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## *A Study of Production in the Gulf of Mexico*<sup>1</sup>

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### ABSTRACT

Theoretical reasons are given to show that midwater chlorophyll maxima may be due to an increase in the chlorophyll content of the plants rather than to an accumulation of plants due to sinking. Data from the Gulf of Mexico are used to support this explanation.

*Introduction.* In the tropics and subtropics, apart from special regions of upwelling or divergence, the general type of marine environment is one having great vertical stability in the water column, low nutrient concentrations down to several hundred meters, and ample surface light (Menzel and Ryther 1960). In many ways this stable tropical environment is an extreme form of the conditions often found in temperate latitudes for a few summer months when production is at a minimum. The main difference is that in temperate latitudes there is usually a sharp increase in phosphate and nitrate just below the euphotic zone (Steele and Yentsch 1960).

Regions having this type of physical environment generally have one major biological feature in common—a maximum in the vertical distribution of chlorophyll *a* near the foot of the euphotic zone, generally at 1–5% of surface

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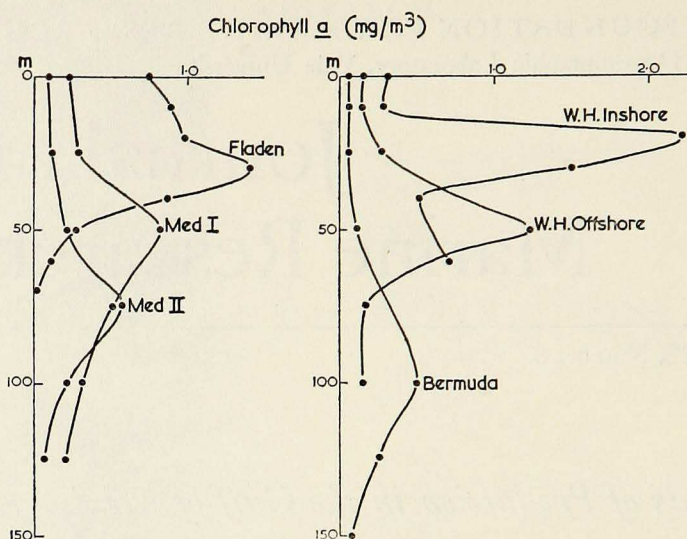


Figure 1. Vertical profiles of chlorophyll *a* from stable low nutrient environments at different latitudes. *Inshore*,  $40^{\circ}02'N$ ,  $73^{\circ}25'W$ ; *Offshore*,  $39^{\circ}11'N$ ,  $71^{\circ}50'W$ ; July 1957. Data from Woods Hole Oceanographic Institution. *Bermuda*, average of six stations in a diurnal experiment, April 1960 (Ryther et al. 1961). *Fladen*,  $58^{\circ}20'N$ ,  $0^{\circ}30'E$ , August 1962. *Med I*, N.E. Mediterranean; *Med II*, S.E. Mediterranean. Data collected on CALYPSO, April 1961, in conjunction with Dr. A. Ivanoff.

light. Since chlorophyll *a* is related to both the population density of the plants and their growth rates, the explanation of this feature would help in understanding the productivity of such areas. Typical features of such maxima are given in Fig. 1 for various latitudes.

Major attempts to explain these changes have been made by Riley et al. (1949) and by Steele (1956). Their main relevant assumptions were:

(1) Chlorophyll *a* concentration is proportional to plant carbon so that the chlorophyll maximum corresponds to a maximum plant population.

(2) Photosynthesis is proportional to light except at high light intensity, where there is some inhibition. This puts the maximum growth rate near the surface.

(3) The grazing rate of the herbivores is assumed to be equal at all depths. It is obvious that, in areas with little vertical mixing, the results of (2) and (3) would show a population maximum near the surface. To prevent such a contradiction with (1), Riley et al. assumed that

(4) The plants sink at a constant rate.

