

Seasonal variations of the parameters
of the photosynthesis-light relationship
during the Fladen Ground Experiment 1976*

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1.- Introduction

Photosynthesis measurements were performed from March to June 1976 at the central station of the Fladen Ground sampling grid or in the immediate vicinity (fig. 1).

The results referred to in this paper relate to $^{14}\text{CO}_2$ fixation rates in particulate matter of samples incubated under a range of daylight intensities (either *in situ* or in a deck incubator). Four teams*** have cooperated to these measurements, using fairly similar experimental procedures, in accordance with the standardisation Workshops held at Texel, 26-27 November 1975 and Brussels, 10-11 February 1976.

An extensive data set has thus become available for the calculation of phytoplanktonic productions. However, the conversion of these raw data into daily integrated figures of primary production is not simple and the various approaches used — for which no total agreement had been found — could lead to poorly intercomparable results.

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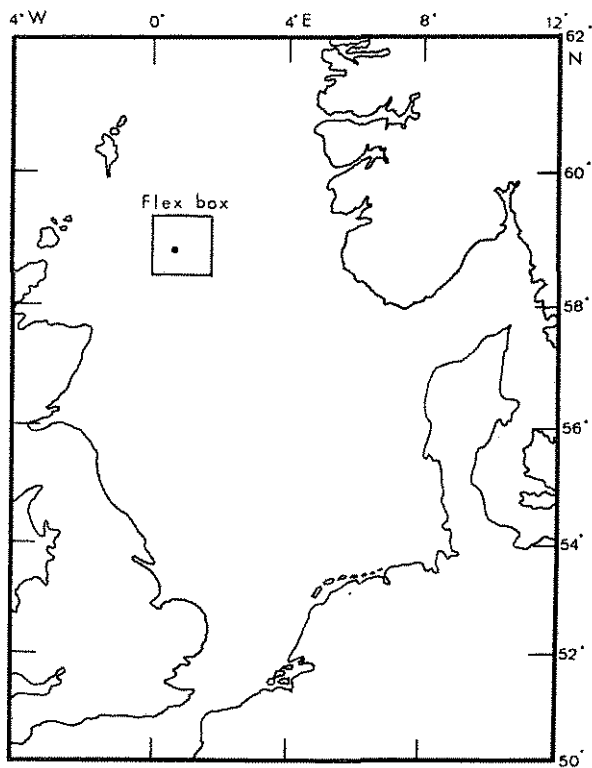


fig. 1.

The North Sea, the Fladen Ground sampling grid ("Flex Box") and its central station

Therefore, the author was given permission by the data originators to handle the entire data set with a single method he had already been using extensively for other areas of the North Sea (Mommarts, 1978). The method uses a simulation model where the photosynthesis-light (PL) relationship occupies a central position (Mommarts, submitted) :

$$k = \frac{\alpha I}{\left[1 + \left(\frac{\alpha I}{b k_{\max}}\right)^2\right]^{\frac{1}{2}} \left[1 + \left(\frac{\gamma \alpha I}{b k_{\max}}\right)^2\right]^{n/2}} \quad (1)$$

where k is the rate of carbon fixation in phytoplankton per unit chlorophyll a (in $\text{mg C m}^{-3} \cdot \text{h}^{-1} / \text{mg chlor.} a \text{ m}^{-3}$), I is the photosynthetic available light energy (400 - 700 nm) [in $\mu\text{einstein} \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$]; k_{\max} , α , γ , b and

n are parameters discussed in this paper. Production figures are normalised to active chlorophyll (*sensu* Lorenzen) values*, thus having the dimensions of the ratio rate/biomass i.e. a kinetic constant.

This paper aims at the analysis of the seasonal variations of the parameters of the PL curves and their relation to environmental or experimental factors.

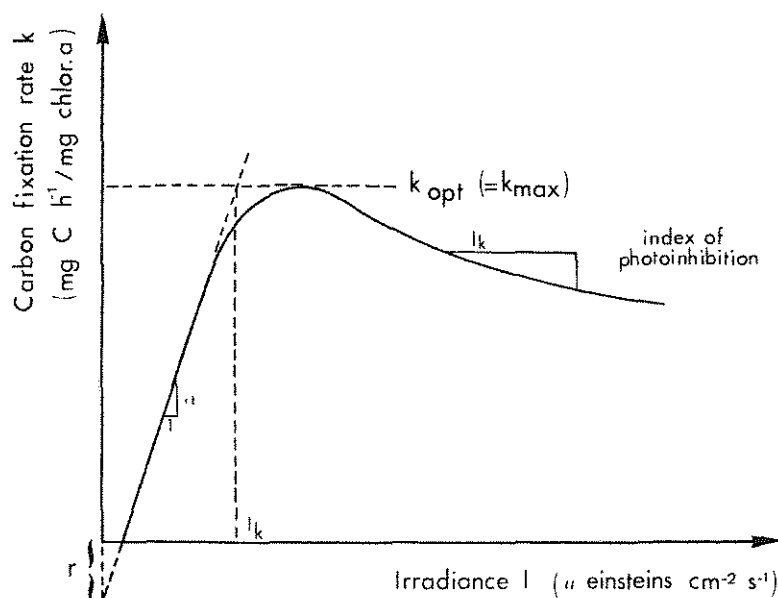


fig. 2.

