226	7·77	109·0	8·46	0	90,000
2	7·00	28·81	1·0226	7.76	108·8	8·44	0	106,000
5	6·77	30·21	1·0237	7·05	99·5	8·24	24	176,000
10	6·73	30·27	1·0238	7·04	99·1	8·24	27	152,000
20	6·27	32·45	1·0255	6·60	93·6	8·22	34	77,000
30	6·28	33·54	1·0264	6·15	88·0	8·20	46	3,500
12–4–28.								
0	7·15	30·32	1·0237	7·47	106·3	8·24	17	225,000
2	7·14	30·21	1·0237	7·47	106·0	8·26	17	220,000
5	7·13	30·32	1·0238	7·51	106·7	8·25	17	169,000
10	6·40	32·31	1·0254	6·83	96·8	8·23	32	83,000
20	6·17	32·89	1·0259	6·43	91·2	8·21	43	10,000
30	6·30	33·55	1·0264	6·04	86·3	8·21	44	2,400

TABLE 2 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
16–4–28.								
0	7·20	29·88	1·0234	7·43	105·4	8·36	17	14,200
2	6·70	30·97	1·0243	7·06	99·7	8·26	24	99,000
5	6·50	31·97	1·0251	6·71	95·1	8·22	28	24,000
10	6·50	32·30	1·0254	6·72	95·6	8·23	28	13,800
20	6·36	32·72	1·0257	6·57	93·4	8·22	34	10,900
30	6·26	33·76	1·0266	6·00	85·8	8·21	48	4,700
19–4–28.								
0	6·32	33·03	1·0260	6·47	92·1	8·22	24	1,120
2	6·32	33·09	1·0260	6·45	91·9	8·21	25	2,015
5	6·29	33·09	1·0260	6·41	91·3	8·21	28	1,400
10	6·29	33·27	1·0262	6·25	89·0	8·21	28	306
20	6·40	33·94	1·0267	5·90	84·7	8·20	33	400
30	6·40	34·20	1·0269	6·06	87·1	8·21	36	1,008
26–4–28.								
0	7·52	32·74	1·0256	7·19	104·7	8·33	17	101
2	7·43	32·77	1·0256	7·18	104·4	8·30	21	138
5	7·18	32·77	1·0257	7·22	104·6	8·30	22	3,072
10	6·67	33·30	1·0261	6·88	98·8	8·25	27	18,400
20	6·50	33·47	1·0263	6·50	93·1	8·23	34	17,800
30	6·47	33·65	1·0265	6·47	92·7	8·22	35	19,600

TABLE 3.

Date	March 19	22	26	29	April 2	3	4	5	6	9	12	16	17	19	20
Compensation-point of culture in metres.	8	14	17	9	6	–	8	–	5	6	4	18	—	13	—
Secchi disc reading in metres.	7	7½	—	6½	4½	3½	2¾	2⅝	2¾	3½	3	7	9½	11	10½

TABLE 4.

Loch Striven. 22–23/3/28. 0·41 hours sunshine.
Diatom culture of Feb. 20th—7,400 cells per c.c.
12.20 p.m.–11.45 a.m. Initial O_2 content 1. 8·21, 2. 8·18, 3. 8·22 } 8·20

Depth in metres.	Light.		Dark.	Av.	Total O_2 produced.	O_2 produced by 10^6 diatoms.
0	11·26 11·65	11·46	7·70	7·73	3·74	0·51
½	11·64 11·88	11·76	7·75	7·73	4·03	0·54
2	11·34 11·41	11·38	7·74	7·73	3·65	0·49
5	9·51 9·55	9·53	7·71	7·73	1·80	0·23
10	8·37 8·29	8·33	—	7·73	0·60	0·08
20	8·01 8·04	8·02	7·79	7·73	0·29	0·04
30	7·95 8·03	7·99	7·68	7·73	0·26	0·04

TABLE 5.

Loch Striven. 6–7/4/28. 4·25 hours sunshine.
Diatom culture of March 7th—8,300 cells per c.c.
11.35 a.m.–11.15 a.m. Initial O_2 content $\left.\begin{matrix}7{\cdot}71\\7{\cdot}72\end{matrix}\right\}$ 7·72

Depth in metres.	Light.		Dark.	Av.	Total O_2 produced.	O_2 produced by 10^6 diatoms.
0	$\left.\begin{matrix}9{\cdot}11\\9{\cdot}04\end{matrix}\right\}$	9·08	6·86	6·89	2·19	0·26
½	$\left.\begin{matrix}10{\cdot}21\\9{\cdot}84\end{matrix}\right\}$	10·02	6·92	6·89	3·13	0·38
2	$\left.\begin{matrix}8{\cdot}98\\9{\cdot}01\end{matrix}\right\}$	8·99	Lost	6·89	2·10	0·25
5	7·56	7·56	6·86	6·89	0·67	0·08
10	7·15	7·15	6·91	6·89	0·26	0·03
20	Lost		6·94	6·89	——	——
30	$\left.\begin{matrix}7{\cdot}10\\7{\cdot}14\end{matrix}\right\}$	7·12	Lost	6·89	0·23	0·03

TABLE 6.

Date.	Diatom cells per c.c.	Oxygen c.c. per litre.	Oxygen produced.	Oxidisable Organic Matter. Total mg. O_2 per litre.	Production mg. O_2 per litre.	In filtered samples mg. O_2 per l.
4–5–28	575	5·89	0	1·36	0	1·24
7–5–28	6,000	9·07	3·18	2·22	0·86	—
9–5–28	15,700	15.48	9·59	3·15	1·79	—
11–5–28	21,300	17·13	11·24	4·46	3·10	1·22