These four assumptions enabled Riley et al. to calculate a range of profiles broadly similar to those given in Fig. 1. However, the accumulation of more

detailed data than those available to the above authors has shown certain inadequacies in this theory; particularly, the maxima appear to be at too shallow a depth relative to the transparency of the water (Steele and Yentsch 1960). It has been necessary, therefore, to consider that some kinds of change occur in the plants themselves, and laboratory experiments suggested that the sinking rate of the plants might decrease at the foot of the euphotic zone, where there is also a marked increase in nutrients. In the tropics, however, where the chlorophyll peaks are often most marked (showing increases of an order of magnitude relative to the surface), there is usually very little increase in nutrients down to depths greater than the depth of the euphotic zone. Further, the plant species of these areas are usually motile, and it seems unrealistic to consider sinking to be a major factor at any depth—especially the high values of 5–10 m/day required by Riley et al. Yet the most important drawback in their theory is that sinking implies a net downward flux of plant nutrients out of the euphotic zone, and this appears to be an extremely inefficient response of a population living in such very stable nutrient-limited regions.

Thus it seems more likely that sinking would be minimal, and in looking for alternative explanations of the chlorophyll distribution, the main requirements must be expressed in terms of changes from the rather fixed values of the plant chlorophyll content and light adaptation as postulated by Riley et al. The great variations in the light response of populations at different depths are now well known (Ryther and Menzel 1959, Steeman-Nielsen and Hansen 1959a). This effect, and also nutrient limitation, can be expected to alter the chlorophyll content of the plants; the possible combined result of these factors in the sea has been expressed in a very simplified set of formulae (Steele, 1962) and applied to seasonal changes in a mixed layer. The first part of this paper attempts to extend these concepts to cover vertical changes in a stable water column, and the second part discusses their relevance to data collected in the Gulf of Mexico.

*Theoretical Considerations.* From Steele (1962), the rate of photosynthesis,  $p$ , per unit chlorophyll  $a$  as a function of average light,  $I$  (g cal/cm<sup>2</sup>/hour), is

$$p = 0.48 I \exp(-I/I_m) \text{ (g C/g Chlor/hour)}, \quad (1)$$

where  $I_m$  is the light intensity at which photosynthesis is a maximum. Variations in adaptation to light are provided by changes in  $I_m$ . Further, for this population, the ratio,  $c$ , of chlorophyll  $a$  to carbon is given by

$$c = \frac{5.7 f(N) p_m}{I_m} \text{ (g chlor/g C)}; \quad (2)$$

here  $p_m$  = the maximum photosynthetic rate = 0.066 (g C/hour) and  $f(N)$  = a factor for the effects of nutrient limitation such that  $f(N) = 1$  when there

