J. Mar. biol. Ass. U.K. (1956) 35, 1–33
Printed in Great Britain

PLANT PRODUCTION ON THE FLADEN GROUND

By John H. Steele
The Marine Laboratory, Aberdeen

(Text-figs. 1–19)

INTRODUCTION

The quantitative study of phytoplankton production may be pursued in many ways, but these ways can be divided into two general methods of approach. There is, first, the direct estimation of a production rate for a particular sample of the population; for example, the light-dark bottle technique for measuring oxygen production (Gaarder & Gran, 1927; Riley, 1939) and the new ^{14}C technique (Steeman Nielsen, 1952). These estimates are made under conditions which must be, to some extent, artificial. Secondly, there is the direct estimation of relevant variables in the sea (phosphate, oxygen, chlorophyll concentration, etc.) from which production is calculated on the basis of hypotheses about the behaviour of phytoplankton. These hypotheses are, of necessity, simplifications of a mass of laboratory experiments and of previous field work. Riley, Stommel & Bumpus (1949) give a full account of this approach and of the difficulties involved in it.

Since it is, in practice, impossible to use all methods at the same time, a choice of techniques must be made. The second approach was chosen in the investigations here described, for the following reasons: (*a*) the estimation of phosphate, oxygen and chlorophyll are, by now, routine techniques, and comparatively large numbers of samples can be analysed; (*b*) the mathematical techniques for working up the chemical results seemed particularly applicable to the Fladen ground, which is the main area studied; (*c*) from this method one can hope to obtain, not merely an estimate of production, but also some insight into causes of variations in that production.

Thus, by this approach one can provide quantitative data about standing crop and production which are not obtainable from the older methods of planktology. Alone, however, it provides no detailed insight into the species composition of the populations. Yet it is likely that purely quantitative results may be of most use ultimately in providing connexions between plankton and fishing theory. For example, the effects of variations in the food supply to larval fish and to the bottom fauna might be studied in this way. But before these problems can be understood it is necessary to obtain quantitative knowledge of the causal relations between the phytoplankton and its environment.

This is the aim of this paper, and it will be obvious that it depends on the work which Riley has done in organizing past data and developing this new approach.

The results given here cover 3 years, 1951–53. During the summer and autumn of 1951 general surveys of the Fladen ground were made as part of a herring research programme. Phosphate, temperature and salinity were sampled at 0, 20, 50, 100 m and near-bottom (approximately 140 m), at ten to eighteen stations on five occasions. Two stations were also worked during the first half of the year, one in April and one in June. The analyses of these data suggested that it would be of interest to obtain as often as possible from this area chemical samples with close vertical spacing. Therefore in 1952, at one station on the Fladen ground, phosphate, temperature and salinity were sampled at 10 m intervals on seven occasions between May and November.

Finally, in 1953, the twelve stations shown in Fig. 1 were visited nine times. At each of these stations samples were taken for phosphate, oxygen, salinity, temperature, chlorophyll and dry weight of net hauls. Also at stations 1, 7, 8, 10 and 11 phosphate samples were taken on five other occasions. On most occasions net hauls were taken for species analysis of the plankton.

The first part of this paper uses the phosphate data to provide estimates of production for the years 1951–53. In the second part the 1953 production on Fladen is linked with the chlorophyll and dry-weight data in an attempt to describe the causes of the variations in plant populations throughout the year.

It is a pleasure to thank Dr H. W. Harvey, F.R.S., and Dr G. A. Riley for reading and criticizing this work, although its final form is the author's responsibility.

PART I. PHOSPHATE AND PRODUCTION

The General Hydrographic Conditions

In estimating the utilization of phosphate by the phytoplankton, it is necessary to estimate the changes in phosphate distribution due to water movement. The possible types of change in this area are large-scale lateral movements, i.e. currents, and small-scale movements, i.e. lateral and vertical turbulence. In this paper it is postulated that the only changes which need be taken into account directly in the calculations of production are those due to vertical turbulence. First, the extent to which this postulate holds for the Fladen ground will be considered.

Fladen is the south-west corner of the central area of the northern North Sea lying between the prime meridian and the Norwegian deeps and having a depth of 100–140 m (Fig. 1). During the winter and early spring there are large-scale hydrographic changes in this region due to the inflow of Atlantic water round the north of Shetland. (This can be seen from the surface salinity charts for the North Sea prepared by the Conseil Permanent International pour l'Exploration de la Mer, 1933.) After March, however, the major changes take place in the uppermost layers only. This is shown by the fact that from April to September of any year the bottom temperatures, 6·0–7·5° C, within the dotted area (Fig. 1) remain approximately constant at a value lower than that of any of the surrounding water masses. Since temperature is also constant from the foot of the thermocline (30–70 m) to the bottom, it follows that most if not all of the water below the thermocline which has this lower temperature during the summer must have been in this area since the spring. This water mass forms a cold, and therefore heavy core in the centre of the northern North Sea; the conditions on Fladen are typical in this respect. The possibility of changes within this core, either as circulation or as shifts of position, will be considered when the 3 years' results are discussed in detail.

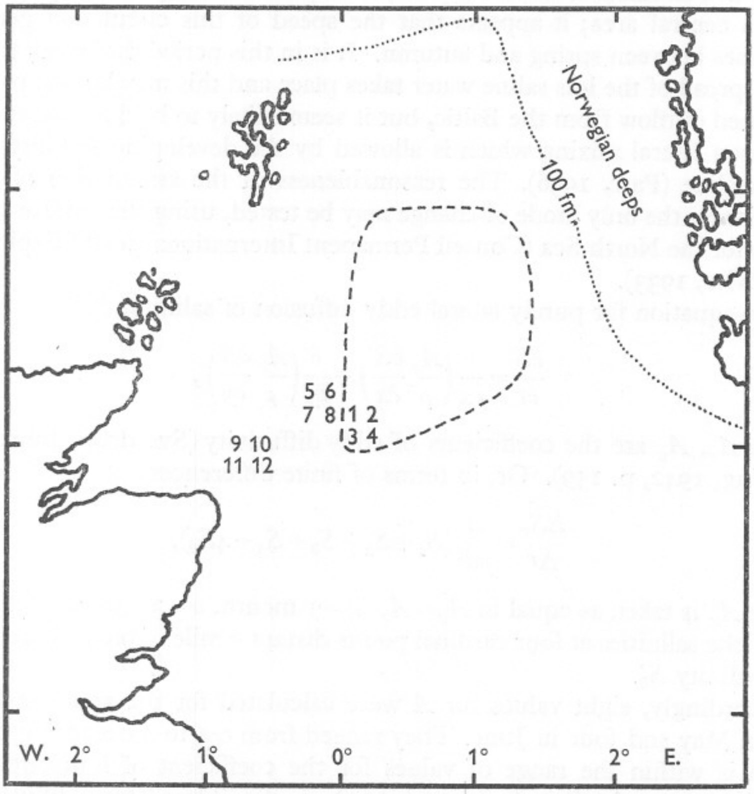

Fig. 1. Positions of stations worked in 1953 in the northern North Sea. 1–4: Fladen Group. 5–8: Northern Group. 9–12: Inshore Group. The dotted line indicates roughly the area inside which there is a nearly constant bottom temperature throughout the spring and summer.

In the surface layers above this cold core, however, large salinity changes occur during the summer and early autumn. These are produced by the westward spread of low salinity water from the current which issues from the Baltic and flows up the Norwegian coast. From the results of drift-bottle experiments, Tait (1937) has inferred that the surface waters of the northern North Sea circulate as an anti-clockwise eddy which occupies nearly the whole of this central area; it appears that the speed of this circulation generally decreases between spring and autumn. It is in this period, however, that the main spread of the less saline water takes place and this may be due partly to increased outflow from the Baltic, but it seems likely to be due largely to the increased lateral mixing which is allowed by the developing stability of the thermocline (Parr, 1936). The reasonableness of the assumption of lateral diffusion as the only mode of change may be tested, using the surface salinity charts for the North Sea (Conseil Permanent International pour l'Exploration de la Mer, 1933).

The equation for purely lateral eddy diffusion of salinity, S, is

$$\frac{\partial S}{\partial t}=\frac{\partial}{\partial x}\left(\frac{A_x}{\rho}\frac{\partial S}{\partial x}\right)+\frac{\partial}{\partial y}\left(\frac{A_y}{\rho}\frac{\partial S}{\partial y}\right),$$

where A_x, A_y are the coefficients of eddy diffusivity (Sverdrup, Johnston & Fleming, 1942, p. 159). Or, in terms of finite differences,

$$\frac{\Delta S_0}{\Delta t}=\frac{A}{\rho a^2}(S_1+S_2+S_3+S_4-4S_0),$$

where A_x is taken as equal to $A_y=A$, $\Delta t=1$ month, $a=30$ miles. S_1, S_2, S_3, S_4 are the salinities at four cardinal points distant a miles from a chosen point with salinity S_0.

Accordingly, eight values for A were calculated for the area considered, four in May and four in June. They ranged from $0{\cdot}3$ to $2{\cdot}0\times10^{+7}$ g/cm/sec, which is within the range of values for the coefficient of horizontal eddy diffusivity given by Sverdrup *et al.* 1942, p. 485. Thus lateral diffusion can be taken as a sufficient explanation of the changes in salinity. It is probable that the effects of this diffusion on the phosphate concentration on Fladen will be negligible since the diffusion has occurred across an area having the same characteristics as Fladen. This is shown in the charts of summer phosphate distribution (Johnston, 1953, fig. 5; and 1954, fig. 8).

Evaluation of 'Biological Change' from Phosphate Observations

By far the largest part of the data collected consists of inorganic phosphate observations. These will be used to provide the estimates of production. The profiles of temperature, phosphate and oxygen for a station on Fladen are shown in Fig. 2.

