PRODUCTION ECOLOGY OF A SANDY BEACH

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ABSTRACT

The vertical distribution of pigments and organic matter and the yearly cycle of production in a sandy beach are described for positions at low water and to a sublittoral depth of 13 m. The chlorophyll and carbon content of the populations attached to the sand grains increases with increasing depth of overlying water. At low-water mark, viable diatom populations are found to 20 cm deep in the sand. The effects of wave action, however, keep these populations at a relatively low level so that the yearly primary production of the benthic flora is in the range 4–9 g C m^{-2}.

INTRODUCTION

A general study of food chains in a small sandy bay in Loch Ewe on the west of Scotland (Fig. 1) is being carried out. As part of this program, the seasonal cycles in organic matter and production, both in the water and in the sand, are being investigated. The results from the water are similar to those in other inshore areas of Scotland (Steele and Baird 1961, 1962) and so are reported briefly. However, the productivity of an exposed beach, including the sublittoral area, has been little studied, especially with reference to the effects of wave action on vertical distributions in the sand.

The detailed topography of the beach is not fixed but the general features (Fig. 1) are sufficient to define the chosen sampling points. From low-water mark to about 8 m below low tide, the substrate is fairly uniform, consisting of well-sorted quartz sand. The cumulative curves for low water and two stations at 5 m, N and S, give an indication of this range (Fig. 2). Sta. M_1, at 10 m, is quite different since it lies in a fairly permanent area of shell gravel. The outer station, M_2, at 13 m, is on the edge of the beach, and the sand, found between rock outcrops, is similar to the 5-m stations except that on occasion Sta. M_2 may contain fine sediment. During routine sampling with small grabs it was often impossible to obtain a sample at M_2 so results from this position are intermittent. A more detailed analysis of the beach material is given by McIntyre and Eleftheriou (in prep.).

METHODS

The methods for analysis of the water samples were standard (Steele and Baird 1961). The ^{14}C uptake was measured from midday to sunset either *in situ* or in a simulated *in situ* incubator. On two occasions, in August and October, the two methods were compared and the differences, corrected to production per day were 0.10 and 0.02 g C m^{-2}.

Particulate organic carbon was measured by wet oxidation, treating 0.2–1.0 g of sand in the same way as filtered water samples (Steele and Baird 1961).

For chlorophyll *a* estimation on sand, 1–7 g of vacuum dried sand were ground in a mortar and extracted with 90% acetone. During the first year, chlorophyll *a* was estimated by the difference between optical densities at 663 and 750 mμ using 89.31 liter/g cm as the coefficient of extinction (SCOR-UNESCO 1964). After 1965, chlorophyll *a* was determined using a Turner fluorometer (Yentsch and Menzel 1963) calibrated by direct comparison with spectrophotometer readings. The greater sensitivity was particularly useful for the low chlorophyll values on the beach.

The proportion of degraded chlorophyll *a* in the samples was determined by acidifying the extracts and remeasuring at the same wavelengths (or in the fluorometer). According to Yentsch and Menzel (1963) the ratio of unacidified to acidified (hereafter referred to as U/A) extracts is 1.7 for pure chlorophyll *a* and 1.0 when the pigment is degraded completely. Intermediate

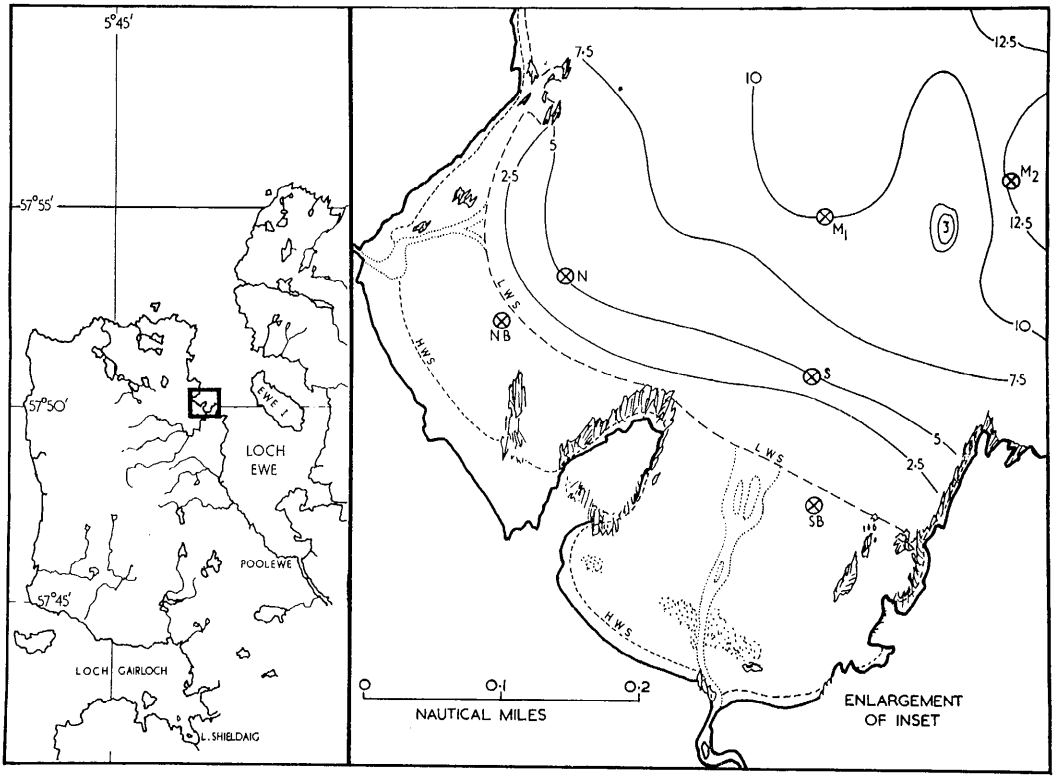

FIG. 1. The position and topography of the beach in Loch Ewe, Wester Ross, Scotland. ⊗ indicates sampling positions. --- limits of low- and high-water spring tides.

values are an indication of the proportion of chlorophyll *a* in the sample.