The photosynthesis-light (PL) relationship and the parameters used for its characterization

Two parameters — presumably mutually independant and biologically significant (Jassby and Platt, 1976) — suffice to characterize most of a PL curve (fig. 2). They are :

- k_{max} measures theoretically the maximum rate of enzymatic processes related to the "dark" reaction of photosynthesis. This rate is also sometimes referred to as "assimilation number";

* Originator for the Meteor data set : A. Weber (Institut für Allgemeine Botanik, Hamburg).

• α is the rate per unit irradiance in the non-photoinhibited range *i.e.* a measure of the photochemical processes. This parameter is similar to the "productivity index" defined by Strickland (1960).

The ratio

$$I_K = \frac{k_{\max}}{\alpha}$$

has often been used as a saturation constant in the literature (*e.g.* Smith, 1936; Talling, 1957; Vollenweider, 1965) but contains obviously less information about the environmental control factors or the physiology of the populations concerned.

Photoinhibition — a possible artefact — has been expressed by an index measuring the fraction of k_{\max} inhibited per I_K -unit, since this can easily be read from the PL curves. It is related to the photoinhibition parameters of the model by an empirical curve (fig. 3) and :

- for $b < 2.6$: $\gamma = b - 1$ and $n = 1$
- for $b = 2.6$: $\gamma = 1$ and $n = 2$.

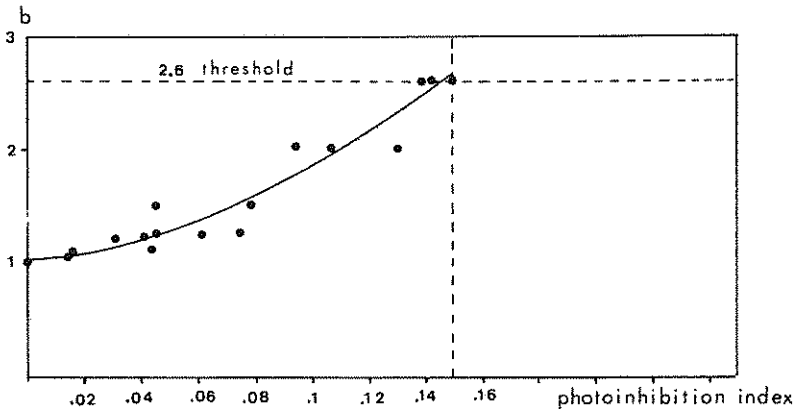


fig. 3.

Empirically determined relationship between the fitted model parameter (b) and the photoinhibition index measured on the curves. Curves with inhibition indices higher than 0.15 cannot be adequately simulated in their photoinhibited range.

r is measured at the intersect of the extrapolated curve with the y -axis. No interpretation is given here for r : apparent loss identified as respiration by several authors (*e.g.* Steemann-Nielsen and Hansen, 1959) but controverted by others (*e.g.* Bunt, 1965).

Measuring these parameters could be considered as a mere necessity of the approach as far as the calculation of primary production with the author's model is concerned. This is however of paramount importance with respect to the study of regulation mechanisms and the design of ecological models.

Thus, k appears in the simplified evolution equation for phytoplanktonic biomass B :

$$\frac{dB}{dt} = kB - \text{grazing} - \text{sinking} + \text{exchanges at the boundaries} \quad (2)$$

where k possibly depends on several factors :

$$k = K_{\max} \cdot [f(I), f(N), f(T), f(t), \dots] \quad (3)$$

where $f(I)$ is a function of photosynthetically available irradiance, *e.g.* the PL curve; $f(N)$ is a function of limiting nutrient concentration, *e.g.* Michaelis-Menten kinetics; $f(T)$ is a function of water temperature, *e.g.* the Arrhenius law; $f(t)$ is a function of time, *e.g.* the diel fluctuations described by Mc Caull and Platt (1977).

