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## COMMENTS ON THE DIEL PERIODICITY OF PHYTOPLANKTON PHOTOSYNTHESIS, WITH AN EXAMPLE FROM THE INDIAN OCEAN

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### ABSTRACT

The well known diel periodicity of phytoplankton photosynthesis under constant light can be explained, to a large extent, by diel periodicity of the photosynthetic activity per unit of chlorophyll; thus, to the same extent, this rhythm is independent of chlorophyll concentration or biomass, and it reflects an endogenous cycle. On the other hand, the periodicity which results from long term (24 hours) exposures under "simulated *in situ*" conditions belongs to a quite different type. Both phenomena are discussed here on the basis of parallel experiments made during cruise 8 of R/V "Anton Bruun" in the Mozambique Channel (International Indian ocean Expedition).

In the natural environment, this periodicity interferes with a number of physical and physiological parameters, so that the background of primary production on the 24-hour scale is not less intricate than the annual pattern, and deserves as much interest as the latter.

### INTRODUCTION

The paper by Doty and Oguri (1957) has now become a classical one; it demonstrated that photosynthetic intensity of phytoplankton samples incubated under constant artificial light for a few hours (photosynthetic "capacity") varies according to time of sampling. This so-called "diurnal" rhythm<sup>1</sup> has been then confirmed by several workers, but it is still interpreted quite diversely in the literature. The fundamental question as to whether this periodicity reflects changes in biomass or changes in the production/biomass ratio, has been rather neglected. The former hypothesis, in fact, could only be sustained by the single observation by Yentsch and Ryther (1957) that variations in photosynthesis are accompanied by parallel variations in chlorophyll content; parallel changes are

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<sup>1</sup> "Diurnal", as the opposite of "nocturnal", is inadequate when applying to a 24-hour cycle: "diel" seems to be here more appropriate. See Sournia and Frontier (1968).

also mentioned by Shimada (1958) and Lorenzen (1963), but with a smaller range for the pigment values; in all other cases, changes in pigment content are opposite or undetectable (Doty and Oguri, 1957; Holmes and Haxo, 1958; Angot, 1961; McAllister, 1963; on monospecific cultures: Hastings *et al.*, 1961, and Palmer *et al.*, 1964). Thus, a diel rhythm of chlorophyll activity, i.e. in photosynthesis per unit of chlorophyll, must be taken into account: such a rhythm has been briefly or hypothetically considered by Lorenzen (1963), McAllister (1963) and Newhouse *et al.* (1967), and demonstrated on natural populations by Hansen (1962), Endo (1967), Newhouse (1967) and Sournia (1967), and on laboratory cultures by Eppley and Coatsworth, 1966 (*Dunaliella*), Jorgensen, 1966 (*Skeletonema*) and Eppley *et al.*, 1967 (*Ditylum*).

An other type of diel periodicity has been described by Ryther and Menzel (1961) and Ryther *et al.* (1961) and was left unexplained by these authors: as resulting from 24-hour experiments in the so-called "simulated *in situ*" conditions (i. e. : samples in a water bath under natural illumination, with appropriate filters "simulating" the fractions of incident light at the respective depths), the highest rates of  $^{14}\text{C}$  assimilation occurred for experiments beginning at midnight (or at night), and the lowest for those initiated at midday (or in the day), while chlorophyll concentrations behaved in a rather opposite way.

In this paper, the diel trends of  $^{14}\text{C}$  uptake *per unit of chlorophyll* will be discussed comparatively from both types of experiments: 1) short-term incubations under constant light, 2) 24-hour simulated *in situ* experiments.

#### METHODS

The present example<sup>2</sup> is taken from R/V "Anton Bruun" investigations in the Mozambique Channel from September to November, 1964 (I. I. O. E., cruise nr. 8).

Samples were taken at any hour of the day or night and from five photometrical depths (100, 50, 25, 10 and 1% of incident light); they were used for: 1) spectrophotometric determination of chlorophyll *a* 2) photosynthetic uptake of  $^{14}\text{C}$  during 4 hours under fluorescent lamps of approximately 1000 foot-candles (or approximately 10000 lx or 3,6 ly.h<sup>-1</sup>), 3) photosynthetic uptake of  $^{14}\text{C}$  during 24 hours on deck in incubator bottles being covered with neutral mesh wire filters which simulated the *in situ* percentages of transmitted light. Hourly rates were obtained by dividing 4-hour rates by 4, and 24-hour rates by 12 (an approximation of daylight length, excluding night time).

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Further details on the cruise are available from the following papers: Menzel, 1962 (a manual of methods), Woods Hole Oceanographic Institution, 1964-65 (methods and stations data) and Ryther *et al.*, 1966 (methods and a synopsis of primary productivity and hydrology).

#### Short-term Experiments Under Constant Light

Timing of maximum and minimum (fig. 1) as well as amplitude agree quite well with the characteristics of the photosynthetic periodicity as described by Doty and Oguri (1957) and others (see a brief compilation in Lorenzen, 1963). Thus, the photosynthesis/chlorophyll cycle can explain to a large extent, if not fully, the photosynthetic cycle. Let us consider now the possible causes of the former cycle.