The unattached organic matter in the sand was determined by putting 25 g of sand in a separating funnel and eluting with 2–4 liters of filtered seawater. This water was divided into equal fractions that were then treated as normal water samples for pigment and carbon analyses.

We needed to develop a method for estimation of ^{14}C uptake by diatoms attached to the sand under natural conditions. The method of Grøntved (1960) provides estimates of "potential productivity" but does not simulate natural conditions. In quartz sand, 99% of the light is absorbed at a depth of 3 mm; thus, in effect, all photosynthesis will occur in a layer 5-mm thick. A layer with this thickness can be settled evenly in the lid of an upturned jar that is filled with filtered seawater inoculated with ^{14}C. The sample can then be exposed in the same way as for labeled water samples in true or simulated *in situ* conditions. After incubation the sand can be washed with clean, filtered seawater and samples of the sand counted routinely in planchets. These counts can be converted to absolute values of uptake using a conversion factor determined by mixing cultures of known activity into the sand and counting this "labeled" sand, or by gas-phase counting of a few samples. A full description of the method is given by Baird and Wetzel (in prep.). The method is best suited to conditions where, in effect, all the photosynthesis is by attached organisms and where the sand is evenly mixed to a depth of a few centimeters by wave action.

Sampling of sand at all stations in 1964 was done by coring, using plastic tubes 2.2-cm I.D. and 20 cm long. Sublittorally

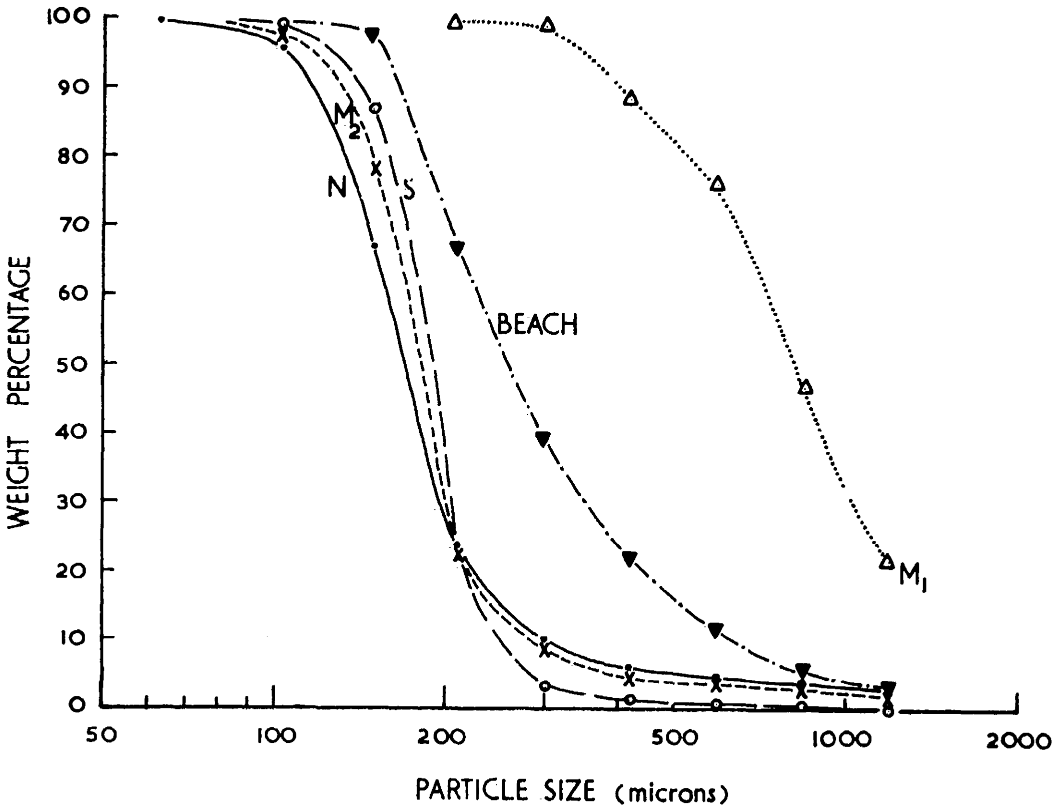

FIG. 2. Cumulative curves of particle-size distribution at the sampling positions. The two low-water stations have been averaged.

these were collected by SCUBA divers. This was not possible in 1965 when sublittoral samples of only the top 2 cm were taken with a small grab.