The calculations are based on two equations (Sverdrup *et al.* 1942, p. 159):

$$\frac{\partial p}{\partial t}=\frac{\partial}{\partial z}\left(\frac{A_p}{\rho}\frac{\partial p}{\partial z}\right)-\frac{\partial C'}{\partial t}+\frac{\partial R'}{\partial t},$$

$$\frac{\partial T}{\partial z}=\frac{\partial}{\partial z}\left(\frac{A_t}{\rho}\frac{\partial T}{\partial z}\right),$$

where p = phosphate concentration, C' = consumption of inorganic phosphate by plants, R' = return of inorganic phosphate due to regeneration from

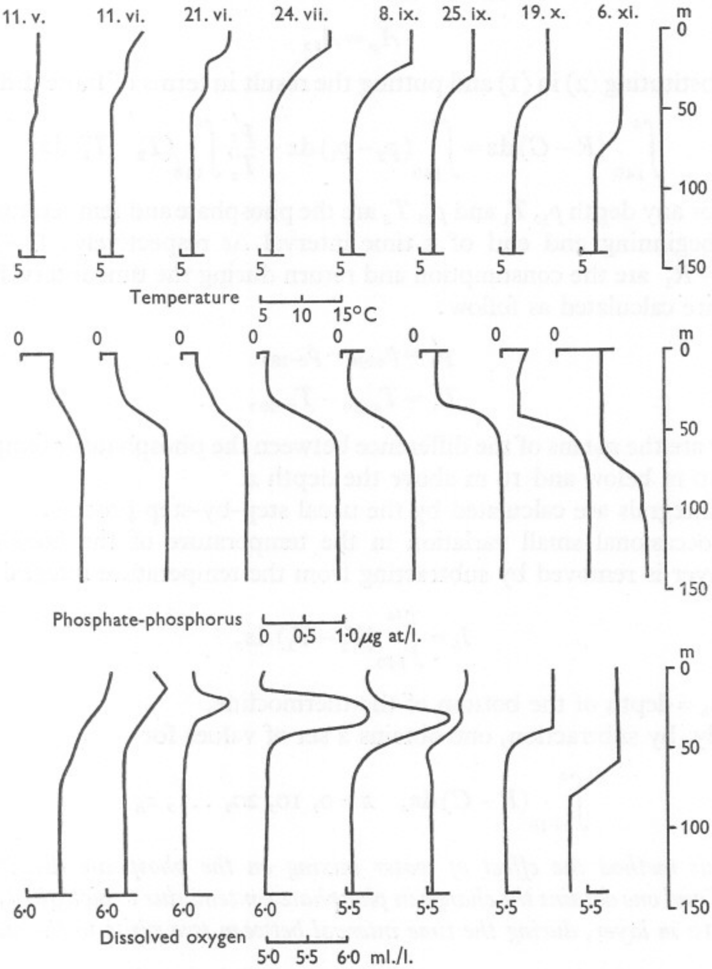

Fig. 2. The profiles of temperature, phosphate-phosphorus and dissolved oxygen at Station 1 during 1953.

organic compounds, T = temperature, z = depth, and A_p, A_t = coefficients of vertical diffusivity of phosphate and temperature respectively.

Integrating both equations from z to 140 m (bottom)

$$\frac{\partial}{\partial t}\int_{140}^{z}(p+C'-R')\,\mathrm{d}z=\left[\frac{A_p}{\rho}\frac{\partial p}{\partial z}\right]_{140}^{z}, \tag{1}$$

$$\frac{\partial}{\partial t}\int_{140}^{z}T\mathrm{d}z=\left[\frac{A_t}{\rho}\frac{\partial T}{\partial z}\right]_{140}^{z}. \tag{2}$$

Taking $$A_p\frac{\partial p}{\partial z}=A_t\frac{\partial T}{\partial z}=0 \text{ at the bottom}$$

and $$A_p=A_t,$$

then substituting (2) in (1) and putting the result in terms of finite differences,

$$\int_{140}^{z}(R-C)\,\mathrm{d}z=\int_{140}^{z}(p_2-p_1)\,\mathrm{d}z-\frac{p'_z}{T'_z}\int_{140}^{z}(T_2-T_1)\,\mathrm{d}z \tag{3}$$

where for any depth p_1, T_1 and p_2, T_2 are the phosphate and temperature values at the beginning and end of a time interval Δt respectively; $C=C'_2-C'_1$, $R=R'_2-R'_1$ are the consumption and return during the time interval Δt, and p'_z, T'_z are calculated as follow:

$$p'_z=p_{z+10}-p_{z-10},$$
$$T'_z=T_{z+10}-T_{z-10},$$

i.e. they are the means of the difference between the phosphate or temperature values 10 m below and 10 m above the depth z.

The integrals are calculated by the usual step-by-step process.

The occasional small variation in the temperature of the homogeneous lower layer is removed by subtracting from the temperature integral

$$I_h=\int_{140}^{z_h}(T_2-T_1)\,\mathrm{d}z,$$

where z_h = depth of the bottom of the thermocline.

Finally, by subtraction, one obtains a set of values for

$$\int_{z+10}^{z}(R-C)\,\mathrm{d}z,\quad z=0, 10, 20, \ldots, z_h. \tag{4}$$

By this method the effect of water mixing on the phosphate distribution is removed and one obtains the change in phosphate content, due to biological activity, in each 10 m layer, during the time interval between two visits to the station.[1]

---

[1] Because equation (3) is an approximation, errors will be introduced whose magnitude will depend on the size of the changes in T, p, $\partial T/\partial z$ and $\partial p/\partial z$ between two stations. These are usually small so long as the time interval is not too large.

In practice, because of the low values of the gradients at 10 m, it is usually necessary to take the 0–10 and 10–20 m layers together. Also, of course, the layer from the depth z_h to the bottom cannot be subdivided.

A typical calculation is shown in Table I.

TABLE I. CALCULATION OF 'BIOLOGICAL CHANGE' IN 10 M LAYERS FOR 11–21 JUNE 1953 AT 58° 25′ N., 0° 20′ E.

m	$\int_{140}^{z}(T_2-T_1)\,dz$	p'_z	T'_z	$^*\frac{pz'}{Tz'}\int_{140}^{z}(T_2-T_1)\,dz$	$\int_{140}^{z}(p_2-p_1)\,dz$	$\int_{140}^{z}(R-C)\,dz$	$\int_{z+10}^{z}(R-C)\,dz$
0	—	—	—	—	0·61	0·61	−0·02
20	8·4	−0·110	1·78	−0·05	0·58	0·63	−0·12
30	9·6	−0·285	1·07	−0·25	0·50	0·75	+0·06
40	5·4	−0·525	1·84	−0·15	0·54	0·69	+0·12
50	0·4	−0·295	0·90	−0·01	0·56	0·57	+0·08
60	0·2	−0·015	0·03	−0·01	0·48	0·49	+0·08
70	0·1	−0·020	0·04	0	0·41	0·41	+0·41
140	0	—	—	0	0	0	

* To convert to μg at/cm² the figures have been multiplied by 10^{-1}.

Analysis of Phosphate Observations

If the figures given by (4) are to be used to provide estimates of production, then it is necessary to make hypotheses about the ways in which consumption and return of inorganic phosphate occur in the sea.

As expected, the values of (4) show a decrease in the upper and an increase in the lower layers, with the change-over occurring at about 30–40 m. This depth of zero change will be called the 'zero level'.

Thus the simplest assumptions would be: (*a*) only production occurs above the zero level and only regeneration below; (*b*) the production in terms of carbon can be found by using a fixed carbon-phosphorus ratio (Sverdrup *et al.* 1942, p. 237).

The objections to these postulates must be considered; the main ones appear to be as follows:

(i) There will be some regeneration above the zero level. This regeneration may occur at a rate equal to the mean rate of regeneration below the zero level, or it may be much greater since there is more phytoplankton above the zero level than below it. The factors involved in regeneration are complex. Since the plants in the euphotic zone are assumed to be living and will not normally die until they sink below the euphotic zone it may be that regeneration from direct decay of plants will be very small. Whether or not regeneration from zooplankton metabolism will be equally spread throughout the water column is at present unknown. Thus no good estimate can be given for the effect of regeneration of phosphate above the zero level. In the conclusion to this part of the paper an estimate is made of the effect of assuming equal regeneration at all depths, but in the body of the paper assumption (*a*) has been used as being the simplest method of stating the results.

(ii) There is evidence that plants can use organic, as well as inorganic, phosphorus compounds to meet their phosphate needs (Chu, 1946; Harvey, 1953). This is an unknown factor to the extent that this evidence comes from laboratory experiments and the process has not been demonstrated under natural conditions. (It has also been suggested (Lwoff, 1951) that some flagellates may be able to ingest particles of organic matter. This, however, does not affect estimates of basic production, which are in terms of the conversion of carbon from inorganic to organic form.)

(iii) The most serious objections to the second postulate comes from laboratory work on phosphate uptake of phytoplankton. Ketchum (1939) showed that in a reduced phosphate concentration ($< 0{\cdot}55$ μg at/l.) diatoms can continue to photosynthesize carbon without a corresponding uptake of phosphate. The phosphate concentration near the surface in the North Sea is less than 0·55 μg at/l. throughout most of the summer. Ketchum showed that cells in a deficient medium could double in number without the uptake of phosphate. To discover the possible effects of this, consider the position at the end of the spring outburst on Fladen. On 11 June 1953 the population in the euphotic zone, as estimated from the chlorophyll content, contained 2·4 g carbon/m^2. If this doubled itself without consuming phosphate then the increase in production would be 2·4 g carbon/m^2. But this is only 5% of the year's production. Further, before this deficient population can again divide, there must be replacement of the phosphate deficiency, and this will be shown by the phosphate changes. For these reasons, the effect of phosphate deficiency may not be appreciable.

These objections must be borne in mind when the validity is considered of the following estimates as absolute measures of production. However, they should not seriously affect conclusions about variations in production from year to year or place to place, and such results are among the main aims of this paper.

Production on Fladen

For 1951, the temperature and phosphate values were obtained by choosing from extensive surveys those stations near the centre of the Fladen Ground that showed similar structure (the stations on the south and west edges of Fladen showed greater mixing and, often, salinity changes). From the average of the chosen stations the changes above and below 35 m were calculated, and the estimated production is given as a histogram (Fig. 3A). These values will not be particularly accurate due to the small number of depths at which chemical observations were made; thus it is not possible to study the data in more detail.

For 1952, the production is again given as a histogram (Fig. 4A), while the profiles for each interval are shown in Fig. 6.

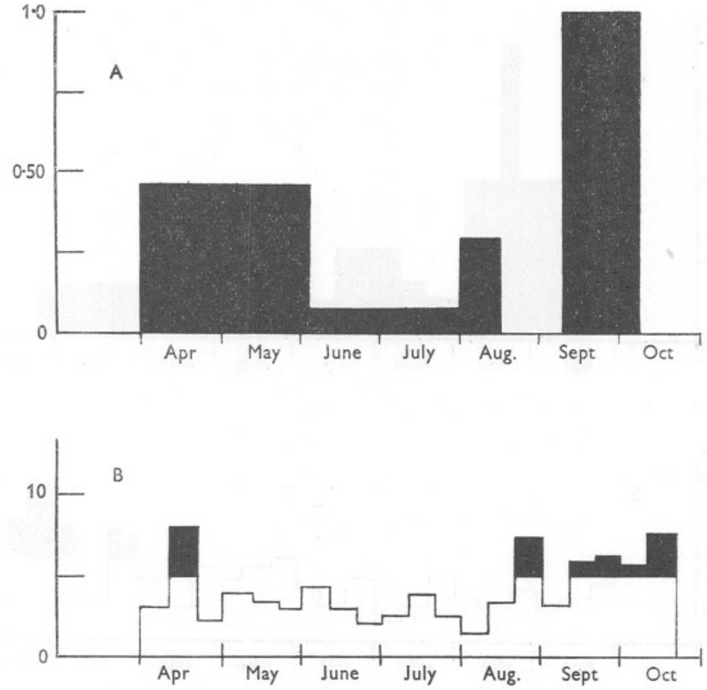

Fig. 3. 1951: A, production rate on Fladen, g carbon/m^2 day; B, wind velocity, m/sec.