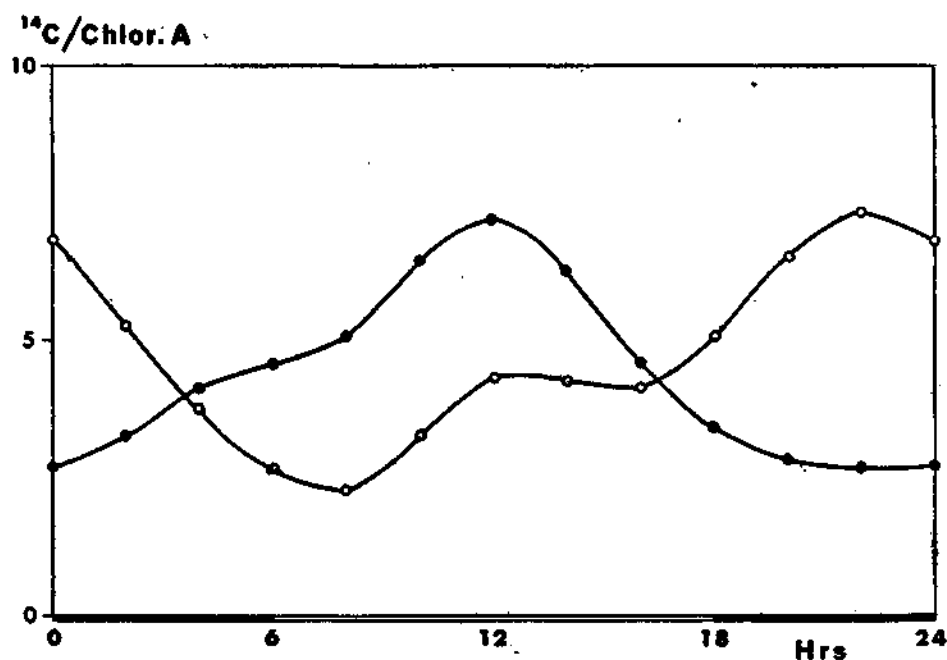


Fig. 1. Photosynthetic uptake of  $^{14}\text{C}$  per unit of chlorophyll ( $\text{mg C/h/mg chlor. a}$ ) as a function of sampling time.

- 4-hour experiments under artificial constant light,
- 24-hour experiments under "simulated in situ" conditions.

As far as production/biomass ratio is concerned, one must exclude variations of biomass itself, though such hypotheses are commonly found in the literature: cell division, transport, migration, sinking, grazing by zooplankton, or amount of pigment per cell. It is hardly to be expected that diel changes in respiration rates could account for so a large range of variations (see e. g. Ohle, 1958 and Lorenzen, 1963). On the other hand, since this rhythm extends to

all levels in the euphotic zone—and since it is measured under constant illumination—injurious effect of light, called forth by Hansen (1962) and Steemann Nielsen and Jorgensen (1962, 1968) must also be discarded. The role of nutrients is suggested by Vollenweider and Nauwerck (1961) but experiments made by Ryther *et al.* (1961) failed to establish a direct relation between diel variations of photosynthesis and availability of nutrients; moreover, work on algal cultures, in which nutrients are supplied at a constant rate, leads to exclude this possibility.

Now, if this phenomenon is replaced in the general frame of plant physiology, an analogy immediately appears with the well known “afternoon depression” (or “midday depression”, “diurnal depression”, “afternoon nap”), which consists in a drop in photosynthetic activity during the second half of the light period, followed by a progressive recovery during the night. Several explanations have been proposed for this depression (Rabinowitch, 1951, chapter 26; Talling, 1961) but the most satisfactory one, in the case of unicellular algae, is an accumulation of photosynthetic products or by-products, or, as pointed out by Sweeney (1965, 1969), an inactivation of enzymes. Whatever the precise cause, it must be looked for inside the cells, that is to say: the rhythm is endogenous.

Studies on synchronous or semi-synchronous cultures of algae suggest that this depression could be connected with the cell division cycle (Hastings and Astrachan, 1959, and Hastings *et al.*, 1961 on *Gonyaulax*; Palmer *et al.*, 1964 on *Phaeodactylum*; Eppley and Coatsworth 1966 on *Dunaliella*; Jorgensen 1966 on *Skeletonema*; Eppley *et al.*, 1967 on *Ditylum*; see also numerous papers by Pirson, Sorokin, Tamiya and others on *Chlorella*, reviewed by Tamiya 1966). However, a photosynthetic rhythm is known in non-dividing (enucleated) cells of *Acetabularia* (Sweeney and Haxo, 1961). Furthermore, natural (mixed) populations of phytoplankton are not likely to divide synchronously and, according to Sorokin (1960), “the amplitude of changes in metabolic activity during the life cycle is expected to be larger in non-synchronized population.” Thus, division cycle must be considered as a connected phenomenon rather than as a causative process.