SEASONAL CYCLES IN THE WATER

During 1965, water samples were taken at M_1, from 0, 2.5, 5, and 10 m. The effects of freshwater runoff appear sporadically in the surface samples, but generally the water is uniform from surface to bottom; the data for 5 m are given in Fig. 3. For ^{14}C uptake, water from 5 m was exposed at 0, 2.5, 5.0, and 7.5 m *in situ* or under a range of filters in the incubator. Integrating the data gives 95 g C m^{-2} as an estimate of the yearly production. An indication of the variability of the phytoplankton is provided by the more frequent chlorophyll *a* data.

The cycles of nutrients and chlorophyll *a*, and the total net production for the year are similar to the surface waters of Loch Nevis (Steele and Baird 1962) and also to Aberdeen Bay on the east coast of Scotland (Steele and Baird 1961). For such inshore areas, the production is more uniform during summer and does not show the summer minimum associated with offshore areas in the North Sea (Steele 1956).

CHLOROPHYLL AND CARBON CONTENT OF THE SAND

The reproducibility of sampling at all stations was tested in 1964 by analysis of the top 2 cm of cores taken approximately 1 m apart. The coefficients of variance in chlorophyll and carbon were 11 and 9%. The samples analyzed for chlorophyll at Sta. S, taken on successive days with a grab sampler, indicate the same magnitude of

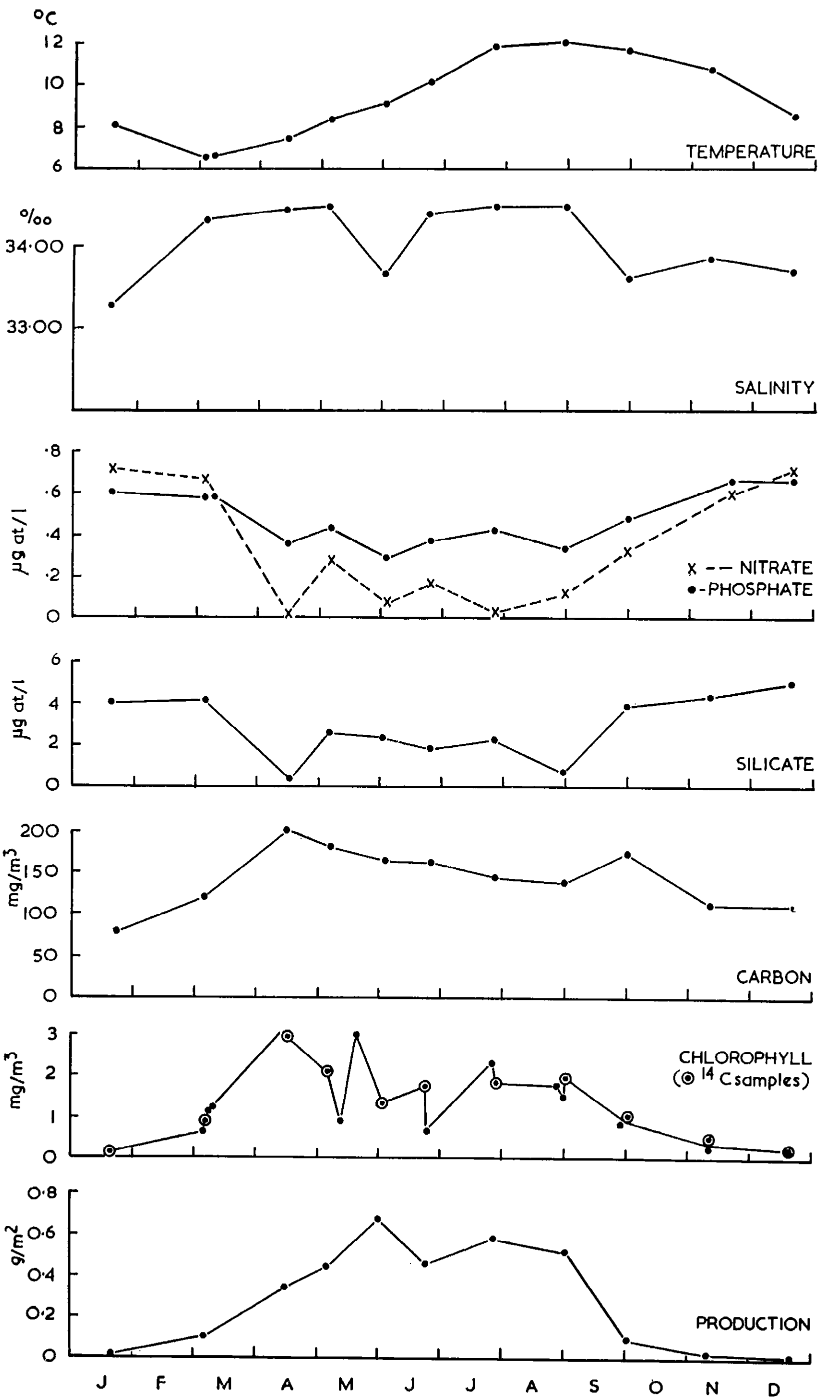

FIG. 3. Seasonal cycles of the environmental data obtained in 1965 from water samples collected at 5 m.