α — a parameter of $f(I)$ — is believed to depend largely on the nature and/or the degree of light adaptation of the phytoplankton populations. With respect to this, the fractionation into size-classes (*e.g.* nanno- and net-plankton) could improve the interpretation of the data markedly. Indeed, a globally measured k ($= k_{\text{tot}}$) can be strongly misleading especially if it is intended to be used in a simulation model, since :

$$k_{\text{tot}} = \frac{1}{B_{\text{tot}}} [B_1 k_1 + B_2 k_2 + \dots + B_n k_n] \quad (4)$$

Moreover, these time-series of PL curve parameters can also be used for a quality check or looked at with respect to experimental conditions (*e.g.* *in situ* versus deck incubations) so that choices or corrections can be decided upon before feeding the data into the production model.

2.- Results

Fig. 4 gives a sample of PL curves measured during the Fladen Ground Experiment. Altogether, the results from the four teams are fairly consistent for all PL curve parameters : no data set departs significantly from the

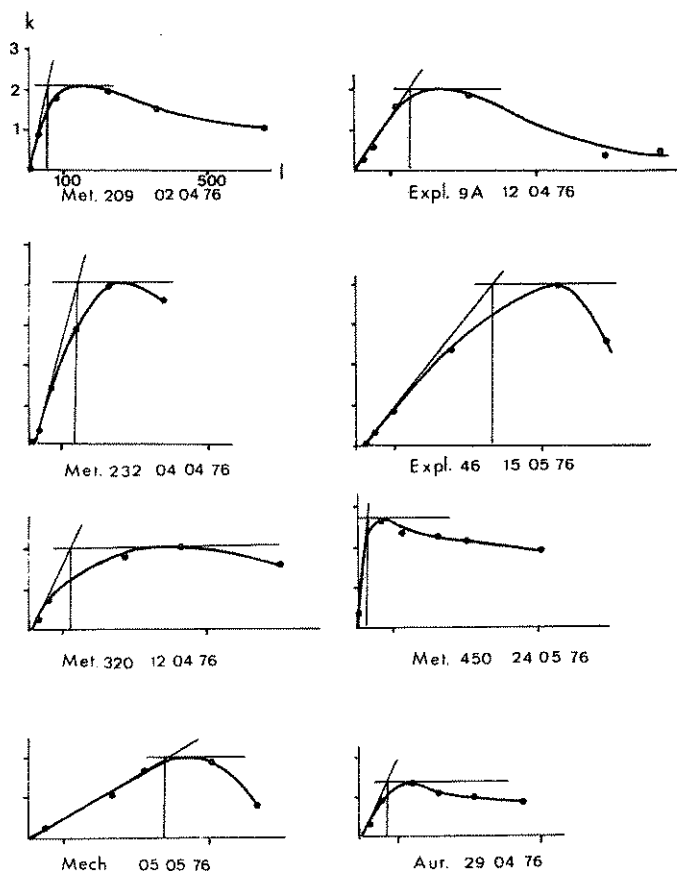


fig. 4.

Representative photosynthesis-light curves measured during the Fladen Ground Experiment. (Units as in fig. 2.)

others. On the other hand, the results are rather scattered (fig. 5). The reasons for this can be multiple : spatial heterogeneity, diel variation, natural variability, cumulated errors on the estimations of the numerous parameters involved in the calculations (irradiance, reflexion, transparency, active chlorophyll *a*, photosynthesis), etc.

Nevertheless, trends can be recognized. A moving average technique, including weighting, has been used to smoothe these variations.

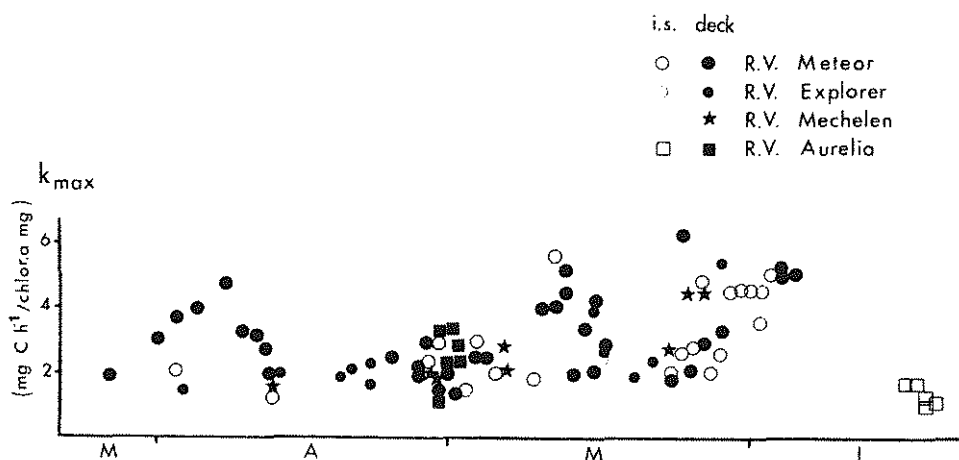


fig. 5.