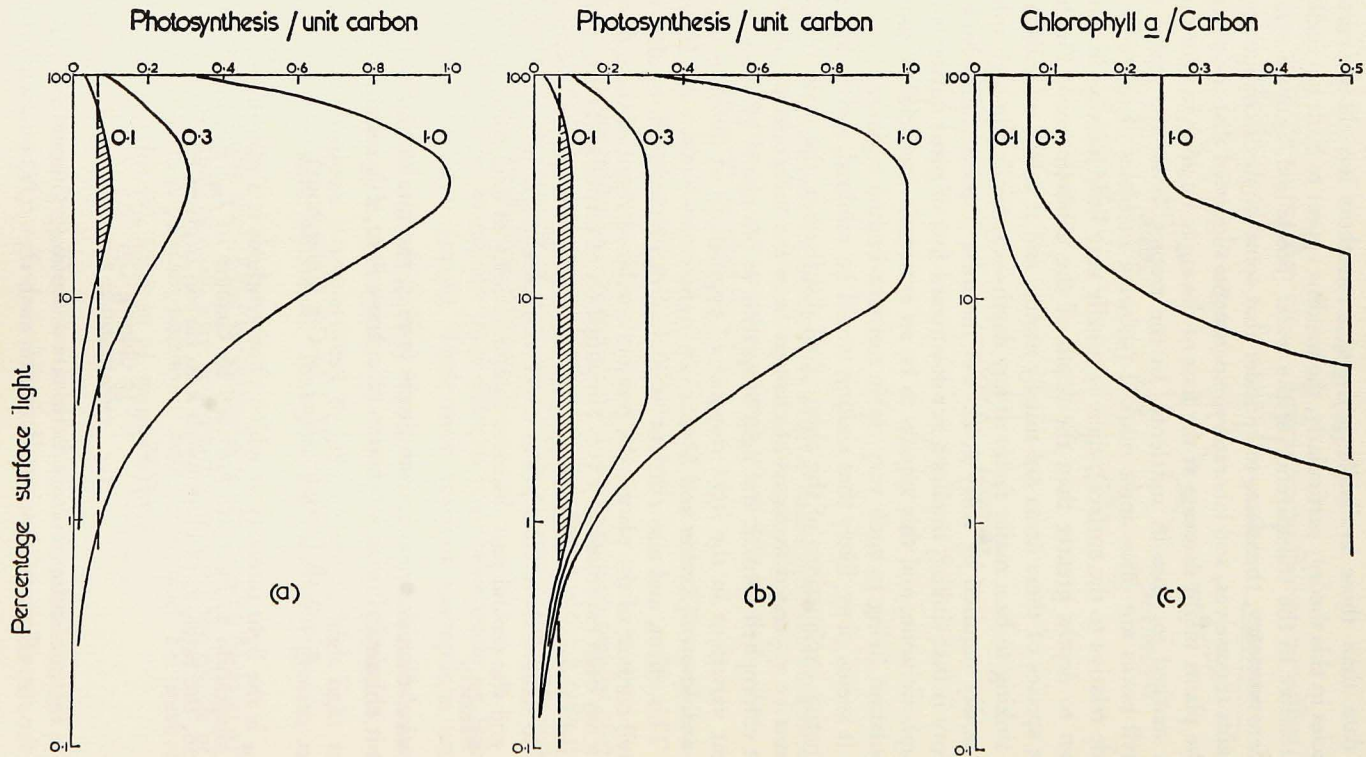


Figure 2. Relative change in photosynthesis for exponentially decreasing light: (a) for unadapted populations; (b) adapted populations; (c) changes in chlorophyll *a*/carbon ratios for adapted populations. The dashed line in (a) and (b) corresponds to a respiratory rate of approximately 5% per day.

is no limiting effect and  $f(N)$  decreases as the effect of limitation increases. From (2) it is seen that chlorophyll per unit carbon decreases with increasing light and decreasing nutrients.

In previous papers (Steele 1962, Steele and Menzel 1962), conditions in a mixed layer were considered, and the plants within this layer were regarded as a single population adapted to the incident light at the surface,  $I_0$ . From observations, the value of  $I_m$  for this population lies between 50% and 30% of  $I_0$ . The latter value will be used here for summer conditions. For the very poor waters of the Sargasso Sea and the central Gulf of Mexico this relative intensity corresponds to a depth of 25 m, which is also approximately the depth of the mixed layer in summer. Thus it is suitable to consider that adaptation by the plants will occur for  $I \leq \frac{1}{3} I_0$  in the stable layers below the surface mixed layer. Although the general features of increasing dark adaptation with increasing depth are known, a detailed relation is not available for these layers. However, it seems reasonable to choose the adaptation that will give the most efficient response in terms of growth rate. From (1) this is obtained by taking  $I_m$  as the average light at any depth. From (2) the maximum photosynthetic rate in carbon units is

$$pc = p_m f(N) \text{ (g C/g C/hour).}$$

There must be a lower limit to dark adaptation, and this is defined by setting an upper limit of  $c = .05$  to the chlorophyll  $a$  content of the plants (Steele 1962). This in turn, from (2), defines the light intensity  $I^*$  (below which adaptation is no longer possible), as

$$I^* = 7.5 f(N). \quad (3)$$

For depths below this light intensity, the photosynthetic rate, from (1), is

$$\begin{aligned} p &= 0.48 I \exp(-I/I^*) \text{ (g C/g chlor/hour),} \\ \text{or} \quad &= 0.024 I \exp(-I/I^*) \text{ (g C/g C/hour).} \end{aligned} \quad (4)$$

In this way the photosynthesis per unit carbon and the chlorophyll  $a$  per carbon ratio are defined as functions of light and the degree of nutrient limitation. The other value required is the average light intensity at the sea surface,  $I_0$ . As an example, 45 g cal/cm<sup>2</sup>/hour is used as a typical value for the subtropics and tropics.