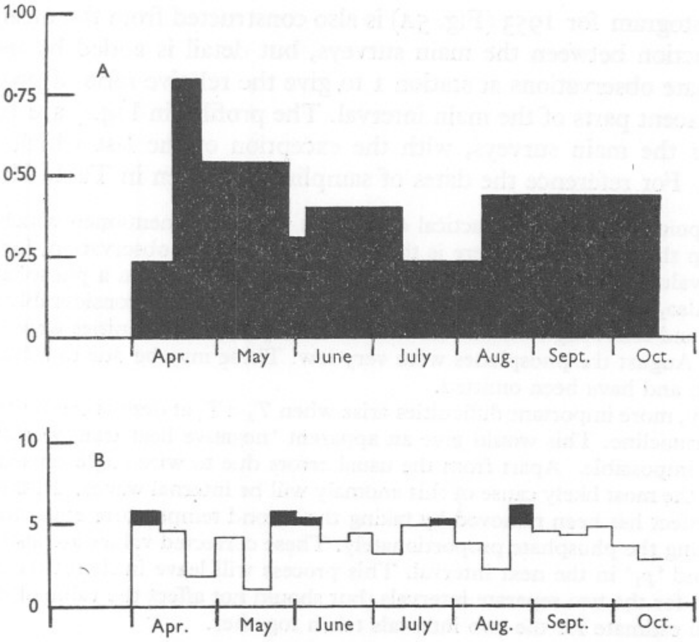

Fig. 4. 1952: A, production rate on Fladen, g carbon/m^2 day; B, wind velocity, m/sec.

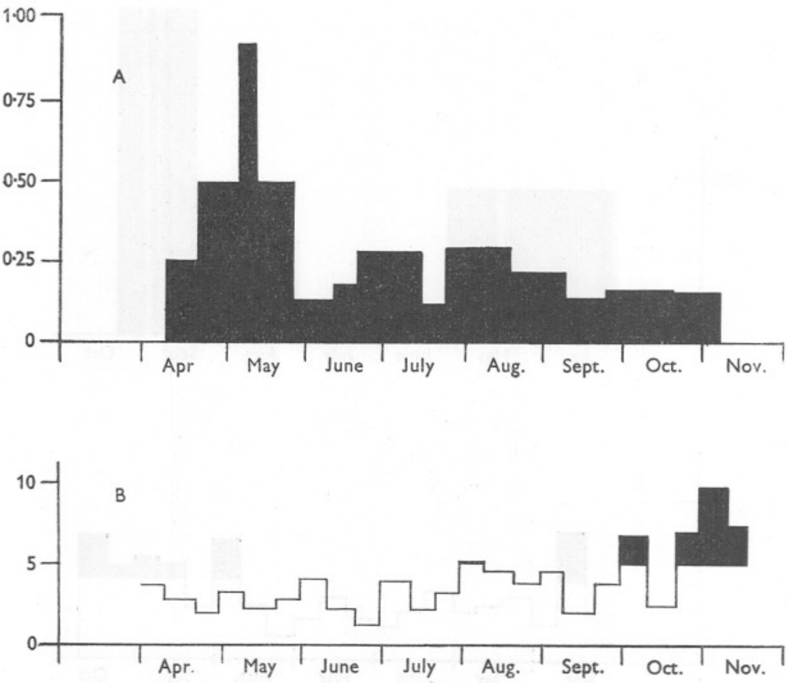

Fig. 5. 1953: A, production rate on Fladen, g carbon/m^2 day; B, wind velocity, m/sec.

The histogram for 1953 (Fig. 5A) is also constructed from the mean values for production between the main surveys, but detail is added by using the intermediate observations at station 1 to give the relative ratio of production in the adjacent parts of the main interval. The profiles in Fig. 7 are from the means for the main surveys, with the exception of the last which is from station 1. For reference the dates of sampling are given in Table II.

At this point some of the practical difficulties should be mentioned which arise in working up the data. First, there is the occasional aberrant observation, for which a corrected value is taken by interpolation from a graph (e.g. from a phosphate-depth profile). Also, on two occasions, all values at one station differed considerably from the preceding and following stations. At station 1 on 15 July the salinities were very low, and on 18 August the phosphates were very low. These may be due to a faulty standardization and have been omitted.

Secondly, more important difficulties arise when $T_2 < T_1$ at depths on the lower part of the thermocline. This would give an apparent 'negative heat transport', which is physically impossible. Apart from the usual errors due to wire angle caused by ship drift, etc., the most likely cause of this anomaly will be internal waves. In the calculations the effect has been removed by taking the second temperature equal to the first and adjusting the phosphate proportionately. These corrected values are also used for the 'T_1' and 'p_1' in the next interval. This process will leave in doubt the values of production for the two separate intervals, but should not affect the value of their sum as the total estimate for the two intervals taken together.

However, once such inaccuracies have been allowed in a few particular cases, it must be admitted that they may occur in others without their presence being noticed (i.e. without $T_2 < T_1$). Until detailed knowledge is available of the variations due to internal waves, the limits of these errors cannot be given.

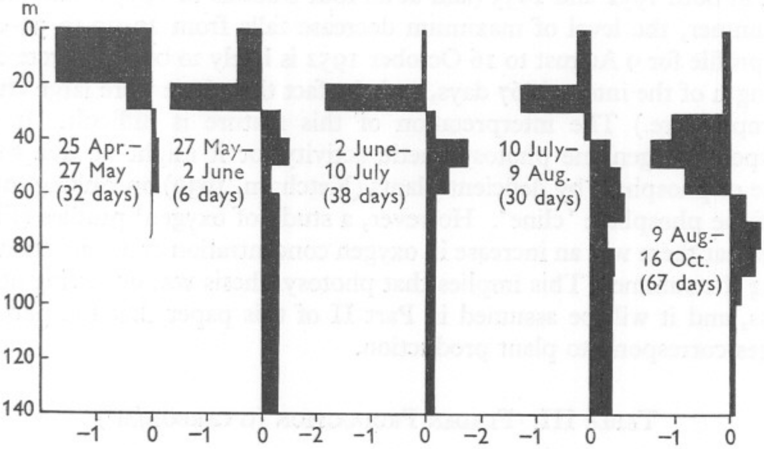

Fig. 6. 1952: profiles of 'biological change' in phosphate on Fladen in $10^2 \times \mu g$ at./cm² day

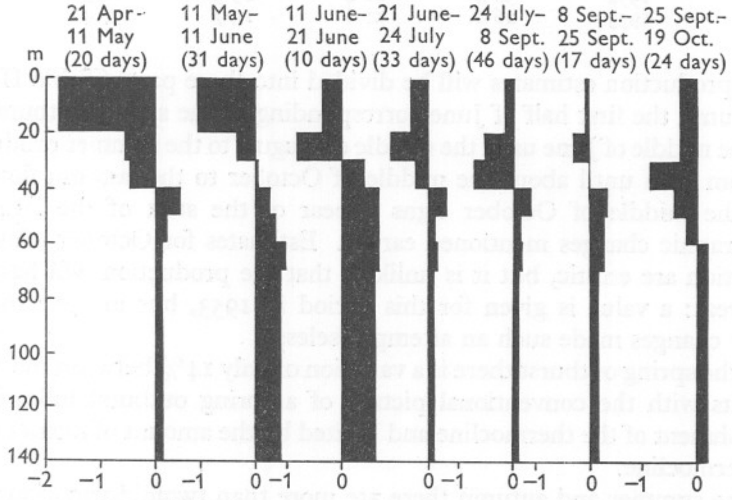

Fig. 7. 1953: profiles of 'biological change' in phosphate on Fladen in $10^2 \times \mu g$ at./cm² day

TABLE II. DATES OF SAMPLING

1951	2. iv, 3. vi, 30. vii, 16. viii, 10. ix, 7. x
1952	15. iv, 25. iv, 27. v, 2. vi, 10. vii, 9. viii, 16. x
1953	5. iv, 21. iv*, 5. v, 11. v*, 26. v, 11. vi*, 21. vi*, 15. vii, 24. vii*, 18. viii, 8. ix*, 25. ix, 19. x, 6. xi

* Main surveys.

The profiles will be discussed first. Until the beginning of June they give the conventional picture of maximum production in the upper 20 m. From June onwards, maximum decrease in phosphate occurs below 20 m. This is found in both 1952 and 1953 (and at all four stations in 1953). Also, during the summer, the level of maximum decrease falls from 20–30 to 30–40 m. (The profile for 9 August to 16 October 1952 is likely to be inaccurate due to the length of the interval, 67 days, and the fact that there were large changes of temperature.) The interpretation of this feature is difficult. It could correspond to genuine photosynthetic activity, or it might be due to dark uptake of phosphate by deficient plants (Ketchum, 1939) on sinking into the top of the phosphate 'cline'. However, a study of oxygen[1] profiles (Fig. 2), shows that there was an increase in oxygen concentration at 20 and then 30 m during the summer. This implies that photosynthesis was occurring at these depths, and it will be assumed in Part II of this paper that the phosphate changes correspond to plant production.

TABLE III. FLADEN PRODUCTION (G CARBON/M^2)

	Spring	Summer	Autumn	Total
1951	28·0	8·9	28·0	64·9
1952	30·4	22·4	29·5	82·3
1953	26·1	17·6	13·7	57·4

The production estimates will be divided into three parts (Table III): the period until the first half of June corresponding to the spring outburst; that from the middle of June until the middle of August to the summer production; and from then until about the middle of October to the autumn flowering. After the middle of October signs appear of the start of the large-scale hydrographic changes mentioned earlier. Estimates for October–November production are erratic, but it is unlikely that the production will have been very great: a value is given for this period in 1953, but in 1952 the large salinity changes made such an attempt useless.

For the spring outburst there is a variation of only 14% between the 3 years. This fits with the conventional picture of a spring outburst following the establishment of the thermocline and limited by the amount of nutrient above this thermocline.

