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A COMPARISON OF PLANT PRODUCTION ESTIMATES USING ^{14}C AND PHOSPHATE DATA

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(Text-figs. 1–6)

In an earlier paper (Steele, 1956) estimates of the yearly cycle of plant production were given for a part of the northern North Sea known as the Fladen Ground. These estimates were made from a study of the changes in inorganic phosphate in relation to the effects of vertical mixing.

The method is indirect since several hypotheses have to be made relating phosphorus and carbon uptake by phytoplankton. The problems which these raise are most acute during the summer when the results show a low rate of production. Either of two factors, a high rate of regeneration of phosphorus to inorganic form in the euphotic zone, or the ability of plants to use organic phosphorus compounds, could make the production rate much greater.

For these reasons a check on the method was desirable and this has been done using the ^{14}C technique devised by Steeman Nielsen (1952) which gives directly a measure of the carbon uptake during a short period of time.

The main purpose of this paper is to show from data collected in 1955 and 1956 that there is general agreement between the two methods. This purpose is attained in so far as the mean daily production calculated from phosphates was 0·20 g C/m^2 between 1 June and 13 August 1955, while the three values found from the ^{14}C experiments during this period were 0·20, 0·21 and 0·15. The results are also used to continue the study of the changing vertical distribution of plants in terms of the effects of sinking and grazing.

It is a pleasure to thank Dr H. W. Harvey for his advice and Mr R. I. Currie of the National Institute of Oceanography for instruction in the details of the ^{14}C technique and for working up the samples collected in 1955.

METHODS

The technique for estimating ^{14}C uptake was essentially that described by Steeman Nielsen (1952). The only variation that was made in the method concerns the estimation of the activity of the ^{14}C solution from the self-absorption curve. It was found difficult to obtain satisfactory precipitates of very small quantities of barium carbonate, and the need for this was avoided by using the known form for the equation of the curve. This gives the activity at thickness T as

$$G(T)=G(O)\,\frac{1-e^{-\mu T}}{\mu T},$$

where μ is a constant and $G(O)$ is the value required (Calvin *et al.*, 1949, p. 30). A curve is fitted to the mean values at three thicknesses; the goodness of the fit acting as a check. Fig. 1 gives the curve for the ampoules used in 1956.

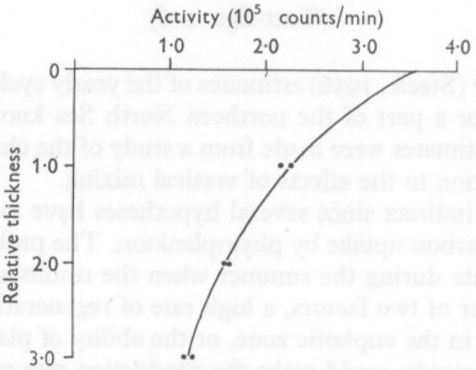

Fig. 1. Self-absorption curve for the ampoules used in 1956.

The bottles used in the experiments were of approximately 170 c.c. capacity. They were filled in pairs from the following depths: 1, 10, 20, 30, 40 and 50 m. The bottles were lowered to the depths from which the water came and left there for the whole (1955) or half (1956) of the period of daylight.

The methods of estimating production from the phosphate data, chlorophyll concentration and zooplankton dry weight have already been described (Steele, 1956).

ESTIMATION OF CARBON ASSIMILATION

In his experiments, Steeman Nielsen collected water samples from different depths and exposed them in a water bath to the same light intensity for 4 h. In converting the measures of ^{14}C uptake to values of carbon assimilation he allowed 6 % for isotope factor and 4 % for loss due to respiration giving a total addition of 10 %.

When samples are exposed at different depths the effect of respiration will be proportionally greater in the deeper water where there is a low rate of photosynthesis. The importance of this effect will depend on the extent to which the ^{14}C is available for respiration during the period of the experiment. Since there is not yet sufficient evidence to estimate this effect, the values for carbon assimilation were calculated by Steeman Nielsen's method. These values are shown in Figs. 2 and 3, together with the profiles of population, estimated from the chlorophyll concentrations.