Fig. 2 shows the photosynthetic rates for unadapted and adapted populations at different levels of nutrient deficiency, as a function of exponentially decreasing light. The effects on net production of a hypothetical respiration rate of 5% of carbon respired per day are shown by the dotted line (Fig. 2a, b); this indicates the increasing importance of adaptive ability as nutrient limitation increases; the shaded area shows that, with extreme nutrient limitation, the net production would be increased by a factor of 3 in this hypothetical case.

The consequences of these adaptive changes on the chlorophyll/carbon ratio (Fig. 2 c) show that maximum chlorophyll in nutrient-poor waters should be found between 1% and 5% of the surface light and that an increase by a factor of ten in chlorophyll concentration relative to the surface could be expected. Below the shallowest level at which maximum chlorophyll/carbon ratios occur there is a decrease in photosynthetic rate. This could be expected to produce a decrease in population density of the plants below the maximum, and so produce a true peak in chlorophyll concentration corresponding to that usually observed in the sea.

Thus these theoretical considerations show how the chlorophyll maxima may be explained in terms that do not require sinking and, further, the population is considered to be a highly efficient rather than an inefficient system. To define the populations in more detail it is necessary to consider the absolute size of the population and the way this size may be determined by nutrient limitation, grazing, and the effects of the population on turbidity. The turbidity can be defined by using the relation between chlorophyll,  $a$  (mg/m<sup>3</sup>), and the extinction coefficient,  $k$ , given by Riley (1956),

$$k = .04 + .088C + 0.54C^2/3; \quad (5)$$

the value for the surface layer,  $k_0$ , as a function of  $C_0$  will be used, partly for simplicity and partly because the relation was deduced in this way. On this basis,  $I = I_0C^{-k_0z}$ .

The other variables will also be interdependent, since an increase in  $f(N)$  is likely to correspond to an increase in the plant population and hence to an increase in the chlorophyll concentration. In turn, an increasing plant population would probably tend to increase the herbivores and therefore the amount of grazing on the plants. To illustrate how these factors might affect the chlorophyll profiles, some very simple assumptions are made.

For a plant population,  $P$  (g C/m<sup>3</sup>), in the region of optimum photosynthesis in a stable water column, with photosynthetic rate,  $p_c$ , and respiration rate,  $r$  (g C/g C/day), being filtered at a rate  $g$  (m<sup>3</sup>/g C) by a herbivore population,  $H$  (g C/m<sup>3</sup>), we take the rate of change of the population to be

$$\frac{dP}{dt} = (p_c - r - gH)P. \quad (6)$$

For the rate of herbivore change,  $(dH)/(dt) = (gP - P - fF)$ , where  $P$  is the respiration rate of herbivores and  $fF$  represents the feeding rate of the carnivores,  $F$ . As Riley et al. have pointed out, it is very difficult to choose numbers for this latter term; they used  $f = 10g$ . The equation will be further simplified by assuming that  $10F = H$ , which provides for a proportional increase of carnivores with the herbivore stock. Thus

$$\frac{dH}{dt} = [g(P - H) - p]H. \quad (7)$$

Considering (6) and (7) as steady states,

$$pc = r + gH = gP + r - P. \quad (8)$$

In the region of optimum photosynthesis for 12 hours of daylight, the photosynthetic rate becomes  $12 pc = 12 p_m f(N) = 0.79 f(N)$ . For the depths below the region of optimum photosynthesis, it is assumed that  $H$  and  $P$  decrease to maintain the relation (8).

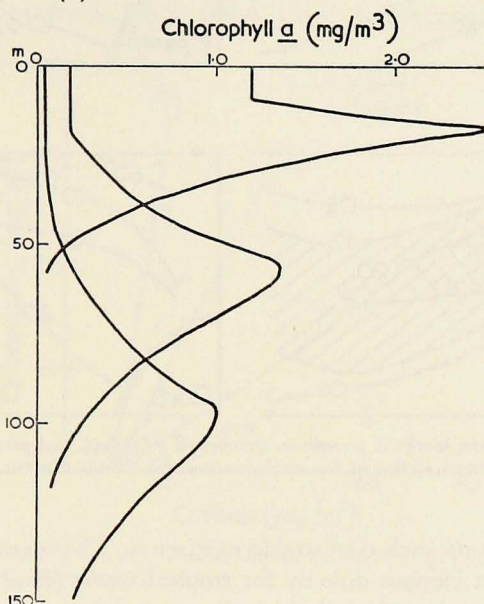


Figure 3. Theoretical chlorophyll  $a$  profiles in a stable water column as a result of differing degrees of nutrient limitation and of grazing.