Actual values of k_{\max} measured in situ or in deck incubator by the four teams during the Fladen Ground Experiment.

2.1.- THE SEASONAL VARIATION OF k_{\max}

The average value of k_{\max} during these three months is $3 \text{ mg C h}^{-1} \text{ mg chlor}^{-1}$, with numbers comprised between 1 and 6. Tentative corrections for r and for the effect of diel variation, using a variant of the Mc Caull and Platt (1977) equation did not lessen the scatter neither could a possible systematic difference between *in situ* and deck incubation results account for it in any appreciable way.

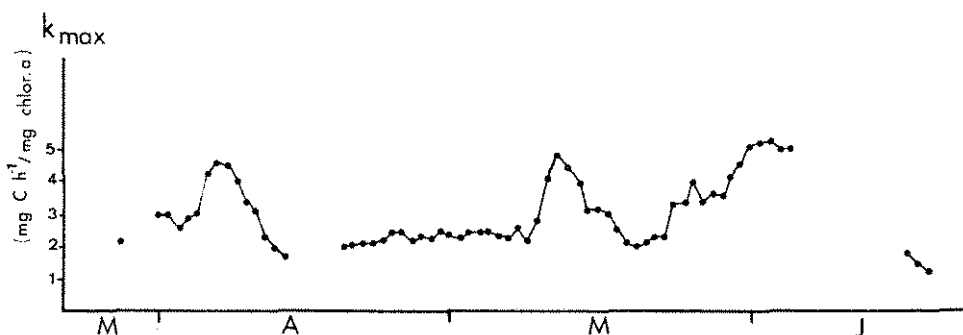


fig. 6.

Seasonal variation of k_{\max} (smoothed curve) during the Fladen Ground Experiment

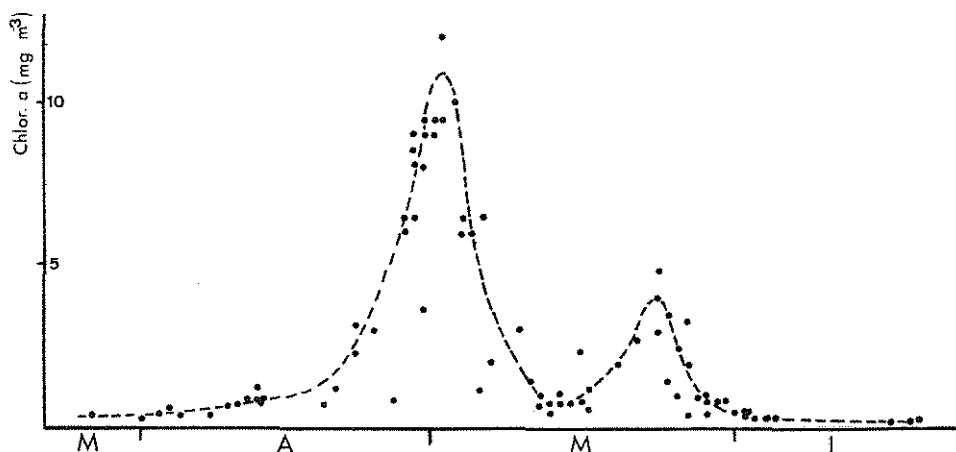


fig. 7.

Seasonal variation of mean chlorophyll *a* concentration in the euphotic zone during the Fladen Ground Experiment (actual numbers and hand-fitted curve).

The smoothed seasonal curve of k_{\max} (fig. 6) shows a trend opposite to that of phytoplankton chlorophyll (fig. 7) since lower values of k are observed during the two consecutive blooms. There is no obvious interpretation for this apparent negative feedback of population density on biological activity: it is at least clear that the major nutrients do not control this evolution in a Michaëlis-Menten mode (fig. 8).

Moreover, the next paragraph casts some doubt on any straightforward interpretation of k_{\max} values.

The ratio of net- to nanoplankton production (fig. 9) varies in the same way as biomass, thus revealing that the first bloom was mainly due to an out-grow of netplankton whereas the second one was due to nanoplankton. This was confirmed by the observations of Gieskes and Kraay (1980), Gillbricht (pers. comm.) and Wandschneider (pers. comm.) who ascertained that the netplankton bloom was mainly due to diatoms (especially *Chaetoceros* spp.) and the nanoplankton bloom to microflagellates (especially *Haptophyceae*, *Chrysophyceae* and *Cryptophyceae*).