In the summer and autumn there are more than twofold variations in the production. The variations in the summer production will depend on three factors: (i) a general reduction in phosphate concentration in the euphotic zone from the June level of approximately 0·25 μg at/l. down to values below 0·10 μg at/l. (this may correspond with the ability of dinoflagellates to

---

[1] The analysis of the oxygen data involves discussion of several difficulties, and it is intended to use these data in conjunction with future and more detailed work in further attempts to understand these problems.

assimilate phosphate at lower concentrations than the spring forms—Barker, 1935; Braarud & Rossavik, 1951); (ii) an increase in the depth at which maximum consumption occurs; (iii) the consumption of any phosphate carried upwards by mixing.

To show that only the third of these factors varies considerably, the figures for phosphate decrease are separated into their components in Table IV. $\int p_2 - p_1 =$ changes above the zero level due to (i) and (ii). $I_p =$ upwards transport through the zero level corresponding to (iii). The net decrease is given by $\int (p_2 - p_1) - I_p$, in μg at /cm.^{2}.

TABLE IV. TRANSPORT THROUGH, AND CHANGE ABOVE, THE ZERO LEVEL

1952	$\int p_2 - p_1$	I_p	1953	$\int p_2 - p_1$	I_p
2. vi–10. vii	−0·71	0·44	11. vi–21. vi	0·07	0·15
10. vii–9. viii	−0·04	0·51	21. vi–24. vii	−0·67	0·03
9. viii–16. x	+0·12	1·92	24. vii–8. ix	0	0·73
			8. ix–25. ix	+0·18	0·27
			25. ix–19. x	−0·20	0·20
Total	−0·63	2·87		−0·62	1·38

Further, in 1951, when there was a very steep thermocline and apparently little transport, the summer decrease is 0·70 μg at/cm.^{2}. This value, with those of 0·75 and 0·60 for 1952 and 1953, shows that the variation in the summer due to the first two factors is comparatively small. This basic summer production is estimated at 8·7 g carbon/m^2 and has its effect at the end of June and the beginning of July. After that, production is solely dependent on the upwards transport of phosphate.

Thus, in the autumn, production depends on the breakdown of the thermocline. This occurred during September in 1951 and 1952, but in 1953 did not take place until after the middle of October, and it appears that owing to this delay the autumn production was less than half that of the previous year.

These variations in transport can best be shown in terms of the heat transported downwards through 40 m. Fig. 8 illustrates the differences between the three years. In a region such as Fladen, which is not subject to strong currents, vertical mixing must be almost entirely due to wind. Below each of the histograms of production is shown the corresponding wind data (Figs. 3B, 4B, 5B) for the northern North Sea (supplied by courtesy of the German Hydrographic Institute, Hamburg, through the Conseil Permanent International pour l'Exploration de la Mer). These are in the form of 10-day means calculated from atmospheric pressure gradients. The exact effect of strong winds on the thermocline is not known, especially in relation to the time factor. Thus it is not possible to say whether 10-day means should be a reliable guide in comparing wind and thermocline changes. However, the main variations noted in mixing can be related to the wind histograms.

The greater amount of summer mixing in 1952 than in the other 2 years was due to the fact that the thermocline, which had half formed by the end of May, was partially broken down at the beginning of June with the result that, for the remainder of the year, the thermocline was not as steep as in 1951 and 1953. From the wind histograms it can be seen that only in 1952 were there mean winds in June exceeding 5 m/sec.

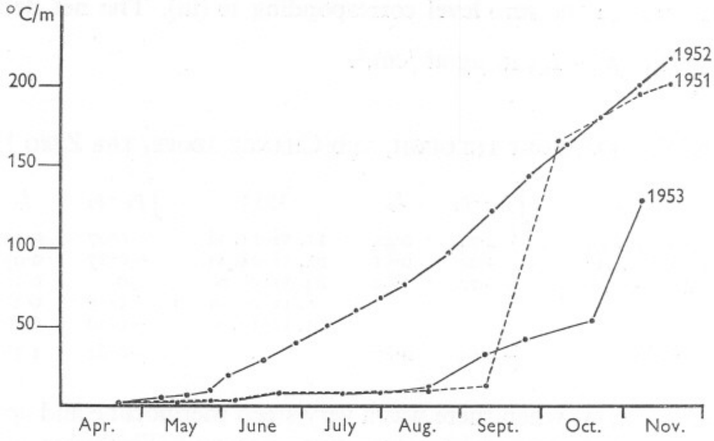

Fig. 8. Increase in the heat content below 40 m on Fladen.

Since it is reasonable to suppose that the strength of wind required to break down the thermocline is roughly inversely proportional to the steepness of the thermocline then, unless the thermocline is partly broken during early June, it is less likely to be broken throughout the remainder of the summer. For this reason, gales at the beginning of June should be critical in determining the excess of summer production over the basic amount previously mentioned.

During the first 10 days of August 1953 there were winds in excess of 5 m/sec which may have caused the transport noted for August. However, from then until October there are no signs of strong winds, and this feature corresponds to the delayed and consequently small production in the autumn, compared with 1951 and 1952 when there were winds greater than 5 m/sec.

Thus the expected chain of relations, strong winds—mixing—production, can be seen to operate on Fladen.

Phosphate Regeneration on Fladen

The estimates of regeneration (Figs. 9, 10) are extremely variable, both within years and between years. To bring any order into them requires a fair amount of 'inspired guessing' at the reasons for these variations, and so the conclusions reached are, to that extent, speculative.

First, it is necessary to consider the effect of known errors in phosphate observations for June 1953. Analyses of duplicate samples from station 1, 21 June 1953, were carried out at the Plymouth Marine Laboratory. These gave consistently lower values than those from the analyses in this laboratory; also there was an apparently greater scatter in our own results. Shortly afterwards the galvanometer in use in this laboratory broke down completely, and it is probable that the onset of the defect caused this difference in results.

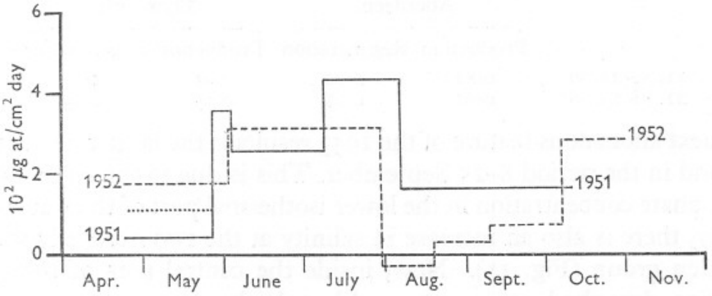

Fig. 9. Regeneration rate of inorganic phosphorus on Fladen in 1951 and 1952. . . ., correction made by taking winter phosphate concentration in 1952 as 0·73 μg at/l. (see text). ($10^2 \times$ μg at/cm² day.)

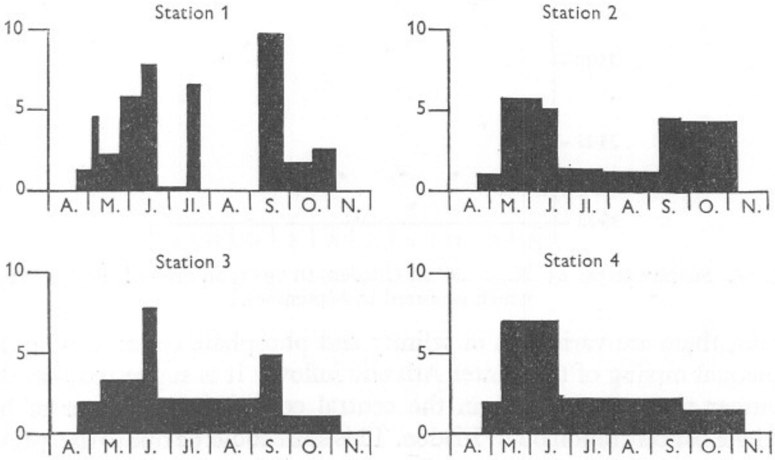

Fig. 10. Regeneration rate of inorganic phosphorus at the four Fladen stations in 1953 (in $10^2 \times$ μg at/cm² day).

In Table V the effects of these differences are given. The effect on production is less than 10% and nearly balances over the two intervals. But, although regeneration also nearly balances, the internal differences are very large. This is due to the fact that regeneration is very sensitive to the absolute value of the phosphate concentration, whereas production depends more on the phosphate gradient. This example is of interest in showing the effect of inaccuracies on the phosphate observations, and because of this, no alterations were made in the production estimates. The data have been used to correct both the 1953 estimates for station 1 and those for the other stations in the Fladen Group, and explains one of the differences between the histograms of regeneration for 1951, 1952 (Fig. 9) and 1953 (Fig. 10).

TABLE V. COMPARISON OF PHOSPHATE ESTIMATES (μg AT/CM^2)

	Aberdeen		Plymouth	
	Production	Regeneration	Production	Regeneration
11. v.–21. vi	0·82	2·02	0·91	1·22
21. vi–15. vii	0·62	0·01	0·55	0·83

The next anomalous feature of the 1953 results is the large rate of regeneration found in the period 8–25 September. This is due to the large increase in the phosphate concentration in the lower isothermal part of the water column. However, there is also an increase in salinity at the two northerly stations of the Fladen group (Fig. 11). Now, inside the central area of the northern North Sea described on pp. 2–4, although the temperature is relatively constant, there are variations in salinity and phosphate concentration due to the unequal mixing of the winter Atlantic inflow. It is suggested that during September there was a shift in the central core, bringing water of higher phosphate concentration on to Fladen. This shift could be due to the 'pressure' begun by another Atlantic inflow. Fraser (1954), from plankton distributions, and Tait (1954) show that during the summer there was a surge of oceanic water round the north of Shetland, and that during the autumn this water penetrated into the North Sea till, by the end of the year, it covered the Fladen Ground. The plankton collections taken on Fladen agree with this general picture, which thus provides a reasonable explanation for the shifting water mass.

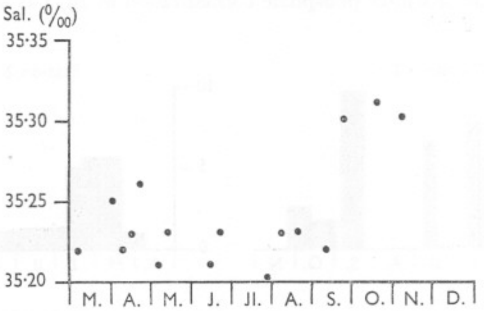

Fig. 11. Salinity at 58° 25′ N., 0° 20′ E. (Fladen) in 1953; an example of the changes which occurred in September.

A further demonstration of the anomalous nature of this feature is shown in the graphs of integrated content of phosphate in the water column (Fig. 12), where the graph for 1953 suddenly rises much above the content at the beginning of the season. This anomaly has been removed by using the mean rate of regeneration of the surrounding intervals.