It is generally thought that photosynthesis varies directly with the light intensity except near the surface where there is some inhibition (Jenkins, 1937; Steeman Nielsen, 1952). To study the present data from this point of view, Secchi disc readings (Table 2) were used to estimate the extinction coefficient, K, defined by the rough conversion factor of Poole & Atkins (1929) as

$$K=\frac{1\cdot 7}{\text{S.D. reading}}.$$

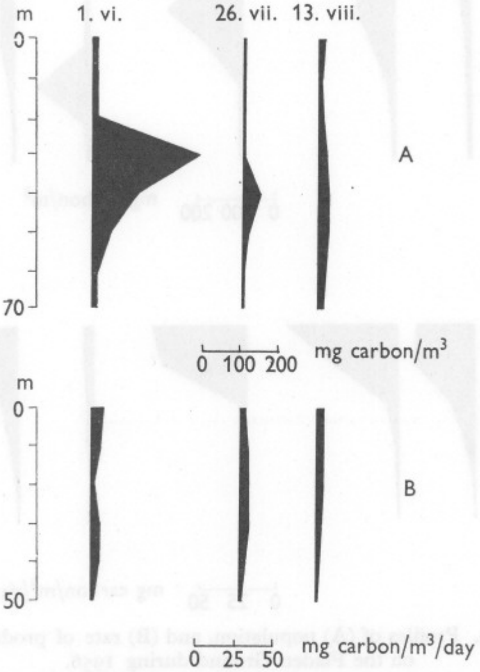

Fig. 2. Profiles of (A) population and (B) rate of production on the Fladen Ground during 1955.

Assuming that the light which is effective for photosynthesis decreases as $\exp(-KZ)$, where Z is the depth in metres, then the light intensity relative to the surface can be found. Since no measurements were made of the absolute light intensity at the surface, the values for each date are not directly comparable. On this basis the values for C shown in Table 1 were calculated where

$$C=\frac{\text{carbon assimilation/day}}{\text{population}\times\text{rel. light intensity}}.$$

Thus *C* provides an index for the increase in cellular carbon in terms of the quantity of chlorophyll present multiplied by a rough measure of the relative light energy at each depth.

There is considerable variation in the values of *C*, but this is not large in terms of the range of values of both assimilation and light intensity which can vary by a factor of several hundreds between surface and 50 m. The expected

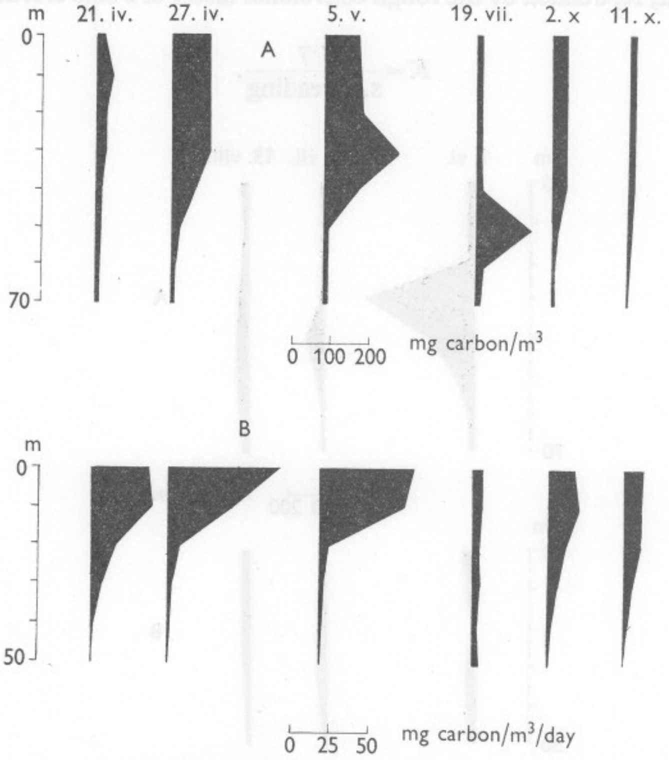

Fig. 3. Profiles of (A) population, and (B) rate of production on the Fladen Ground during 1956.

TABLE 1. VALUES OF *C* DURING 1955 AND 1956 (SEE TEXT)

	Depth (m)					
Date	1	10	20	30	40	50
1. vi. 55	0·5	1·3	1·0	0·5	3·0	1·5
26. vii. 55	0·5	2·1	3·8	12·0	3·2	5·0
13. viii. 55	0·2	0·8	1·6	1·0	0·8	0·5
21. iv. 56	1·8	2·8	5·8	8·6	6·6	20·0
27. iv. 56	0·8	2·4	2·4	2·0	16·0	22·0
5. v. 56	0·8	3·4	1·8	1·4	2·0	—
19. vii. 56	—	1·4	2·8	8·8	10·0	5·2
2. x. 56	0·5	1·4	2·0	2·8	2·4	3·1
11. x. 56	0·7	2·0	5·8	7·6	11·2	16·4

decrease in C near the surface is found and it occurs also to some extent at 10 m. At 40 and 50 m the values are more variable, but in general they tend to be larger. It is at these depths, however, that lower values of C would be expected if much of the ^{14}C were being lost through respiration. On this rather tenuous basis it would appear that ^{14}C estimates more nearly represent total photosynthesis rather than net assimilation.