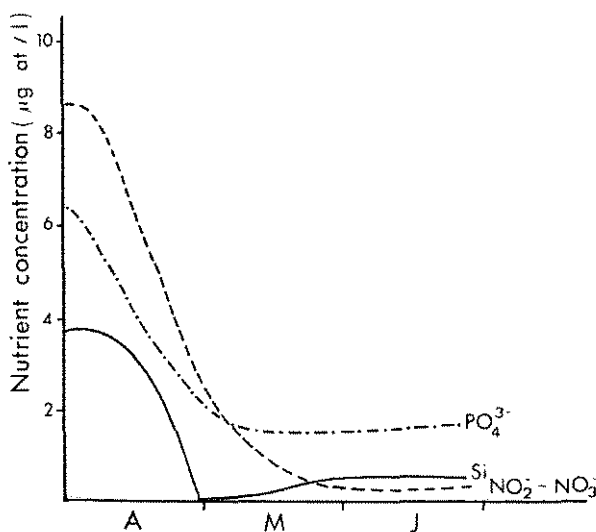


fig. 9.

Evolution of the concentrations of the major nutrients in the euphotic zone during the Fladen Ground Experiment (trends as figured out from the time-depth concentration patterns published in the Draft Flex Atlas by Hanner, Kähler and Eberlein, SFB 94, Hamburg).

Unit: : $\text{NO}_2^- + \text{NO}_3^-$: $\times 1$
 PO_4^{3-} : $\times 10^{-1}$
 Si : $\times 10^{-1}$

The ratio of net- to nanoplankton chlorophyll *a* has also been measured on three occasions, thus allowing separate estimations for $k_{\text{max-nanno}}$ and $k_{\text{max-netpl}}$. These measurements covered the period comprised between the two blooms. Table 1 shows that the photosynthesis rate of nanoplankton is quickly increasing during this time, whereas that of netplankton is rather diminishing: the coming population change is clearly announced.

This also demonstrates that, in some circumstances at least, globally measured rates only give a poor reflexion of the processes at work.

Whether this is the reason why no visible relationship exists between k_{max} and the concentrations of the major nutrients is only one of the possibilities. A microscale nutrient distribution ("marine snow") might account as well for the results obtained (cf. Shanks and Trent, 1979). It must also be remembered that these results are pertinent to the carbon cycle only and that there is no direct coupling between the nutrient uptake kinetics and photosynthetic carbon assimilation.

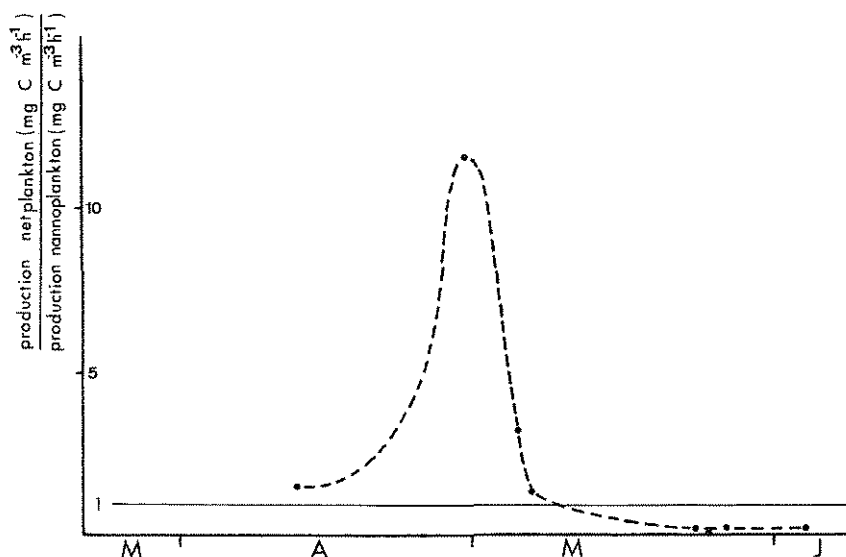


fig. 9.

Ratio of net- to nannoplankton production during the Fladen Ground Experiment, showing the dominance of nannoplankton from early May on.

Table 1

Comparison of the production and chlorophyll a ratios and the rates of carbon fixation by netplankton and nannoplankton in the beginning of May 1976

Date	$\frac{\text{Prod. netpl.}}{\text{Prod. nanno.}}$	$\frac{\text{Chlor. netpl.}}{\text{Chlor. nanno.}}$	k_{tot}	$k_{\text{netpl.}}$	$k_{\text{nanno.}}$
29-04-76	11.50	2.00	2.06	2.85	0.49
05-05-76	3.20	4.30	1.92	1.80	2.42
06-05-76	1.25	2.30	2.74	2.18	4.01

The sole relationship with an environmental factor that could be ascertained is temperature dependency. Indeed, the general trend towards an increase of k_{max} is linearly correlated with the logarithm of water temperature ($r = 0.983$). The computed Q_{10} value was 2.29 .