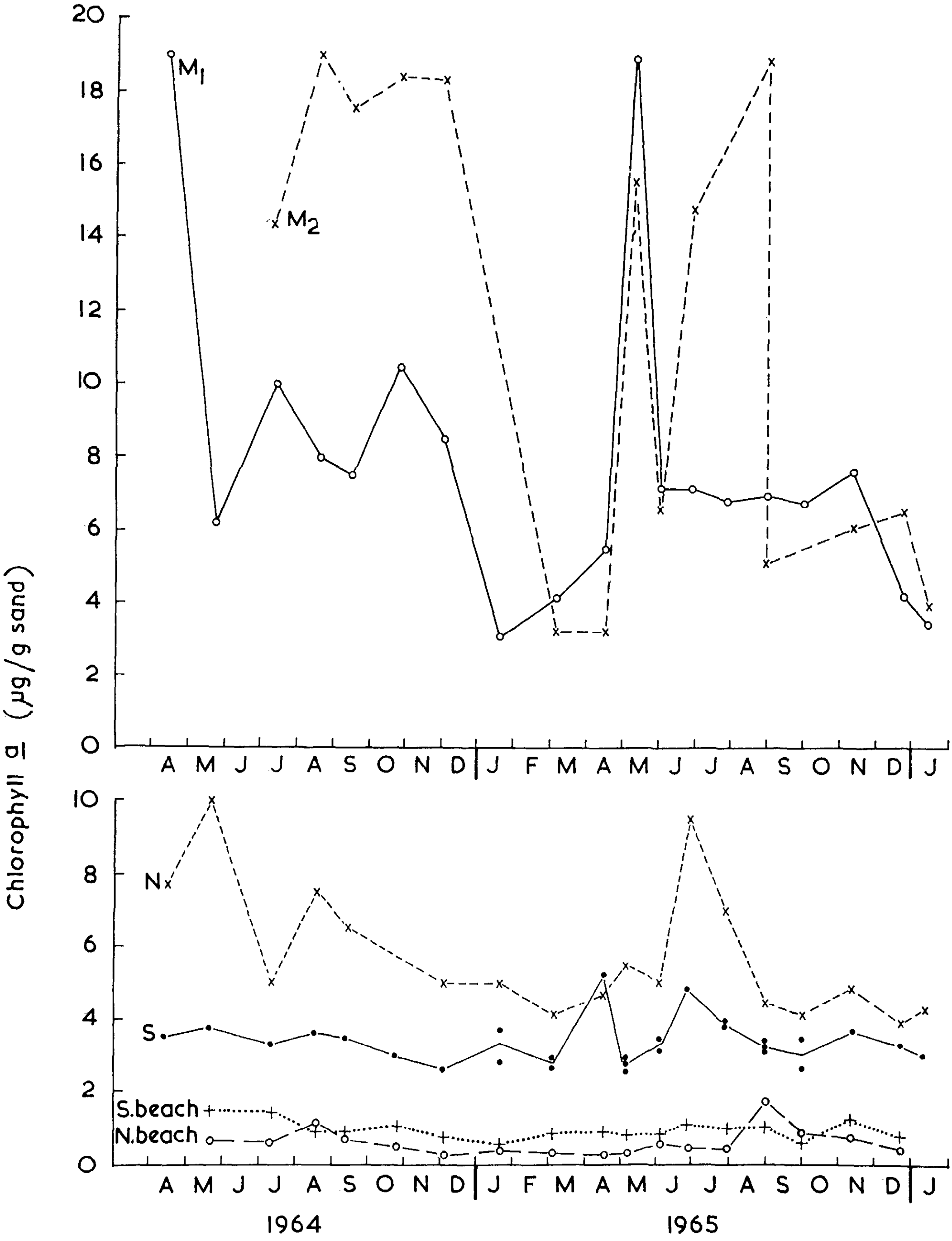

FIG. 4. The chlorophyll *a* content of sand from the top 2 cm of the beach at the sampling positions.