Again, from Fig. 12, it is possible to notice another anomaly. In 1952 the spring regeneration was much lower than in the other 2 years. Now the winter phosphate concentration is obtained from three phosphate values, 0·73, 0·76, 0·79 μg at/l., in the lower part of the water column on 25 April; the mean 0·76 μg at/l. was chosen, but in Fig. 12 this is seen to put the winter level abnormally high compared with the remainder of the curve (even though there was more production in this year than in the other two). A reduction in the winter level to 0·73 μg at/l. would raise the estimate of spring regeneration from 0·32 μg at/cm^2 to 0·56 μg at/l.; at the same time the reduction in the spring production would be 1·7 g carbon/m^2, bringing the total down to 28·7 g carbon/m^2, which is in fact nearer to the other two estimates.

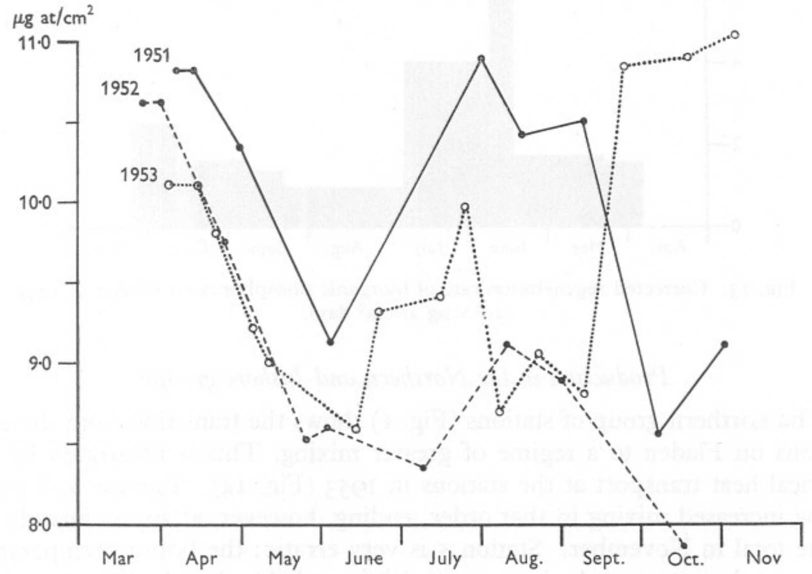

Fig. 12. Integrated content of inorganic phosphorus on Fladen in the years 1951–3 (μg at/cm^2).

The results of these various corrections are shown in Figs. 9 and 13, which are the histograms of regeneration for Fladen. They show that the main regeneration after the spring outburst occurs between the middle of June and end of July. Thus, the maximum rate of regeneration occurs about 2 months after the maximum rate of production, and this interval also corresponds to the interval between the end of the spring outburst (end of May) and the beginning (end of July) of the low rate of regeneration found in the summer of 1951 and 1953.

From this it appears that regeneration occurs about 2 months after production. Again, this effect can be seen from the graphs of Fig. 12, where the interval between the spring trough and summer peak is approximately 2 months, and the phosphate content at this summer peak in 1951 and 1953 is about the same as the winter level.

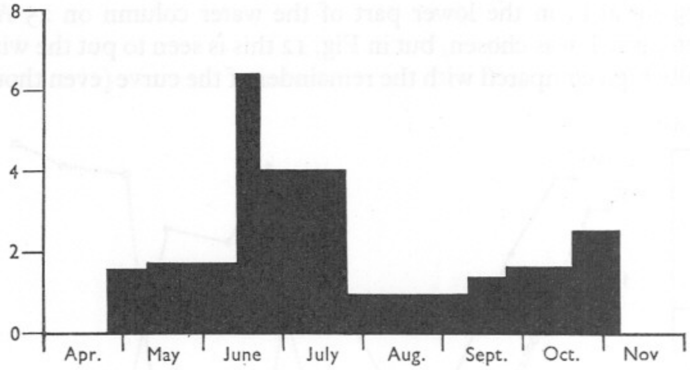

Fig. 13. Corrected regeneration rate of inorganic phosphorus on Fladen in 1953 ($10^2 \times \mu$g at/cm² day).

Production in the Northern and Inshore groups

The northern group of stations (Fig. 1) shows the transition from the conditions on Fladen to a regime of greater mixing. This is illustrated by the vertical heat transport at the stations in 1953 (Fig. 14). Stations 6, 8 and 7 show increased mixing in that order, ending, however, at approximately the same total in November. Station 5 is very erratic; the bottom temperature does not show any regular increase, and it is probable that the lateral gradient in the amount of mixing is sufficiently steep for these changes to be due to small horizontal shifts in the water between times of sampling. The temperature profiles for station 7 are given in Fig. 15A.

Calculations for production were made in the same way as for Fladen, although the postulate of purely vertical water movement may not always be satisfactory.

During the summer of 1953, the greater mixing gave rise to an increased production which probably equals that of the summer production on Fladen in 1952 (the maximum on Fladen in the three years considered).

In the autumn of 1953, there is much larger production than on Fladen. An explanation of this may be found in Fig. 14. The heat transport by 6 November is much higher than on Fladen 1953 and is almost the same as that found on Fladen in 1951 and 1952. Thus it appears that the breakdown of the thermocline occurred earlier than on Fladen. This is confirmed by the production figures for station 7, where it is shown that the main part of the autumn flowering occurred before 19 October. On Fladen (station 1) there was but little production before that date in 1953.

Thus the northern group, which is in an area of hydrographic change between the conditions on Fladen and those inshore, shows corresponding changes in the production.

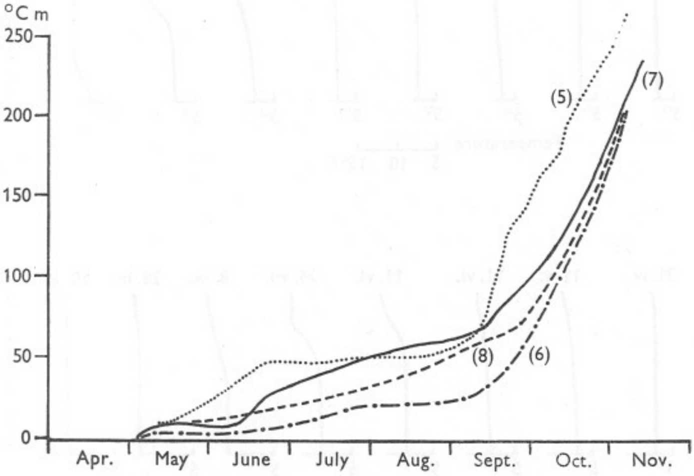

Fig. 14. Increase in heat content below 40 m at the Northern group of stations in 1953.

TABLE VI. 1953: PRODUCTION IN NORTHERN GROUP (G CARBON/M^2)

Station no.	15. iv–11. vi	11. vi–8. ix	8. ix–25. ix	25. ix–19. x	19. x–6. xi	Total
5	24·2	20·5	8·3	27·0		80·0
6	23·2	18·7	5·7	20·9		68·5
7	23·7	36·5	19·0		7·1	86·3
8	28·9	25·7	4·3	11·6		70·5

The inshore group of stations lies in an area of confused water movement with large changes in salinity. From an examination of the salinities it seems likely that most of the time these changes are due to local wind drift which will produce variations in the seawards limit of the less saline coastal water. However, there will be occasions when the changes are not local, but will involve the intrusion of water from other regions. The temperature profiles for station 11 are given in Fig. 15B.

Thus it is obvious that the postulate of purely vertical water movement does not hold, yet, since these lateral changes may be of an oscillatory nature for much of the year, the total estimates of production, considered as a balance of these variations may give a reasonable estimate for the year.

The values of yearly production for the four stations were 103·9, 108·1, 108·4 and 127·2 g carbon/m².

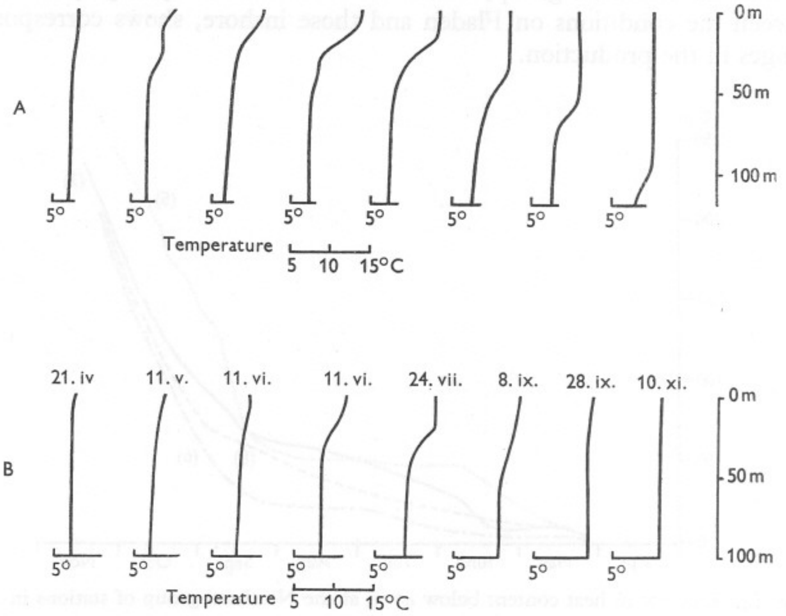

Fig. 15. The profiles of temperature, at A a station in the Northern group, and B a station in the Inshore group.

TABLE VII. SUMMARY OF THE ESTIMATES OF PRODUCTION (G CARBON/M²)

Group	1951	1952		1953			
			Station	1	2	3	4
Fladen	64·9	82·3		59·5	53·6	56·3	62·2
			Station	5	6	7	8
Northern	—	—		79·9	68·4	86·2	70·5
			Station	9	10	11	12
Inshore	—	—		127·2	103·9	108·1	108·4

Discussion

The values for yearly production given in Table VII show variations between years on Fladen and between groups in the year 1953. The main conclusion of this part is that the differences in the Fladen results can be explained by the variations in mixing, and these variations in turn can be linked with the wind data and show the critical effects of high winds near the beginning of June and at the middle of September.

Fladen was chosen as typical of those parts of the North Sea where least mixing occurs. The other groups were added to show the effects of increased mixing and in their values for production they reflect this. Thus in 1953 the inshore group had a production nearly twice that of the Fladen group, while the northern stations had intermediate values.

This increased mixing will be largely due to the increase in the effect of tidal movement. On Fladen the wind effectively controls mixing, and it was possible to relate the two. Such relations would not be demonstrated in the more complex cases when wind and tide combine.

As was stated earlier (p. 7) the effect of regeneration above the zero level has been ignored. In Figs. 6 and 7 the depth distribution of regeneration below the zero level is shown. Although there are variations with depths, there is no sign of a consistent increase in the rate of regeneration just below the zero level. Thus the assumption that the regeneration rate is constant with depth may be satisfactory. On this basis the addition to the values of production already given would be about 17 g carbon/m^2 on the Fladen and Northern groups and about 31 g at the Inshore group. This is an increase of between a quarter and a third of the original estimates.