2.2.- THE SEASONAL VARIATION OF α AND PHOTOINHIBITION INDEX

From the second bloom onwards, the results for *in situ* and deck incubations depart clearly from each other as far as α and photoinhibition (fig. 10 and 11) are concerned. As these results associate a particular type of phytoplankton (microflagellates) with a given experimental condition (the incubators), one may conclude that this could be an artefact (e.g. ill effects due to an excess of UV radiation, cf. Steemann-Nielsen, 1975) detrimental to more delicate organisms.

Therefore, only *in situ* results will be considered in the next paragraphs from mid-May onwards.

2.2.1.- The parameter α (fig. 10)

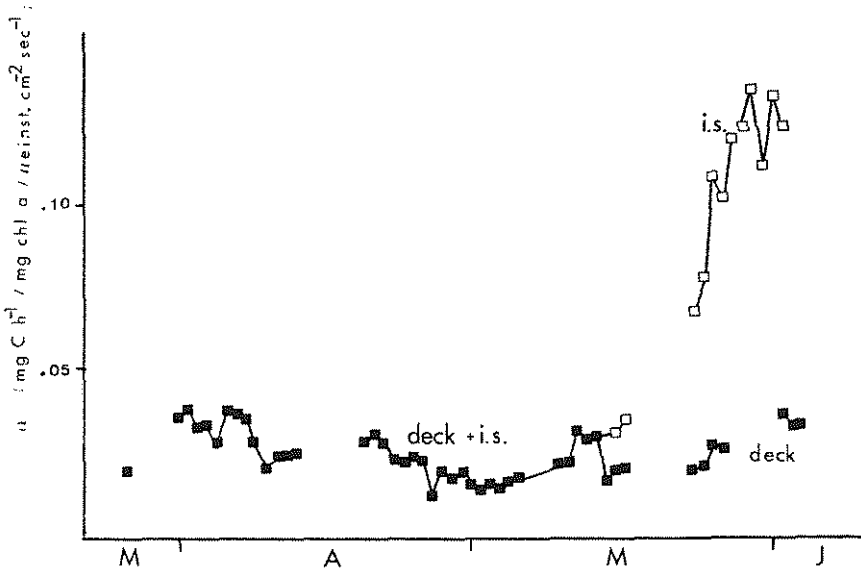


fig. 10.

Evolution of the parameter α (smoothed curve) during the Fladen Ground Experiment. From mid-May on, the results from *in situ* (i.s.) and deck incubations are given separately.

The average value of α is $0.25 \text{ mg Chl } a / \text{mg chl } a / \mu\text{Einst. cm}^2 \text{ s}^{-1}$ in the period preceding the microflagellates bloom. During the microflagellates

bloom it reaches a peak value of 3, demonstrating a photosynthetic efficiency six times as high as during the first bloom.

This different behaviour of nanoplanktonic algae might be related to a better light harvesting ability in those organisms, depending on cellular architecture and pigment composition (see discussion in Platt and Jassby, 1976). To our knowledge, the higher efficiency of nanoplankton had until now mostly been ascribed to higher assimilation numbers i.e. k_{\max} (e.g. Malone, 1971).

There is no statistical relation between α and k_{\max} . This confirms the assumptions made in the introduction about the independence of these parameters.

2.2.2.- The photoinhibition index (fig. 11)

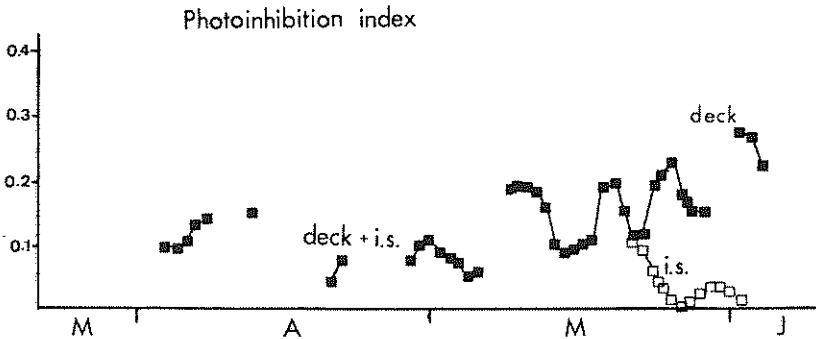


fig. 11.

Variation of the photoinhibition index (smoothed curve) during the Fladen Ground Experiment. From mid-May on, the results from in situ (i.s.) and deck incubations are given separately.