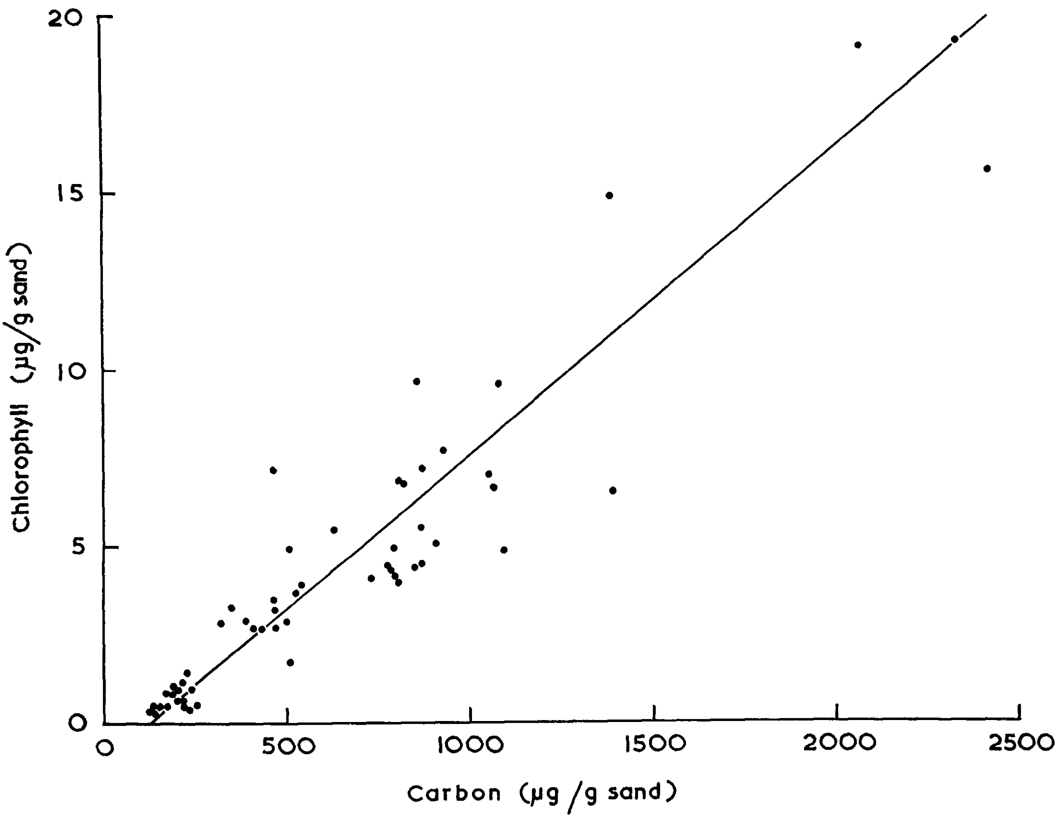

FIG. 5. The relation of chlorophyll *a* to carbon in the top 2 cm of the sand.

variation. In this respect, the samples from Sta. M_2 may be more irregular when a grab sampler is used because of its position on the edge of the beach.

The results (Fig. 4) show two main features in the chlorophyll *a* distribution in the top 2 cm of sand: marked increases with depth of water and much greater fluctuations at the deeper stations. At the low-tide stations, NB and SB, and at S, although there are occasionally higher values in spring and summer, the main feature is the relative constancy of the seasonal picture. Values from Stas. N and M_1 show larger relative variation and some evidence of a seasonal cycle with a winter minimum and a maximum in late spring or summer. Values from Sta. M_2, on the edge of the beach, are very erratic but confirm the trend of highest values in the deeper water.

The particulate organic carbon in the top 2 cm of sand shows a close relation with chlorophyll *a* concentration for all stations in 1965 (Fig. 5). There are, however, significant seasonal changes. For all sampling dates in the period March–October, a single regression is adequate (SE given in parentheses).

$$\text{Carbon} = 115\ (\pm 4) \times \text{chl} + 124\ (\pm 5).$$

During winter months there are significant differences in the regression.

$$\text{Carbon} = 115\ (\pm 4)\ \text{chl} + 40\ (\pm 18)\text{—Jan.}$$
$$\text{Carbon} = 82\ (\pm 8)\ \text{chl} + 167\ (\pm 16)\text{—Nov.}$$
$$\text{Carbon} = 162\ (\pm 9)\ \text{chl} + 80\ (\pm 18)\text{—Dec.}$$

The close relationship of chlorophyll and carbon in the top 2 cm does not hold when vertical distributions in the sand are examined. At all the deeper stations, particularly N and M_1 where cores were taken during 1964, there is usually a rapid decrease in chlorophyll with depth but a