It should be recalled that we are dealing here with experiments under artificial constant light, so that “capacity” of photosynthesis is measured instead of actual *in situ* photosynthesis. If we refer for a moment to *in situ* conditions, it will be noticed that the afternoon depression in this case is not so general as it appears in artificial conditions: when measuring *in situ* primary production, some workers observe that photosynthesis is more active during forenoon than during afternoon (Verduin, 1957; Ohle, 1958; Vollenweider and Nauwerck, 1961), but this is far from being the rule. The reason is that, besides changes in natural illumination, some environmental factors such as turbulence must be taken into account (Verduin, 1957; Ohle, 1961). So, the afternoon depression, which is of general occurrence in the plant kingdom, is expected to undergo fre-

quent exceptions in natural populations of plankton living in actual *in situ* conditions.

#### Simulated *In Situ* Experiments

The "simulated *in situ*" experiments are subjected to natural day-to-day variations of incident light; on the other hand, such prolonged expositions over 24 hours can be suspected of some unreliability, particularly in oligotrophic waters (Steemann Nielsen, 1964). However, it is clear from fig. 1 that photosynthesis is higher in night samples and the lowest in morning samples.

These observations agree with the periodicity described by Ryther and Menzel (1961) and Ryther *et al.* (1961), who could not explain it. Explanation, however, looks very simple (Steemann Nielsen, 1964): when experiments begin during daylight, a notable fraction of photosynthesized  $^{14}\text{C}$  is subsequently lost through respiration in the course of the night, whereas this effect is minimum for samples taken during night (moreover, the afternoon depression is expected to interfere at some degree with this cycle and make it more complex). It follows that, unlike the cycle resulting from short-term exposures under constant light, the present cycle can hardly be considered as a photosynthetic rhythm and should be merely designated as a pseudo-rhythm.

Fig. 1 shows that the two cycles described in the present paper are nearly opposite with respect to time; this is explained by the different processes which are involved in each of them. In the two cases, on the other hand, timing is expected to vary if other conditions of light and duration of exposures are used. This is probably the reason why the two cycles described by Doty *et al.* (1967) and Newhouse *et al.* (1967) do not differ markedly from each other, and differ slightly from our own curves; procedure used by these workers were a) short-term experiments: 2 hours, 1500 foot-candles, b) 24-hour experiments: using this artificial light source, instead of natural daylight, between 06.00 and 18.00 hours.

#### CONCLUSIONS

The well known diel periodicity of photosynthetic capacity, as described by Doty and Oguri (1957) and others, mainly reflects a periodicity of photosynthesizing ability of chlorophyll. To what extent the latter cycle can account for the former one is difficult to say but, whatever that may be, indisputable evidence is now available of diel variations in photosynthesis per unit chlorophyll or, as diversely called by workers, "assimilation number" or "assimilationszahl". Such variations are of the utmost importance in field studies of primary production.

First, this constitutes one reason more to think that chlorophyll measurements can provide only but a rough estimate, or a mean estimate, of potential productivity. So the "chlorophyll-radiation" method of Ryther and Yentsch

(1957) and similar ones cannot be used without extreme caution. In fact, a constant value of the photosynthesis/chlorophyll ratio would be found if "plankton originates from approximately the same area, the same season, the same depth and the same time of the day" (Steemann Nielsen and Jorgensen, 1962), that is nearly to say: if duplicate samples are considered. It must still be added, concerning chlorophyll, that all the data presented or cited in this paper apply to total concentrations of both active and inactive or "dead" pigment; further researches are needed on possible diel variation of active and inactive chlorophyll proportions.

A second consequence of practical interest concerns the choice of adequate sampling time and duration of experiments in routine work, in view of assessing daily production. This problem has been approached by several workers (e. g. : Angot, 1961; Vollenweider and Nauwerck, 1961; Doty *et al.*, 1963, 1967; Strickland, 1965; Newhouse, 1967; Qasim *et al.*, 1969; Doty, in press). In fact, it seems doubtful that a standard procedure could be established, as diel characteristics depend on experimental conditions: then, it would be necessary to standardize experimental conditions too, but this subject is beyond the scope of the present paper. Furthermore, in addition to the diel photosynthetic periodicity, the time course of primary production *in situ* is subjected to a number of factors such as light intensity, turbulence, cell growth, synthesis of chlorophyll, excretion of photosynthesized matter, respiration, horizontal transport and grazing. For these reasons, any extrapolation of *in situ* daily production, whether gross or net, from a single experiment, encounters insuperable difficulties. Actually, as far as natural populations of phytoplankton are concerned, diel variations are not less complex than seasonal ones, and there is no doubt that a single measurement during the course of the year could hardly be extrapolated to annual production. Much more information about the numerous aspects of diel phytoplankton cycle must be gathered before the problem of daily primary production could be reasonably treated.

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