TABLE VIII. COMPARISON OF NORTHERN NORTH SEA, ENGLISH CHANNEL AND GEORGES BANK

	Winter phosphate (g at/l.)	Yearly production (g. carbon/m^2)	Maximum plant population (mg chlorophyll/m^2)	Maximum zooplankton (g carbon/m^2)
Fladen	0·7	54–82	100	5
Inshore	0·6	104–127	175	5
English Channel	0·35	55–91	210	5
Georges Bank	1·1	120–300	660	30

These estimates of production can be compared with those from other areas. It is pointless to compare production values by themselves, so three other relevant figures are given in Table VIII. It will be seen that the English Channel (station E. 1), although having a lower winter phosphate concentration than the northern North Sea, has a production which is probably between Fladen and Inshore values. This is due to the fact that there is at E. 1 vertical mixing similar to that occurring at the Inshore group. Georges Bank, which has both a large winter phosphate concentration and considerable mixing, gives a production which is certainly greater than any of the other regions, and these differences are reflected in the maximum plant and zooplankton populations.

Thus the estimates of production given in this paper fit reasonably into the pattern of previous results. Because of this, and because of the internal consistency of the Fladen results, it seems that the use of phosphate data can be considered as a comparatively satisfactory method of studying production.

PART II. PLANT POPULATION AND PRODUCTION

The first part of this paper was mainly concerned with the problem of estimating the production from the sea area typified by Fladen. The various assumptions required for these estimates were each more or less open to question, and thus the results are to that extent uncertain.

In this second part, these results will be linked with chlorophyll and dry-weight data, again on the basis of hypotheses whose validity is uncertain. The picture obtained, however, proves to be to some extent internally consistent and agrees reasonably with the results of other workers. To this extent the various methods of sampling and their attendant hypotheses can be held to be justified.

The attempts to describe quantitatively the causal relationships which control plant population and production began with the work of Fleming (1939) and were continued by Riley and his colleagues (Riley, 1946; Riley *et al.* 1949). The development of this approach is summarized by Riley (1953).

Any model of the plant population should take account of many factors, but there are three principal ones which must be considered: production, predation and water movement. Fleming (1939) and Riley (1946) did not deal with the effects of vertical mixing, and thus said nothing about the vertical distribution of the plants. Instead they concentrated on changes with time and obtained reasonable fits with the mean populations. The problem of explaining the distributions with depth was studied by Riley *et al.* (1949) but, in order to do this, areas and times of year were chosen in which the plankton was changing slowly and this was idealized by assuming a steady state. Again fairly good fits were obtained.

Thus the present position is that changes in mean population with time, and stationary distributions with depth, have been studied separately, but no attempts have yet been made to provide an example where these two factors occur together. The main obstacle to this is caused by the generally continuous lateral changes which occur in the sea. These ensure that the water sampled on a given date will frequently not be the same as that sampled previously. This is most serious when detailed vertical distributions are being studied.

However, it was shown in the first part of this paper that the Fladen area appears to approximate sufficiently to the required conditions. For this reason an attempt will be made to compare calculated and observed distributions of chlorophyll throughout 1953.

Ideally one should start from measurements of the physical environment alone and, by means of a set of simultaneous equations, build up models of the distribution of nutrients, plants, herbivores, etc. This will not be attempted here, and only the distribution of the plants as shown by chlorophyll concentration will be considered.

Also, there should be a genuine prediction which can be tested, but this is impossible since, in the end, wind strength is unpredictable. Thus to explain the chlorophyll distribution at the end of a time interval, the information used is as follows: chlorophyll distribution at the beginning of the interval, phosphate, temperature and dry-weight of a net haul at both ends of the interval. In this way, for a series of intervals, a series of calculated chlorophyll distribution is obtained for comparison with the observed distributions.

Before giving the calculations, the chlorophyll and dry-weight observations will be described.

In 1953, when it was decided to supplement the chemical observations by estimates of the chlorophyll concentration, the following simple method was devised.

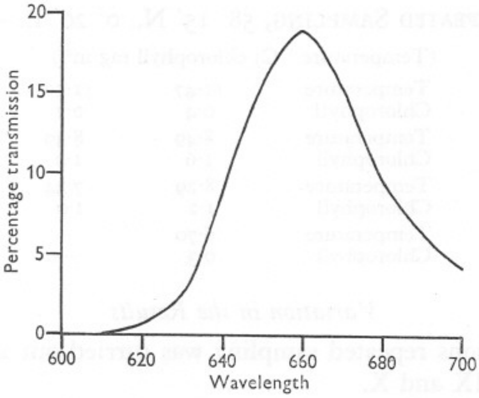

Fig. 16. Calculated spectral response of combination of photocell and I608 filter.

The Chlorophyll Observations

Water samples were taken from 10, 30, 50 and 100 m. The quantity of water used for each estimation was either 1·6 or 2·4 l. This was filtered under suction through a no. 542 Whatman filter-paper and the paper preserved in 80% acetone. The sample was kept in the dark until it was taken to the laboratory where it was made up to 25 ml. after filtering and its light absorption measured. The measurement was made on the long cell model of the Hilger and Watts 'Spekker', using a 3 in. cell and Ilford 608 filters. The spectral response given by the combination of the filter and the cut-off of the photoelectric cell is shown in Fig. 16. Since the secondary chlorophyll maximum, which is used in this type of work, lies at about 655 mμ, the response curve used should be satisfactory. The main drawbacks are (*a*) less than half of the light beam is used, and (*b*) the maximum transmission of 19% is low.

The instrument was calibrated with a known chlorophyll concentration kindly provided by Dr de Kock of the Macaulay Institute for Soil Research, Aberdeen.

One source of error which should be mentioned is the possible loss of the smallest plants, which may pass through the filter-paper. Using a no. 2 Whatman paper, Riley (1941) concluded that he caught 90% of the phytoplankton, a membrane filter catching little more. Harvey (1950), however, found that a no. 2 paper caught just over half of what was retained on a Gradocol membrane. The no. 542 paper used here is probably more retentive than the no. 2, but the probability of the small flagellates escaping cannot be ignored.

Thus this arrangement cannot be expected to be very accurate. However, apart from inaccuracies in the method, one can expect significant and perhaps large errors to arise from sampling variations.

TABLE IX. REPEATED SAMPLING, 58° 15′ N., 0° 20′ E.—21 JUNE 1953

(Temperature ° C; chlorophyll mg/m³.)

10 m	Temperature	11·47	11·50	11·52
	Chlorophyll	0·4	0·2	0·4
30 m	Temperature	8·49	8·49	8·51
	Chlorophyll	1·6	1·0	1·4
50 m	Temperature	8·29	7·34	6·79
	Chlorophyll	1·2	1·0	0·4
100 m	Temperature	6·70	—	—
	Chlorophyll	0·3	—	—

Variation in the Results

On three occasions repeated sampling was carried out and the values are shown in Tables IX and X.

In Table IX are shown the results from a station of the Fladen Group. The temperature of each water sample was also taken. It will be seen that the largest variation in concentration occurs at 50 m where there are large temperature changes. These variations are related; the highest temperature at 50 m is near the 30 m temperature and the chlorophyll concentration lies within the range of the 30 m values; similarly, the lowest temperature at 50 m is near the temperature of the homogeneous lower layer and the corresponding concentrations do not differ significantly. Thus, at this particularly steep point of the thermocline, the variations in concentration depend upon the part of the thermocline from which the sample was taken.

Considering the further results from Table X, it may be said that, when the 50 m case in Table IX is omitted, the standard deviation is not more than 25% of the mean, except at such low concentration as 10 m on 21 June 1953.

The next form of variation to be considered is that between stations of the Fladen group at any given time. All the observations are given in Table XI.

This shows that on Fladen, although there are differences between the four stations on any occasion, the maximum concentrations nearly always occur at the same depth. That is to say, the samples from the four stations appear to be samples of populations having the same distribution with depth. Thus it is reasonable to take the mean values of the four stations, as shown in Fig. 18, as representing the chlorophyll distribution on Fladen.

Since the chlorophyll observations are to be used in conjunction with phosphate and dry-weight data, some common quantity is required and, as in the phosphate results, carbon content will be used. However, the initial question is whether it is possible to have a single conversion factor from chlorophyll to carbon content. It has been shown that the concentration of pigments in plant cells varies with the light intensity in which they are grown (Rabinowitch, 1945). Similar variations have been found in the sea and appear to include differences with season and with depth. This may explain the large variations which are to be found in the figures quoted by workers in this field. Both Harvey and Riley have made several estimates of the relevant quantities. Riley (1949, 1952) decides on a factor

TABLE X. REPEATED SAMPLING FROM THE INSHORE GROUP

57° 55′ N., 1° 00′ W., 25. vii. 53	10 m	0·6	—	0·7	—
	30 m	2·1	2·0	2·6	—
58° 05′ N., 1° 00′ W., 8. ix. 53	10 m	1·8	1·5	1·6	1·9

TABLE XI. CHLOROPHYLL CONCENTRATION IN MG/M³ ON FLADEN IN 1953

	21. iv				11. v				11. vi				21. vi			
Station no. ...	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
10 m	0·6	—	1·0	0	2·9	1·9	—	2·9	0·8	0·4	1·2	1·1	0·4	0·4	0·4	1·0
30 m	0	—	0·8	0	1·6	0·7	—	—	1·5	1·3	1·4	1·2	1·4	1·2	1·6	1·7
50 m	0	—	0·6	0	0·2	0·3	—	0·4	0·4	0·4	0·6	1·4	0·8	0·4	1·1	0·7
100 m	0	—	0·2	0	0	0·3	—	0·5	0·2	0·6	0·4	0·6	0·4	0·4	0·3	0·4

	24. vii				8. ix				25. ix			
Station no. ...	1	2	3	4	1	2	3	4	1	2	3	4
10 m	0·2	0·2	0·2	0·1	0·4	0·4	—	0·4	0·7	0·3	0·8	0·9
30 m	0·3	0·4	0·5	0·4	0·4	0·8	—	0·6	0·3	1·0	0·7	1·2
50 m	1·0	1·0	0·6	1·7	0·8	0·8	—	0·7	0	0·2	0·3	0·6
100 m	0·2	0·3	0·6	0·5	0·4	0·4	—	0·1	0·2	0·2	0·2	0·2

$$1 \text{ mg chlorophyll} \equiv 54 \text{ mg carbon.}$$

Harvey's value (1950) is in terms of units of plant pigments which on conversion gives

$$1 \text{ mg chlorophyll} \equiv 27 \text{ mg carbon.}$$

Harvey says of his own figure—'This estimated ratio is no more than a rough approximation. It is unlikely to be less than half or more than double the true mean ratio.'