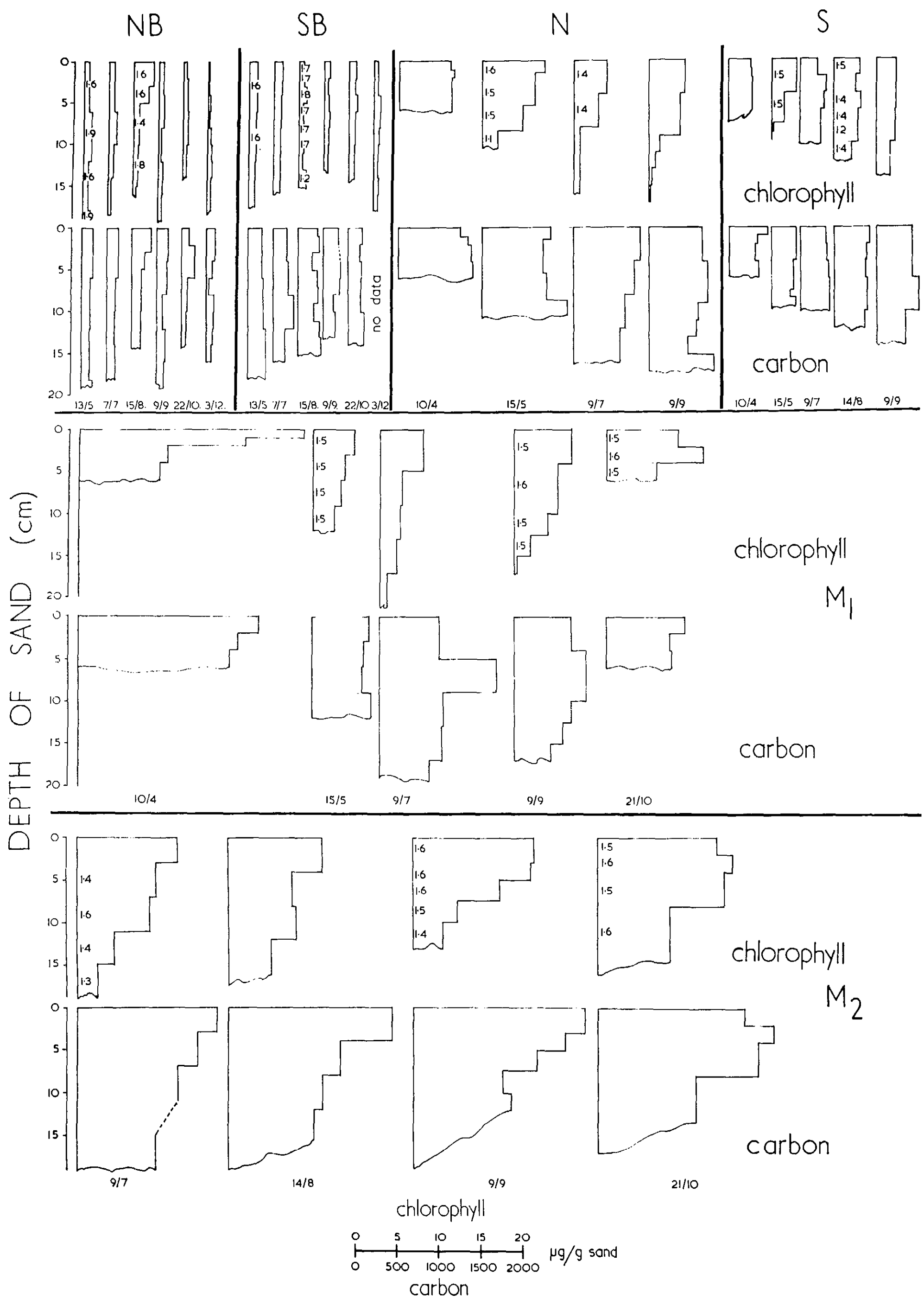

FIG. 6. The depth distribution of chlorophyll *a* and carbon from cores taken in 1964. The numbers in the profiles give the U/A ratios for these samples (*see* text).

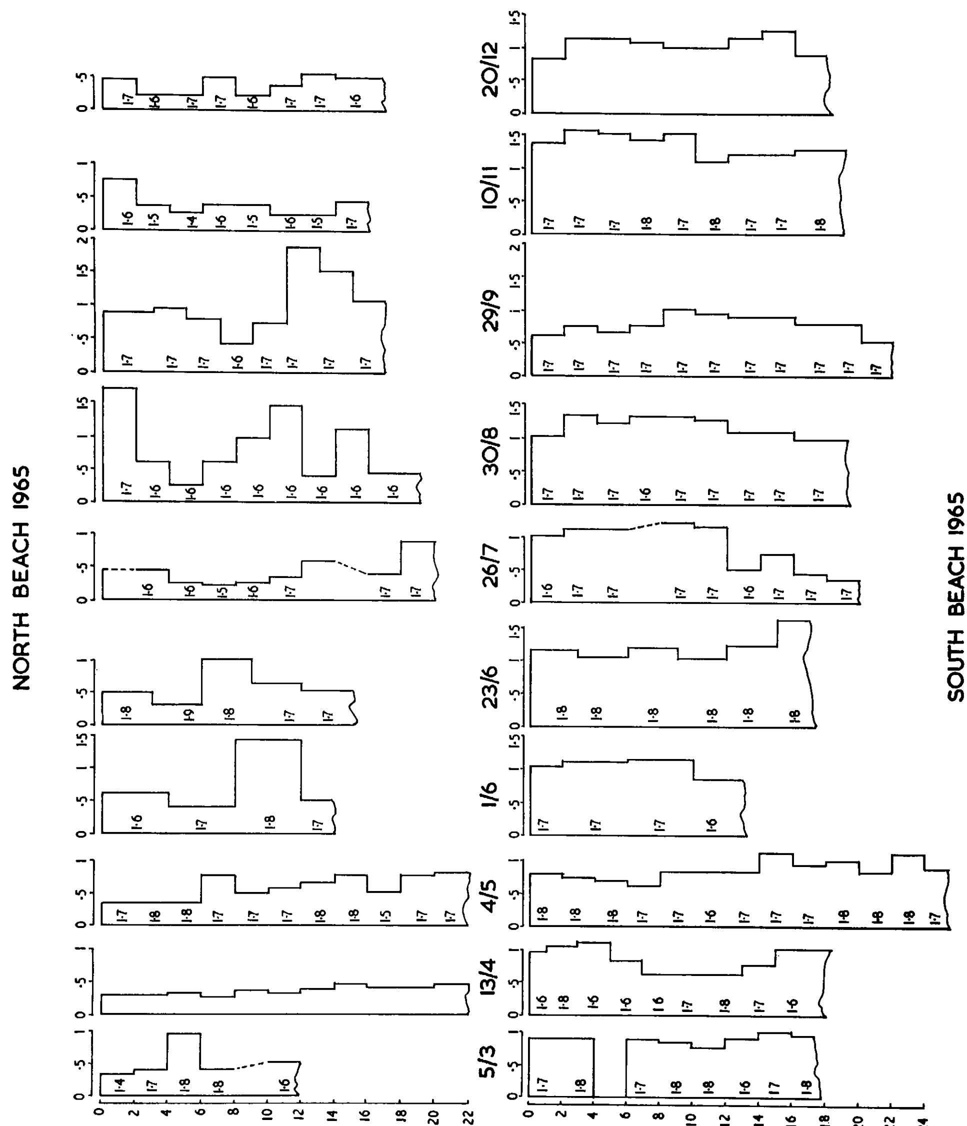

FIG. 7. Chlorophyll *a* distribution in cores from stations at low water in 1965. The inset numbers give the U/A ratios.

much slower change in carbon (Fig. 6). The data on U/A ratios available for several cores indicate that with a few exceptions these ratios do not decrease markedly with depth, so that although some breakdown of the chlorophyll pigment seems to occur at depth in the sand, this does not provide a complete explanation of the vertical gradients.