Generally comprised between 0 and .2 I_K -units this parameter shows no identifiable seasonal pattern of variation. The little oscillations observed in May-June are not believed to have a particular significance either since the smoothing technique used could produce such artefacts. The photoinhibition effect is believed to be an artefact altogether. Indeed, phytoplankton cells in nature circulate whereas the incubation system locks them into position so that there is an exposure problem next to the instantaneous response to light intensity.

2.3.- THE PARAMETER r (fig. 12)

Unlike α and the photoinhibition index, the extrapolated parameter r is depending on the experimental conditions of incubation since the beginning of the sampling period : 19 on 23 (i.e. 83 %) *in situ* experiments show null or low r values whereas 44 on 54 (i.e. 81 %) deck incubation results show a r value averaging about 10 % of k_{max} . The latter percentage is consistent with the observations of Steemann-Nielsen and Hansen (1959) who assumed this was related to respiration (or more exactly to 60 % of it, if there is such a reassimilation of respiratory CO_2 that k_{max} is comprised between gross and net rates). Since then, this 10 % figure has been used extensively in primary production research and ecosystem modelling for correcting for algal respiratory losses.

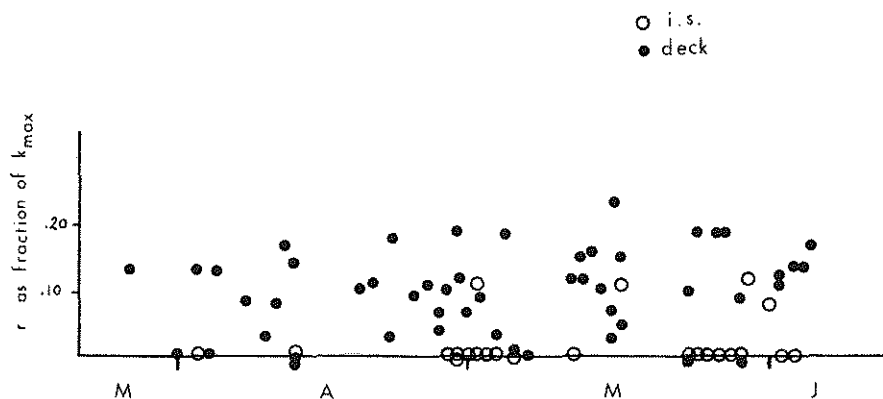


fig. 12.

Values of r measured during the Fladen Ground Experiment and given separately for *in situ* and deck incubations.

However, the fact that this kind of result strongly depends on the experimental set up casts doubt on the validity of such a practice. Moreover, the assumption that r measures respiration is neither supported by other primary production studies (Bunt, 1965) nor by recent ecosystem budget evaluations (Joiris et al., 1979) or by direct determinations of phytoplanktonic respiration (Hoch et al., 1963; Radmer and Kok, 1976; Nijs and Nihoul, pers. comm.).

It seems therefore that the recurrent discussions on the interpretation of PL curves in terms of net, gross or in-between production should be founded on more recent findings.

3.- Synthesis : the seasonal evolution of the $f(I_0)$ function

As discussed in the introduction, photosynthesis varies with light intensity according to a relationship for which a model has been suggested (eq. 1). Integrated over depth, this equation has the form :

$$\int_{d=0}^{d=\infty} k_z \cdot d_z = \frac{k_{\max}}{\eta} f(I_0)$$

where I_0 is the surface irradiance and η the vertical attenuation coefficient (in m^{-1}).

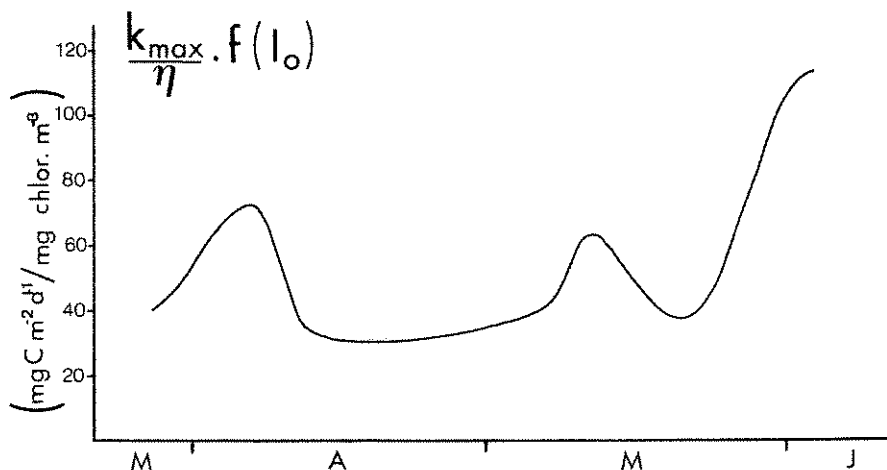


fig. 13.