The ratio given by Riley will be used since one purpose of this paper is to compare certain results obtained here with those of Riley.

Dry Weights of Zooplankton

Since knowledge is required of predation on the plants, some figures must be found that will represent the herbivore population. It is probable that the dry weight of a net haul is the best compromise between simplicity and accuracy.

A Hensen egg-net was used with no. 3 silk (60 meshes per inch). The net was hauled vertically from bottom to surface. The collections were preserved in ethyl alcohol and, on return to the laboratory, dried for 12–18 h at 90° C and then weighed. The values used for the subsequent calculations are the means of the four stations as shown in Fig. 17, with the figure for 21 June found by interpolation.

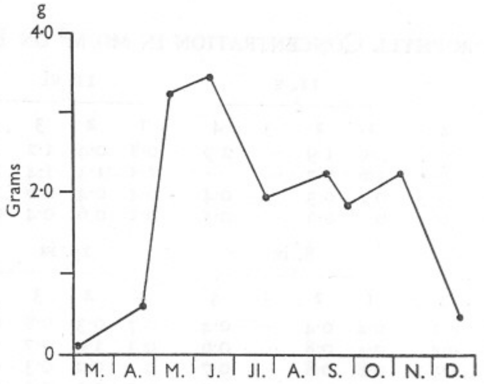

Fig. 17. Mean dry weights of net hauls on Fladen in 1953.

As with chlorophyll data, these results are converted into carbon content. Since the opening of the net has an area of approximately one-third of a square metre, then, assuming 100% filtration and taking the carbon content to be half the dry-weight, the values in Fig. 17 should be multiplied by 1·5 to give carbon content below 1 m^2.

These results are not only very variable, but they are also very much minimum values, since a no. 3 silk catches but a small proportion of the smaller animals. This effect is important when considering the assumptions necessary for using these data in the subsequent calculations.

These data are intended to provide information about the grazing on the plants, and the simplest assumptions which would be required for the calculations are that (*a*) the animals are filter feeders and filter a constant quantity of water per unit of dry weight in a net haul, and (*b*) the zooplankton population spends equal time at all depths.

The most serious objection to (*a*) has been pointed out by Raymont & Gauld (1951) and Gauld & Raymont (1953), who drew attention to the fact that, whereas weight is approximately proportional to the cube of the length, respiration is approximately proportional to the square. Thus the food requirements of the zooplankton will depend on the size frequency-distribution of the population, with the smaller animals having much higher requirements per unit of weight.

Concerning the second assumption, Nicholls (1933) showed that copepodite stages I–III of *Calanus* in Loch Fyne were always most abundant above 30 m during 1932. If this result was regarded as generally applicable, which is not obviously the case, then these two facts together could thus upset the postulates suggested to describe the grazing effects. However, these postulates are not merely the simplest but probably provide the only available approach for linking predation to the plant population.

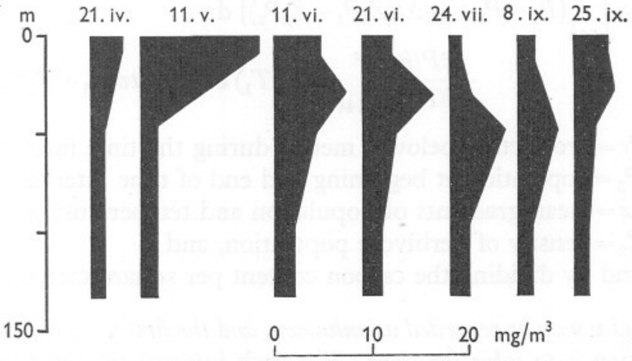

Fig. 18. Profiles of chlorophyll concentration (mg/m³) on Fladen in 1953 constructed from the mean values at 10, 30, 50 and 100 m.

Sinking Rate and Filtering Rate

The value of the constant which converts dry weight to filtering rate will be one of the two unknowns which must first be evaluated. The other initially unknown quantity is the rate at which the plants sink through the water. This and the filtering rate must be evaluated to give a quantitative picture of the reasons for the changing distribution of the plants.

Qualitatively, this sequence of events can be seen in Fig. 18. After the spring outburst, production does not occur at a high rate and, during the summer, the gradual sinking of the population and its grazing down is shown by the successively greater depths at which maximum concentration occurs and by the decreasing total chlorophyll content.

The basic mathematical form which will express these various effects is as follows (see Riley *et al.* 1949):

$$\frac{\partial P}{\partial t}=(p_h-r-gZ)P+\frac{\partial}{\partial z}\left(\frac{A}{\rho}\frac{\partial P}{\partial z}\right)-v\frac{\partial P}{\partial z}, \qquad (1)$$

where P = density of the plant population, p_h = photosynthetic rate, r = respiration rate, g = filtering rate, Z = density of herbivore population, A = coefficient of vertical diffusivity, v = sinking rate, z = depth. The units used here are grams, metres, days. The term $(p_h - r)\,P$ can be replaced here by the estimates of production rate derived from the phosphate results.

Riley *et al.* (1949) also made the further assumption throughout their work that $\partial P/\partial t = 0$, which allowed them to study each station separately. It is obvious from the profiles shown in Fig. 18 that the phytoplankton on Fladen cannot be considered as existing in a steady state. Thus the methods used by Riley could not be applied here. It is necessary to consider the changes between two stations and, as with the phosphate, this involves making several approximations. The integrated approximate form of (1) is

$$Pr = \int_{140}^{z} [P_2 - P_1 + \tfrac{1}{2} g \Delta t (Z_1 P_1 + Z_2 P_2)]\,\mathrm{d}z - \frac{\partial P/\partial z}{\partial T/\partial z} \int_{140}^{z} (T_2 - T_1)\,\mathrm{d}z - \tfrac{1}{2} \Delta t v [P_1 + P_2]_{140}^{z}, \qquad (2)$$

where Pr = production below z metres during the time interval Δt,
P_1, P_2 = population at beginning and end of time interval Δt,
$\partial P/\partial z$, $\partial T/\partial z$ = mean gradients of population and temperature at depth z,
Z_1 and Z_2 = density of herbivore population, and
Z_r is found by dividing the carbon content per square metre by 140.

In (2) *g and v may be regarded as unknown, and the first use which will be made of this equation is to solve for them.* For each interval two equations can be found, corresponding to the depth intervals $0 - z_0$ metres and $z_0 - 140$ m, where z_0 is the zero level. These equations can be solved simultaneously to give values for g and v.

Of the results shown in Table XII, those for the first interval appear to be abnormally high; the reasons for this will be discussed later. Excluding this interval the others show a comparatively small range of variation with mean values of 3·0 m/day and 1·34 m^3/day/g zooplankton carbon.

The sinking rates proposed by Riley were dependent on temperature, but such a variation is small compared with the overall variation of the results and has not been included here. Over the temperature range found here Riley's choice of sinking rate varies between 3·5 and 4·3 m/day. The values given here cover this range but have a lower mean value. However, when one remembers the great range of values for sinking rate which has been found previously (Riley *et al.* 1949, pp. 84–5), the agreement between the figures given here and

TABLE XII. SINKING RATES AND FILTERING RATES

	21. iv.–11. v.	11. v.–11. vi.	11. vi.–21. vi.	21. vi.–24. vii.	24. vii.–8. ix.	8. ix.–25. ix.
Sinking rate (m/day)	13·0	2·4	2·1	4·2	4·9	1·4
Filtering rate (m^3/day/g carbon)	2·9	1·0	1·2	1·7	1·4	1·4

those of Riley can be taken as very satisfactory. Similarly, the mean filtering rate does not differ greatly from Riley's estimate of 1·26 m³/day/g C.

With values for filtering and sinking rates available, the detailed shape of the profiles can now be considered. Equation (2) can be put in the form

$$(1+\tfrac{1}{2}g\Delta tZ_2)\int_{140}^{z} P_2\,\mathrm{d}z-\tfrac{1}{2}\Delta tvP_2=Pr+(1-\tfrac{1}{2}g\Delta tZ_1)\int_{140}^{z} P_1\,\mathrm{d}z + \frac{\partial P/\partial z}{\partial T/\partial z}\int_{140}^{z}(T_2-T_1)\,\mathrm{d}z+\tfrac{1}{2}\Delta tv\,(P_1-[P_1+P_2]_{140}^{z}), \tag{3}$$

where

$$\frac{\partial P}{\partial z}=\tfrac{1}{40}[P_1+P_2]_{z+10}^{z-10}. \tag{4}$$

The left-hand side of (3) contains P_2 alone, but the right-hand side, beside terms in P_1, involves P_2 in the term $\partial P/\partial z$, as shown in (4). The third term on the right-hand side is, however, found to be much smaller than the others and *thus* (3) *can be used to predict* P_2 *by successive approximation.* In fact, because of the low degree of accuracy, no second approximation is necessary.

As a first step, a mean value is found for the 0–20 m layer; then this value is used to find the 30 m value; and so on to the top of the homogeneous bottom layer. In this way a profile is obtained from surface to about 50–70 m. This profile can be compared with the three observed values at 10, 30 and 50 m. With the exception of the first time interval, the computations were first made with the values for sinking and filtering rates given in Table XII. Then, for the first interval and some of the subsequent ones, other values were used in search of a better fit. The results of these calculations are shown in Fig. 19.

It is in the first four cases that the observed points show the greatest changes with depth, so that these cases are of the most interest from the point of view of predicting results.

These four profiles show the same type of distribution with depth as the observed points. The last two profiles also show quite large changes with depth, but these are not borne out by the observed points.

The two profiles which have been drawn for the first interval show that a high filtering rate and low sinking rate are required to give a reasonably shaped profile with approximately the observed quantity of plankton above 50 m. Similarly, increasing the filtering rate in the second and third cases brings the profiles into better agreement with the observed points. In the fourth interval the initial profile is as good a fit as can be obtained. The fifth profile does show an increase with depth which is also true of the observed points; decreasing the sinking rate will give a rather better fit, but because of the small number of observed points there is no confirmation of the predicted maximum at 40 m. In the last case it was not found possible to obtain a reasonable fit.

Returning to the first interval, in both sets of calculations it gives results which are very different from the succeeding intervals. This interval covers the spring outburst and so it is likely that the population will consist largely of juvenile stages of the copepods. This would provide the conditions which, as suggested on p. 27, would not fulfil the postulates on which the grazing effects were based. During this period it is possible that grazing, dominated by the juveniles with their proportionately higher metabolic rate, was confined to the water above 50 m which, in turn, provides an explanation of the anomalous results of the first calculation and of the high filtering rates given by the second. Such a hypothesis might well be necessary since the juveniles, with their proportionally greater food requirements, would perhaps be unable to obtain sufficient food if they spent only a small part of their time in the zone of high plant concentration. Later, when they are adult and when the maximum concentration of phytoplankton may occur at widely varying depths, vertical migration could be expected to be more extensive, and the postulate of equal depth concentration over long time intervals becomes more acceptable.