For the stations at low-water mark, the data on chlorophyll from 1965, and especially on U/A ratios (Fig. 7), show that there is no evidence for gradients nor for any breakdown of pigments. The chlorophyll data, however, do suggest some stratification since the 95% confidence limits on chlorophyll measured in each section of a core are ± 0.1 $\mu g/g$ of sand. These

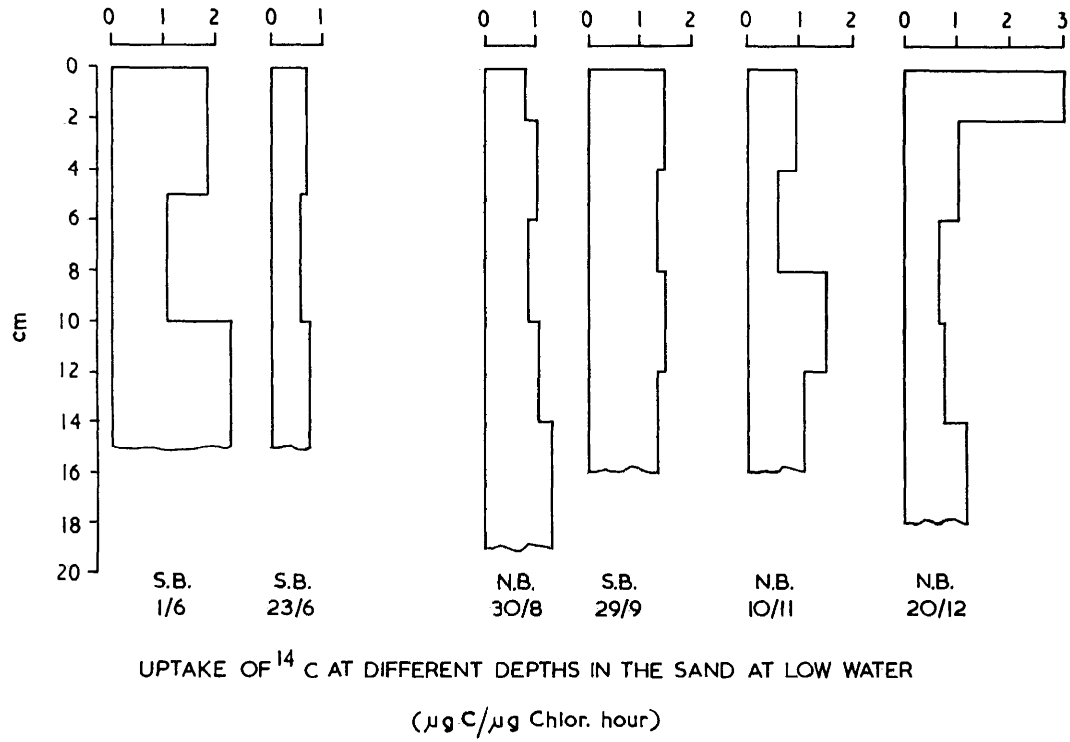

FIG. 8. Uptake of ^{14}C at different depths in sand collected at low water.

results imply that the diatoms at all levels in the sand at low tide are in viable conditions. As further evidence, Fig. 8 shows the rate of ^{14}C uptake, at a fixed light intensity, of sand taken from different levels. Again there are variations with depth but no evidence of decreased ability for photosynthesis at greater depths in the sand.

Microscopic examination of the sand shows that diatoms firmly attached to the sand are the dominant flora (Munro and Brock, in press). However, there are small quantities of organic matter in the interstitial water, and part of this appears to be finely divided seaweed. The organic carbon content of this material shows considerable variation but no seasonal pattern and is most closely related to the total carbon. In Table 1 the proportion of unattached organic matter, expressed as a percentage, is relatively constant compared with the total carbon, which varies by more than an order of magnitude between the low-water and offshore stations. Measurements of the pigments showed that, on the average, the eluted material had a U/A value of 1.3 compared with 1.7 for the sand at low water; sublittorally, the eluted material gave a ratio of 1.2 compared with 1.6 for the sand. Thus, plant material not attached to the sand grains is considerably degraded. Table 1 also shows the equivalent percentages of chlorophyll *a* if the pigments were not degraded. These imply that the interstitial material had a much higher chlorophyll content than the organic matter attached to the sand (carbon : chlorophyll ratio of approximately 65 : 1). During summer the ratio for particulate matter in the water varies between 65 and 115.

PRIMARY PRODUCTION IN THE SAND

Uptake of ^{14}C by sand collected at Sta. S and incubated as described earlier was used to estimate daily production per unit

TABLE 1. *The carbon and pigment estimates of material in the interstitial water expressed as a percentage of the totals for sand. The last line shows the calculated percentage for the pigment as undegraded chlorophyll* a

	Station				
	Beach	N	S	M_1	M_2
Carbon (%)	1.7	3.7	3.5	4.9	5.2
Pigment (%)	2.2	4.3	4.7	7.5	6.3
"Chl *a*" (%)	2.8	6.0	6.6	10.5	8.8

of chlorophyll at different light intensities corresponding to the mean depths of the other stations. Samples from all stations were exposed for 4 hr in an incubator at a fixed light (approx 10,000 lux). These data (Table 2) have been used to provide average factors for the differences between stations that are due to the effects of light adaptation on the ^{14}C uptake per unit chlorophyll. These, together with the data from 1965 on chlorophyll (Fig. 4), permit calculations of the rates of primary production at each station. Since this method is indirect, no great accuracy attaches to any individual value. However, when integrated over a whole year, the results (Table 3) permit two main conclusions. First, although there are large increases in chlorophyll with depth, these are balanced by decreases in light, so that there is a very narrow range in production values with no particular depth giving much larger rates than the others. Second, these yearly values of 4–9 g C m^{-2} are at least an order of magnitude lower than the production in the water (95 g C m^{-2}).