Some idea of the magnitude of the respiration loss can be obtained from the formula given by Riley, Stommel & Bumpus (1949),

$$r_T = 0{\cdot}0175 \exp(0{\cdot}069\,T),$$

where r_T is the respiratory coefficient in g C/day/g phytoplankton carbon at temperature T. In Table 2 the ratios of respiration to production are given as the average for the layer 0–50 m. Only one value exceeds one third and the mean is about 0·22 which can be considered a reasonable general value (Steeman Nielsen, 1952). There is a considerable fluctuation in the figures, and for this reason no allowance has been made for respiration in the following discussion.

TABLE 2. OBSERVATIONS ASSOCIATED WITH ^{14}C EXPERIMENTS (SEE TEXT)

	1955			1956					
	1. vi.	26. vii.	13. viii.	21. iv.	27. iv.	5. v.	19. vii.	2. x.	11. x.
Secchi disc reading (m)	15·5	19·0	21·0	15·0	10·0	10·0	17·0	18·0	14·5
Respiration/production	0·65	0·15	0·33	0·04	0·11	0·19	0·21	0·18	0·09
Mean dry weight of zooplankton (g C/m²)	2·2	1·4	2·3	0·7	2·1	2·7	4·0	0·6	0·4

COMPARISON OF PRODUCTION ESTIMATES

The general comparison of the estimates of production given by ^{14}C and by phosphate change is shown in Fig. 4. A detailed comparison is difficult since the ^{14}C uptake measures production rate on a given day, whereas the phosphate data give a value for production between two dates. The main point is that there is no large and systematic discrepancy between the two sets of data. The ^{14}C values are on the average slightly less than the phosphate values and the difference would be accentuated if respiration were taken into account. This is important for, on this basis, there is no evidence that the phosphate estimates are fallaciously low due to regeneration or to the use of organic phosphorus compounds by the phytoplankton. To this extent the phosphate method is validated.

Given this general agreement between phosphate and ^{14}C estimates one main difference must be noted; this is found in the depth distribution of production. The most suitable examples are the four occasions when two ^{14}C experiments were made within a short time interval. The phosphate profiles for these intervals are shown in Fig. 5, and it can be seen that they differ from the relevant ^{14}C profiles of Figs. 2 and 3.

For the final interval, 2–11 October 1956, the difference can be explained by the fact that the water column is homogeneous from 0 to 40 m. This means that, although the production rate at any moment has the depth distribution shown by the ^{14}C data, mixing spreads this production evenly through the homogeneous layer so that, effectively, production is constant in this depth range. However, this type of explanation is not sufficient to account

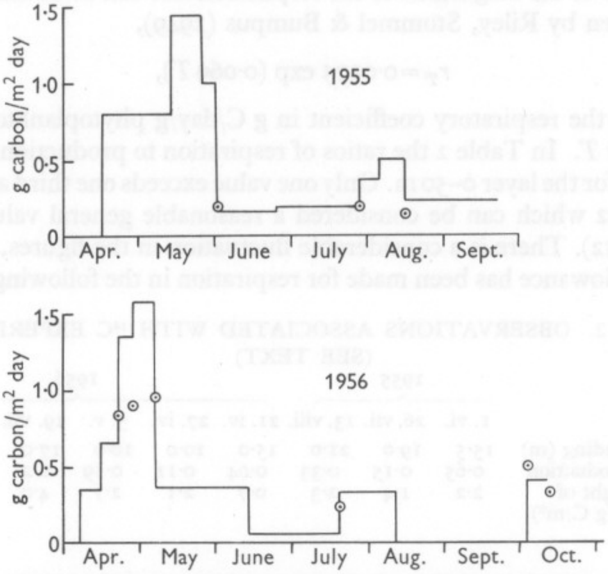

Fig. 4. Histograms of production for the years 1955 and 1956 derived from the phosphate data. The circles show the rates of production estimated by the ^{14}C method.

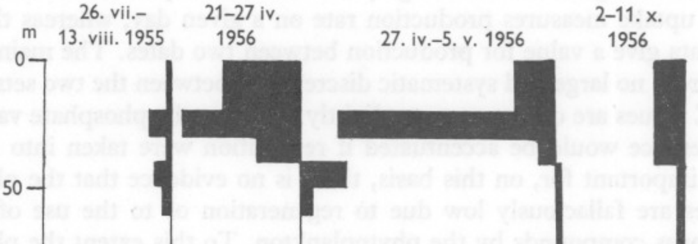

Fig. 5. Some profiles of 'biological change' of phosphate on Fladen in $10^2 \times \mu$g at./cm² day.

for the fact that maximum phosphate consumption in the summer seems to occur between 20 and 30 m (Steele, 1956). Oxygen data appear to support the phosphate results (Steele, 1957) but, although the anomaly remains, it seems probable that the ^{14}C values are more trustworthy.