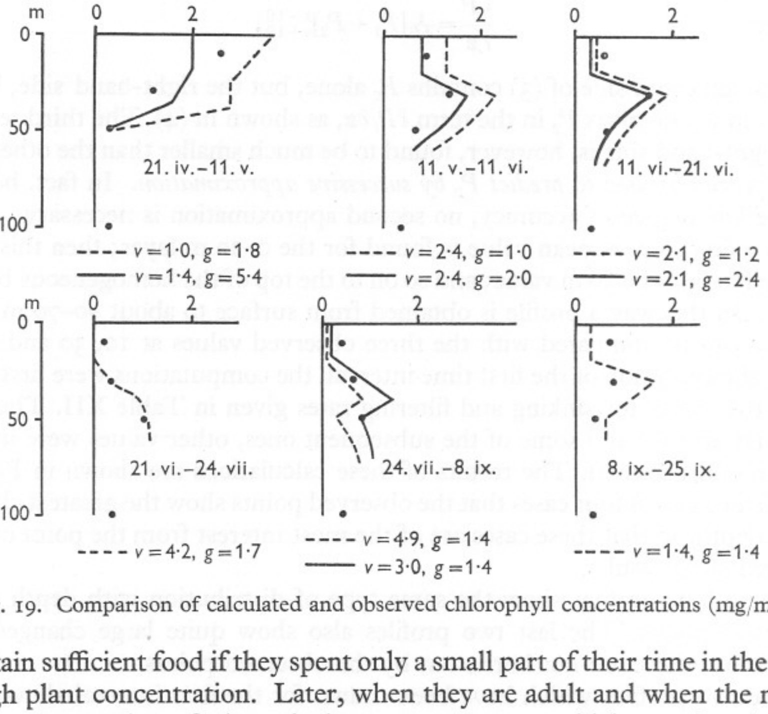

Fig. 19. Comparison of calculated and observed chlorophyll concentrations (mg/m^3).

The need for a greater filtering rate is still apparent in May, but by June the differences between observed and calculated values are so small that a greater filtering rate does not provide a significantly better fit. Thus the anomalies between the two calculations decrease from April onwards, perhaps because of the progressive domination of the population by the later stages of copepods.

Regarding the interval 8–25 September, it will be remembered that the phosphate results for this interval were somewhat erratic (p. 16), and it was suggested (p. 16) that there was some shift in the water during this period.

Possibly this could also explain the poor fit for the chlorophyll data on the 25th.

It also seems possible that there are significant changes in the sinking rate. The values deduced here start at about 1·4 m/day, rise to above 4 m/day at the end of July and then in September return to 1·4 m/day. Gross & Zeuthen (1948) have suggested that under suitable conditions diatoms do not sink, since their specific gravity equals that of the surrounding sea water. But to maintain this buoyancy requires the expenditure of energy and so sinking occurs when these energy requirements cannot be met. This situation is most likely to occur in a senescent population. Thus it is possible that the variations in the calculated sinking rate may correspond to the gradual change from a new plant population in April and May, living in a suitable environment, to a senescent population in July, with a return in the autumn to a population of comparatively recent origin.

From this discussion it would appear that neither the sinking rate, v, nor the filtering rate, g, will be constant throughout the year but will depend on the age composition of the phytoplankton and zooplankton respectively.

Finally, it has not proved possible to start with given constant rates of sinking and filtering and from them to predict the cycle of plant distribution throughout the year. Yet it does seem that by varying the sinking and filtering rates from one interval to the next the changes in plant distribution can be largely explained in terms of the factors listed at the outset; further, these variations in the rates of sinking and filtering are not unreasonable.

CONCLUSIONS

The aim of the first part of this paper was to develop a method of estimating the basic plant production. The second part was designed to measure the factors which control the distribution of the plants with time and with depth. In each there has been some measure of success, but most of the results are open to question and, further, in this paper the methods have been applied in detail to one area only.

This type of work requires chemical and biological data collected over many years to provide information on the possible kinds of variation that may occur. The results from the northern North Sea cover, at most, three years, with only one year's data for the areas outside Fladen. Thus the problems tackled so far have been concerned with the basic regularities and the more important variations. For this purpose Fladen is very suitable since it appears to give a good approximation to the case of purely vertical mixing.

In the areas outside Fladen the difficulties which arise are due mainly to the effects of lateral water movements. The measurement of these would be required before the changes at, say, the Inshore group could be properly understood. Similarly, features in the Fladen results such as the apparent production between 20 and 30 m in the summer, or the anomalous results in the chlorophyll prediction, probably require knowledge of the metabolism of plants and animals which is not at present available. But these are problems which face any method of studying production.

SUMMARY

In the first part of the paper estimates of the plant production are given for the years 1951–53 in one area, Fladen, of the northern North Sea. These estimates, based on the changes in inorganic phosphate, give values for the yearly production of 55–81 g carbon under each square metre of surface—a range which is nearly the same as that in the English Channel; its variation can be related to the varying occurrence of high winds in the different years. It appears that the zone of phosphate utilization sinks progressively during spring and summer to a depth around 30–40 m.

In the second part these estimates are then used, together with chlorophyll and zooplankton data, (*a*) to study the changes in the vertical distribution of the plants, and (*b*) by comparing calculated and observed vertical chlorophyll profiles, to discover to what extent a few simple postulates can explain the changing vertical distribution of plants throughout one year.

REFERENCES

BARKER, H. A., 1935. Culture and physiology of the marine dinoflagellates. *Arch. Mikrobiol.*, Bd. 6, pp. 157–81.

BRAARUD, T. & ROSSAVIK, E., 1951. Observations on the marine dinoflagellate *Prorocentrum micans* Ehrenb. in culture. *Avh. norske VidenskAkad.* (1, Mat. Kl), No. 1, 18 pp.

CHU, S. P., 1946. Utilization of organic phosphorus by phytoplankton. *J. Mar. biol. Ass. U.K.*, Vol. 26, pp. 285–95.

CONSEIL PERM. INTERNAT. POUR L'EXPLOR. DE LA MER, 1933. *Atlas de température et salinité de l'eau de surface de la Mer du Nord et de la Manche.* 32 pp. Copenhagen: Bureau du Conseil.

FLEMING, R. H., 1939. The control of diatom populations by grazing. *J. Cons. int. Explor. Mer*, Vol. 14, pp. 210–27.

FRASER, J. H., 1954. Zooplankton collections made by Scottish research vessels during 1953. *Ann. biol., Copenhague*, Vol. 10 (1953), pp. 99–101.

GAARDER, T. C. & GRAN, H. H., 1927. Investigations of the production of plankton in the Oslo Fjord. *Rapp. Cons. Explor. Mer*, Vol. 42, 48 pp.

GAULD, D. T. & RAYMONT, J. E. G., 1953. The respiration of some planktonic copepods, II. *J. Mar. biol. Ass. U.K.*, Vol. 31, pp. 447–60.

GROSS, F. & ZEUTHEN, E., 1948. The buoyancy of plankton diatoms: a problem of cell physiology. *Proc. roy. Soc.* B, Vol. 135, pp. 382–9.

HARVEY, H. W., 1950. On the production of living matter in the sea off Plymouth. *J. Mar. biol. Ass. U.K.*, Vol. 29, pp. 97–137.

—— 1953. Note on the absorption of organic phosphorus compounds by *Nitzschia closterium* in the dark. *J. Mar. biol. Ass. U.K.*, Vol. 31, pp. 475–6.

JOHNSTON, R., 1953. Hydrography. North Sea. Chemical observations. *Ann. biol., Copenhague*, Vol. 9 (1952), pp. 99–103.

—— 1954. Hydrography. North Sea. Chemical observations. *Ann. biol., Copenhague*, Vol. 10 (1953), pp. 84–6.

KETCHUM, B. H., 1939. The development and restoration of deficiencies in the phosphorus and nitrogen composition of unicellular plants. *J. cell. comp. Physiol.*, Vol. 13, pp. 373–81.

LWOFF, A., ed., 1951. *Biochemistry and Physiology of Protozoa*, Vol. 1, 434 pp. New York: Academic Press.

NICHOLLS, A. V., 1933. On the biology of *Calanus finmarchicus*. III. Vertical distribution and diurnal migration in the Clyde sea area. *J. Mar. biol. Ass. U.K.*, Vol. 19, pp. 139–64.

PARR, A. E., 1936. On the probable relationship between vertical stability and lateral mixing processes. *J. Cons. int. Explor. Mer*, Vol. 11, pp. 308–13.

RABINOWITCH, E. I., 1945. *Photosynthesis and Related Processes*, Vol. 1, 599 pp. New York: Interscience Publishers.

RAYMONT, J. E. G. & GAULD, D. T., 1951. The respiration of some planktonic copepods. *J. Mar. biol. Ass. U.K.*, Vol. 29, pp. 681–93.

RILEY, G. A., 1939. Plankton studies. II. The western North Atlantic, May–June 1939. *J. Mar. Res.*, Vol. 2, pp. 145–62.

—— 1941. Plankton studies. III. Long Island Sound. *Bull. Bingham oceanogr. Coll.*, Vol. 7, Art. 3, 93 pp.

—— 1946. Factors controlling phytoplankton population on Georges Bank. *J. Mar. Res.*, Vol. 6, pp. 54–73.

—— 1952. Phytoplankton of Block Island Sound. *Bull. Bingham oceanogr. Coll.*, Vol. 13, Art. 3, pp. 40–64.

—— 1953. Theory of growth and competition in natural populations. *J. Fish. Res. Bd Can.*, Vol. 10, pp. 211–23.

RILEY, G. A., STOMMEL, H. & BUMPUS, D. F., 1949. Quantitative ecology of the plankton of the western North Atlantic. *Bull. Bingham oceanogr. Coll.*, Vol. 12, Art. 3, 169 pp.

STEEMAN NIELSEN, E., 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. *J. Cons. int. Explor. Mer*, Vol. 18, pp. 117–40.

SVERDRUP, H. U., JOHNSTON, M. W. & FLEMING, R. H., 1942. *The Oceans; their Physics, Chemistry and general Biology*. 1087 pp. New York: Prentice-Hall.

TAIT, J. B., 1937. Surface water drift in the North Sea and Faroe-Shetland Channel. *Sci. Invest. Fish. Scot.*, 1937, No. 1, 60 pp.

—— 1954. Hydrography, North Sea, northern North Sea and approaches. *Ann. biol., Copenhague*, Vol. 10 (1953), pp. 82–4.