The following estimates for the several parameters have been chosen:  $g = 5 \text{ m}^3/\text{day}$  (Steele 1959),  $r = 0.07 - g \text{ C/g C/day}$  (Steele and Menzel 1962, Riley et al. 1949),  $P = 0.10 - g \text{ C/g C/day}$  (Riley et al. 1949).

With these values, using eqs. (1), (2), (4), (5), and (8), it is possible to derive the depth distribution of chlorophyll  $a$  corresponding to any value of  $f(N)$ , and in Fig. 3 the curves are shown for three degrees of nutrient limitation. A comparison of the curves in Figs. 1 and 3 shows that the curves in Fig. 3 describe roughly the main trends found in the observations.

*Observations in the Gulf of Mexico.* The problems involved in testing these ideas can be derived from a comparison of the postulates of Riley et al. (1949) with those put forward here.

The main difference is that the former would require a maximum in the plant biomass corresponding to that in chlorophyll  $a$  while the latter would



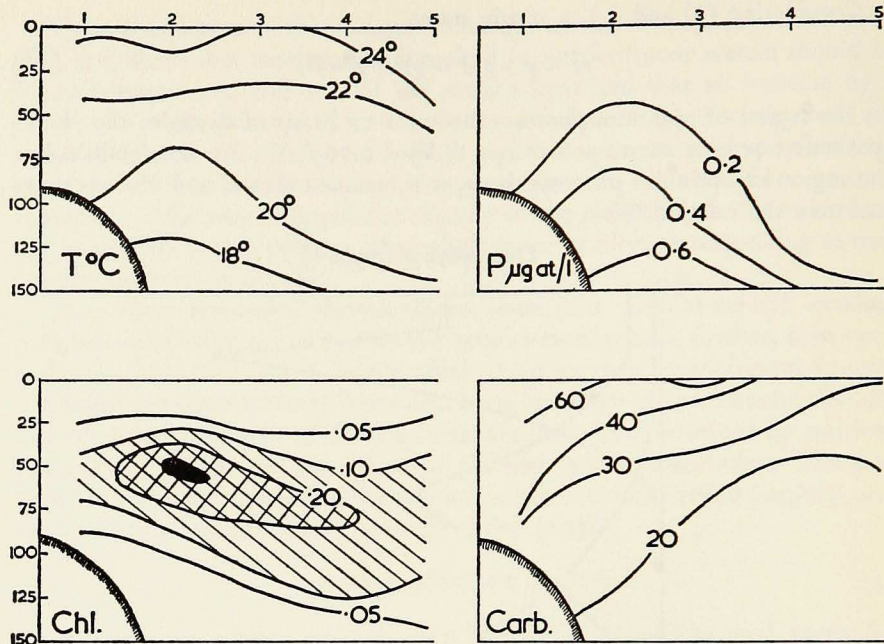


Figure 4. Temperature, inorganic phosphate, chlorophyll *a* (mg/m<sup>3</sup>), and particulate organic carbon (mg/m<sup>3</sup>) from a section of five stations across the Florida Current.

imply that there is no such comparable maximum. There are great difficulties in estimating plant biomass directly for tropical water (Hulburt et al. 1960). The total particulate organic carbon can be measured by wet oxidation (Strickland and Parsons 1960), but the disadvantage here is that such estimates include detrital carbon which, in areas of low plant growth, may be a large fraction of the total carbon. Further, the possible separation by statistical regression of carbon on chlorophyll (Steele and Baird 1962) would not be possible for stable water columns if the chlorophyll *a* content of the plants is expected to vary greatly with depth.