TABLE 2. *Uptake of ^{14}C carbon by sand at fixed light intensity measured during 1965 (mg C mg chl^{-1} hr^{-1})*

Date	Station SB	NB	S	N	M_1	M_2
1 Jun	1.78	—	0.87	0.70	0.58	0.70
30 Aug	—	0.77	0.65	0.52	0.52	0.22
30 Sep	1.34	—	0.64	0.42	0.25	—
10 Nov	—	0.93	0.56	0.30	0.31	0.22
20 Dec	1.03	—	0.48	0.48	0.78	0.14
Avg	1.38	0.85	0.64	0.48	0.49	0.32

TABLE 3. *Production (g C m^{-2} year^{-1}) in the sand. The value for M_2 is based on a small number of samples*

Station	SB	NB	S	N	M_1	M_2
Production	7.3	4.3	7.8	9.2	4.9	(8.3)

DISCUSSION

The main feature of the results is the increase of chlorophyll and organic carbon with depth below low-water mark. This does not appear to depend on particle size, particularly since the two deepest positions with high chlorophyll and carbon in the summer have very different particle composition. Further, the offshore stations show definite vertical gradients in chlorophyll values, and to a lesser extent in carbon values, within the sand column. This suggests that vertical mixing is a major controlling factor, with wave action on the beach producing conditions that most limit growth of diatoms attached to the sand grains. The difference between the two 5-m stations is consistent with this since Sta. N, which is more sheltered than Sta. S, has higher chlorophyll values and more evidence of vertical gradients.

One survey, in March 1965, of the sand between high and low water gave values between 0 and 1 μg chl/g of sand, indicating that the limiting effects of wave action apply to the whole intertidal area. For this exposed beach it would appear that in the littoral area, wave action is so limiting that seasonal changes in incident radiation have comparatively little effect. Sublittorally, periods of relative calm could permit the build-up of plant populations attached to sand grains near the surface. Thus, for the deeper sublittoral stations, the seasonal changes in incident radiation combined with short term variations in disturbance of the sand could produce the observed fluctuations in chlorophyll values with the main peaks occurring sporadically during summer.

Although nearly all the organic matter is present in forms attached to the sand grains, the low productivity of the sand could mean that the small fraction of unattached organic matter is important in the interstitial food chains if it has a rapid turnover. The presence of some weed debris in the sand is an indication of an external source for some of the unattached material. However, one might expect that increased sand mixing at low water would permit greater incorporation of debris (or "detritus") from the water into the sand. Yet the results show that this debris is most nearly proportional to the content of attached organic matter, which is greatest at the deeper stations. This suggests that this debris is mainly composed of breakdown products, perhaps of diatoms from the sand.

The method devised to measure production by benthic diatoms attempts to provide an estimate of *in situ* production. The results indicate that, for an exposed beach, production per m^2 is low compared with that in water and also compared with sheltered areas where the bottom is little disturbed and where large growths of motile benthic diatoms occur (Pomeroy 1959). On the other hand, the effect of mixing and disturbing the sand is to distribute an apparently viable population to considerable depth relative to the thickness of the euphotic zone in the sand.

Investigations in more sheltered areas usually show the benthic plant population within the top cm (Pomeroy 1959) and often dominated by motile forms that can migrate to the surface (Aleem 1950). Grøntved (1966), working in the Danish Wadden Sea, has recorded ^{14}C uptake to a depth of 10 cm, but it was much decreased below 5 cm. The results presented here, particularly those for low-water stations, demonstrate the presence throughout the year of viable populations to a depth of 20 cm. These results raise several problems concerning metabolism under such conditions.

The organic carbon content under 1 m^2 of the sand to a depth of 20 cm is about 50 g C. If 40% of this carbon is composed of diatoms (equivalent to a carbon : chlorophyll ratio of 50 : 1 in the living plant), then a plant population of 20 g C m^{-2} has a yearly production less than 10 g C m^{-2} $year^{-1}$. In other words, this would permit less than 0.2% loss of carbon per day by the cells for maintenance—neglecting grazing by animals on this stock. Further, during summer, preliminary results on mixing of the sand show that for long periods mixing may be only to a depth of 5–10 cm, so that populations below this have no access to light for several months. A possible explanation is that these diatoms assimilate carbon heterotrophically, as suggested by the results of Lewin and Lewin (1960), but work by Munro and Brock (in press) shows that this is unlikely. The other possibility is that these organisms are specially adapted to spend long periods in the dark at low metabolic rates and with negligible degradation of pigment. In a preliminary experiment, we have shown that an axenic culture of a diatom isolated from the sand at Loch Ewe (by M. R. Droop) can exist in the dark for 23 days with no measurable loss of carbon or pigment degradation. Long term experiments are planned.

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