Variation of the depth-integrated photosynthesis-light profile at 12 h (with average values for irradiance and light attenuation in water) during the Fladen Ground Experiment (based on the smoothed curves of the PL parameters).

At constant water penetration and surface irradiance levels, the seasonal evolution of this integral pictures the evolution of the production potential per m^2 of the phytoplankton during the Fladen Ground Experiment (fig. 13). It is clear that this pattern is greatly determined by the evolution of k_{\max} (fig. 6). An amplification is however observed for the second bloom. It is accounted for by the seasonal evolution of $f(I_0)$ (fig. 14) which reflects the changes of adaptative properties of the phytoplankton as well as taxonomic

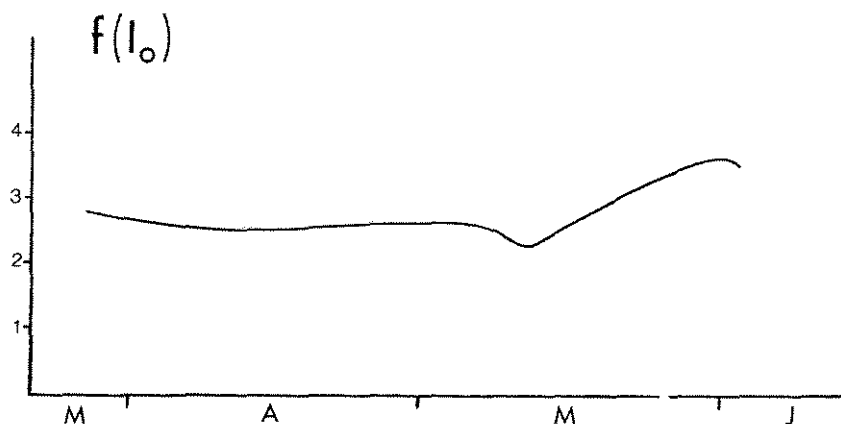


fig. 14.

Variation of the depth-integrated light-dependent function $f(I_0)$ during the Fladen Ground Experiment (based on the smoothed curves of the PL parameters).

composition. In this case, an increase of 50 % of the production potential of biomass was relevant to that term *i.e.* essentially to the increase of α at the end of May 1976.

4.- Conclusion

The analysis of the seasonal fluctuations of the parameters of the photosynthesis-light relationship during the Fladen Ground Experiment has been conceived as a means of studying the regulation of photosynthesis in the environment without having to depend on laboratory experiments and monospecific cultures. Our interest was particularly focused on the control possibly exercised by limiting nutrients.

With respect to the latter point, this approach has not proven successful. Yet, this work has thrown some light on several aspects both methodological or fundamental.

The methodological aspects concern the artefacts caused by the deck incubator with respect to the efficiency of light energy conversion and to photoinhibition : both effects might be related to overexposure to UV radiation. "Respiration" as measured by the extrapolated photosynthesis-light curve might be an artefact as well, perhaps with similar causes.

The fundamental aspects relate mostly to the implications of community changes (i.e. nannoplankton versus netplankton) in this study. These are important with respect to the two major parameters of the photosynthesis-light relationship. The photosynthetic yield at undersaturating light intensity (slope α) is markedly higher (by a factor 6) when nannoplankton predominates. In addition, the light-saturated rate of photosynthesis (k_{\max}), however fluctuating in a quite different way, also depends on the populations assemblage. Yet, this will appear only when the specific rates are uncoupled.

The environmental control on the photosynthesis-light curve parameters or, indirectly, on the succession pattern is much less evident. There are several hypotheses which could explain why nutrients seem not to control the maximal rate of carbon intake (e.g. in a Michaelis-Menten way). An obvious one is that nutrient assimilation and carbon uptake are only loosely coupled. Hence, far better results could be expected from nutrient uptake (e.g. ^{15}N) measurements.

On the other hand, the control exercised by temperature on k_{\max} could be observed on the long term. The observed short-time fluctuations can however not be explained by temperature changes.

This important data set and the present study have provided an opportunity to look more directly at parameters and relations that are usually hypothesised in ecosystem models. One of the lessons that can be drawn from these results is that existing models could fail to simulate the evolution of phytoplanktonic biomass adequately because they totally ignore such problems as have been discussed above, and possible others just as significant which have thus far escaped identification. Without making a case for the development of mammoth models, the author believes however that the reductionist approach that has been chosen by a majority of modellers is meaningless if it is not driven to the complexity level that will satisfy minimal requirements. Whether there is such a compromise between complexity and tractability is a question as yet unsolved.

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