Data from a line of stations in the Gulf of Mexico across a loop of the Florida Current (Duxbury 1962) at 25°N is shown in Fig. 4. The geostrophic slope is associated with an uplift of phosphate; this in turn corresponds to the region where chlorophyll *a* is the shallowest and most highly concentrated. This general trend fits the theoretical concepts. The carbon values measured by wet oxidation, on the other hand, show a quite different distribution. The higher surface values to the east may be associated with detritus from inshore, but the main feature is the lack of any maximum associated with the maximum in chlorophyll *a*. A plot of chlorophyll *a* and carbon (Fig. 5) suggests that in the deeper water the level of detrital carbon is about 10 mg/m<sup>3</sup> and that, except

for the surface mixed layer, the range in ratios of chlorophyll *a* to carbon in excess of the detrital level may be in the range  $1/30$  to  $1/300$ . A similar possible interpretation for data collected in the subtropical Atlantic has been made by Menzel and Ryther (in press). Thus, although methods are still required for a more detailed insight into the chlorophyll *a* content of living plants, the data given here at least do not conflict with the theoretical concepts.

The other main predicted feature concerns the light adaptation of the communities at different depths. Such adaptation is well known from the results

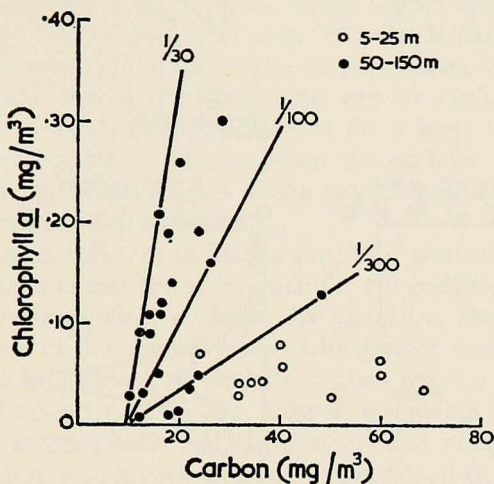


Figure 5. Chlorophyll *a* as a function of carbon for the stations in Fig. 5. The solid lines indicate various chlorophyll *a*/carbon ratios.

of Steeman Nielsen and Hansen (1959) and Ryther and Menzel (1959); they used  $C^{14}$  uptake at a range of light intensities to show progressive dark adaptation at increasing depths in a stable water column. The results obtained in the Gulf of Mexico have the same general character.<sup>3</sup>

In addition to this general adaptation, the ideas put forward here require that the maximum photosynthetic rate should be constant down to the depth at which light is limiting. In poor tropical waters this depth will be in the region of 80–100 m.

Ryther and Menzel's result from  $32^{\circ}N$  gave the following maximum uptake rates: for 0, 50, and 100 m (corresponding to 100, 10, and 1% of surface light), 2.95, 2.25, and 2.84 mgC/m<sup>3</sup>/hr, respectively; these rates do not suggest any major change with depth. Similar experiments in the Gulf of Mexico

3. The light source was provided by Sylvania "Grolux" very high output fluorescent tubes arranged in pairs on either side of the sample bottles; these tubes have a spectrum with a peak at 665 m $\mu$ . They were used because they are designed to give high plant-growth rates. The intensity as recorded on an ordinary selenium photocell was 700 foot-candles, but this value cannot be compared directly with natural radiation. Fine wire mesh was used to provide light filters.