SINKING AND FILTERING RATES

In the earlier paper (Steele, 1956) an attempt was made to explain variations in plant population throughout 1953 in terms of production, sinking, grazing and vertical mixing. The first step was to calculate sinking rates of phytoplankton and filtering rates of zooplankton from the mean changes in and below the euphotic zone during the interval between two sampling dates. Using these values and the population profile at the beginning of the interval, a profile was derived for the end of the interval which could be compared with the observed profile. As a continuation of this work the four intervals discussed in the previous section were analysed in the same way using the ^{14}C estimates of production. The values for dry weight of zooplankton used in the equations are given in Table 2.

TABLE 3. SINKING AND FILTERING RATES

	1955	1956		
	26. vii.–13. viii.	21–27. iv.	27. iv.–5. v.	2–11. x.
Sinking rate (m/day)	2·2	3·3	1·9	6·0
Filtering rate (m^3/day/g carbon)	5·8	7·7	7·7	78·0

Table 3 gives the estimated sinking and filtering rates. The values for the last interval are excessively high and no satisfactory explanation can be given. The remaining values are comparable with those of 1953. In particular, the higher filtering rate in the spring agrees with the conclusions made in the earlier paper.

Fig. 6 shows the comparison of observed and calculated profiles for the first three intervals. The agreement between them is not very good; in particular the sharp increase at 30 m on 5 May 1956 cannot be explained. The use of the phosphate estimates of production does not give any appreciable improvement.

CONCLUSIONS

As so often happens in this type of work the results are not completely consistent. Hypotheses are partly supported, partly disproved, and further data alter previous conclusions. Such difficulties have arisen in these attempts to explain in detail the changing vertical distribution of production and of population.

In three out of the four cases considered, a broad division of the water column into the euphotic zone and the region below leads to estimates of sinking and filtering rates which are in good agreement with previous values.

The profiles deduced from these rates are not always satisfactory, and the question remains whether this defect is due to some combination of sampling errors, inadequacy of approximating over periods of weeks, and arithmetical artifacts; or are the hypotheses themselves insufficient to explain such detail? One obvious conclusion is that much further study is required on these basic problems.

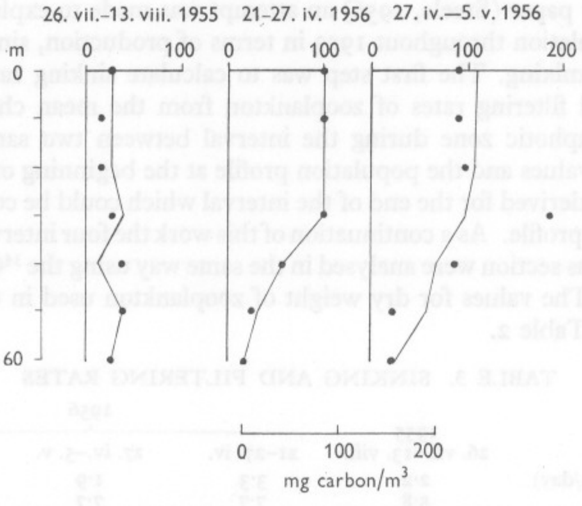

Fig. 6. Comparison of observed and calculated population profiles.

A rough analysis of the depth distributions of ^{14}C uptake gives some evidence that these agree with the accepted relations of photosynthesis and light intensity. For this reason these distributions are more acceptable than those given by the phosphate data.

There remains the fact that as measures of production below a given area of sea surface the two methods are in good agreement. Differences are to be expected since there will be day-to-day variations in carbon uptake due to changes in weather, vertical mixing, etc. From this point of view phosphate estimates are valuable since they measure production during an interval of weeks. Further, because of the way they are derived, phosphate estimates display the relations between production and such features of the environment as vertical mixing and nutrient deficiency. For these reasons the two methods may be regarded as complementary.

SUMMARY

Organic production in the sea can be measured by studying the changes in phosphate throughout the water column. Results obtained by this method are compared with estimates of carbon uptake using ^{14}C made on the Fladen

Ground during 1955 and 1956. There is good general agreement between the two methods but some differences in the vertical distribution.

The results are also used to calculate filtering rates of phytoplankton and sinking rates of zooplankton, and to compare observed and predicted vertical distributions of chlorophyll.

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