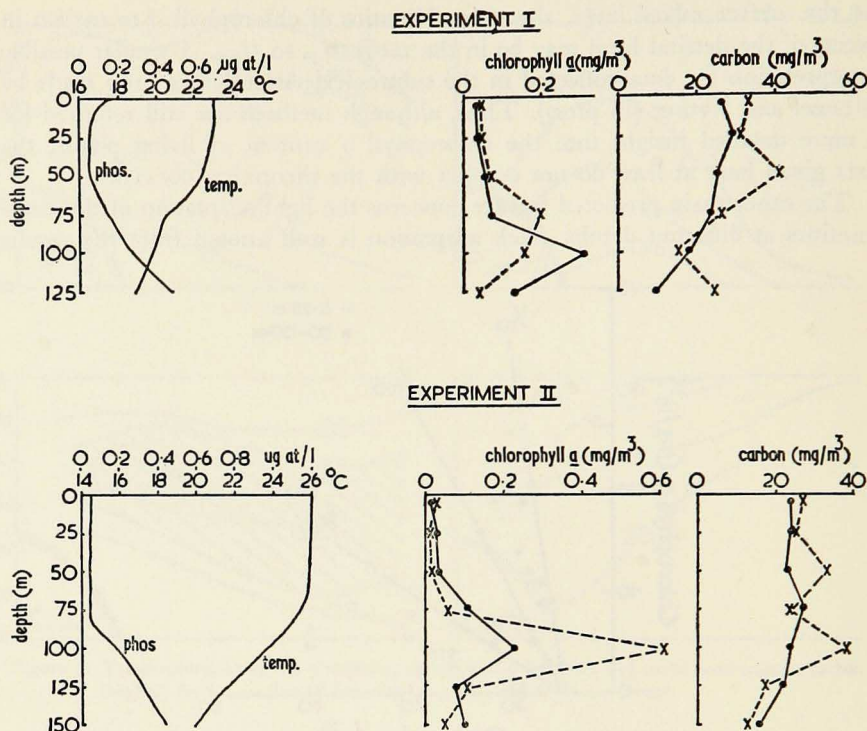


Figure 6. Vertical distributions of temperature, phosphate, chlorophyll *a*, and carbon for  $C^{14}$  experiments. I ( $24^{\circ}57'N$ ,  $84^{\circ}08'W$ ; 24-IV-62), II ( $24^{\circ}53'N$ ,  $84^{\circ}39'W$ ; 25-IV-62). For chlorophyll *a* and carbon: solid line, 1200 hours; dashed line, 0000 hours.

were undertaken to discover the degree of constancy of the maximum photosynthetic rate with depth. Three sets of experiments were run; samples were collected at mid-day, local time, from 5, 50, and 100 m and incubated for four hours. Five meters rather than surface was chosen for the upper sample in order to avoid contamination from surface material, especially from fragments of Sargassum; unfortunately, contamination still occurred, particularly in the third set of experiments.

The distribution of temperature, phosphate, chlorophyll *a*, and particulate carbon for the first two experiments is given in Fig. 6. The range in size

TABLE I. MAXIMUM PRODUCTION RATES (MG C/M<sup>3</sup>/HOUR), IN THREE  $C^{14}$  EXPERIMENTS.

	I	II	III	Average
5 m . . . .	.30	.70	.32	.37
50 m . . . .	.35	1.08	.25	.43
100 m . . . .	.60	.57	.43	.43

of the chlorophyll *a* maxima is probably the result of the rather wide sampling intervals. The carbon profiles, in spite of some variability, demonstrate the lack of comparable midwater maxima. The  $C^{14}$  uptake data also show

considerable variability, probably due to the very low levels of plant growth in this area. Table I summarizes the results of the three experiments. The average results in the final column suggest that the maximum production rate could be considered constant with depth.

*Discussion.* In tropical waters, the main feature of the nutrient cycle is that the supply of nutrients to the plants comes mainly from *in situ* regeneration rather than through upward mixing, as in temperate latitudes. Efficiency of the productive cycle, in these terms, would require that loss of nutrients from the euphotic zone is at a minimum. The simple theoretical picture of the population response to such conditions, developed here, shows that the main features of vertical chlorophyll distribution can be explained without the necessity of introducing a factor to account for a large loss of plants, and therefore of nutrients, due to sinking below the euphotic zone. These concepts are, essentially, a development of the general approach by Riley et al., although they contradict certain details.

The disadvantages inherent in such a simplified picture of reality will be apparent. A definite choice has to be made for the coefficients used, and this is often based on insufficient evidence. In particular, there is little understanding at present of the physical means whereby the required grazing rates of herbivores can be achieved, particularly in areas where a particulate carbon concentration of 10–30 mg/m<sup>3</sup> is one order of magnitude lower than that in open temperate waters (Steele and Baird 1961) and nearly two orders less than that in inshore waters such as Long Island Sound or Plymouth Sound, where agreement is possible between experimental feeding rates and available food (Conover 1956, Corner 1961). Further, the excessively simple conditions ignore the fact that some mixing may occur and that this would tend to smooth out vertical profiles. In temperate waters there is an increase in nutrients at the foot of the euphotic zone, so that nutrient limitation may be less severe there; this gives a true maximum in plant biomass that would accentuate the chlorophyll peak (Steele and Yentsch 1960). There is also the more general problem recently of the presence of phaeophytin in “chlorophyll *a*” estimates (Yentsch 1963), and this could affect depth distributions.

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