

Diel variations in photosynthetic activity of summer phytoplankton in Lindåspollene, western Norway

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ABSTRACT: Diel patterns in photosynthesis of natural phytoplankton were studied during a 5 d period during midsummer in Lindåspollene, a land-locked fjord of western Norway. Samples were taken from depths of 0.5, 5, 10 and 21 m at 3 to 4 h intervals. The natural light:dark cycle was 19:5 h. The coccolithophorid *Emiliana huxleyi* and ultraplankton (< 5 µm) flagellates were predominant in the upper 10 m, while diatoms and silicoflagellates were predominant at 21 m. No clear diel pattern was seen in the variations of chlorophyll *a* and cell numbers. The photosynthesis vs light relationship (P-I) was studied at 0.5 and 10 m, and the parameters P_{max}^B , α^B and I_K showed pronounced diel rhythms. Maximum and minimum values of α^B and P_{max}^B differed by a factor of 3 to 4 and occurred in the morning and evening periods, respectively. These parameters were linearly correlated at both 0.5 and 10 m, indicating a phased diel periodicity. I_K showed a clear diel variation at 0.5 m with minimum values at night, whereas no persistent diel rhythm could be seen at 10 m. P_{max}^B and I_K were correlated at 0.5 m but not at 10 m, while I_K and α^B were weakly correlated at both 0.5 and 10 m. In vivo fluorescence per unit chlorophyll *a* showed a diel variation pattern that was the opposite to that of P_{max}^B and α^B . Our results indicate that an endogenous rhythm is regulating the diel oscillations in photosynthesis. This endogenous mechanism is possibly entrained by environmental signals such as cycles in nutrient availability and light conditions.

INTRODUCTION

During the last 2 decades a research program has been in progress on the plankton community of Lindåspollene, a land-locked fjord of western Norway (Lännergren 1976, Lännergren & Skjoldal 1976, Skjoldal & Lännergren 1978, Aksnes & Magnesen 1983, 1988, Lie et al. 1983, Skjoldal et al. 1983, Wassmann 1983, Aksnes et al. 1985, Skjoldal & Wassmann 1986). One aim of the investigations has been to establish a deterministic simulation model of the phytoplankton and zooplankton growth dynamics and their trophic interactions. Fundamental in this context is the assessment of daily primary production. Great errors may occur when estimating production if the influence of diel variations in photosynthesis is neglected (MacCaull & Platt 1977).

The occurrence of periodic diel variations in photosynthetic properties of natural marine phytoplankton was first reported by Doty & Oguri (1957) and has since then been frequently observed (e.g. Lorenzen 1963, McAllister 1963, Malone 1971, Sournia 1974, Taguchi

1976, MacCaull & Platt 1977, Pearl & Mackenzie 1977, Gargas et al. 1979, Prézelin & Ley 1980, Harding et al. 1982a, b, Setser et al. 1982, Fuhrman et al. 1985, Putt & Prézelin 1985, 1988, Prézelin et al. 1986, 1987, Glover & Smith 1988, Legendre et al. 1988, Putt et al. 1988, Rivkin & Putt 1988). Diel patterns in photosynthetic capacity occur among a wide range of phytoplankton species (Eppley & Coatsworth 1966, Prézelin & Sweeney 1977, Hitchcock 1980, Marra 1980, Owens et al. 1980, Prézelin & Matlick 1980, Harding et al. 1981a, b, Brand 1982, Cosper 1982, Marra & Heinemann 1982, Harding et al. 1983, Samuelsson et al. 1983, Harding & Heinbokel 1984, Vårum et al. 1986, Putt & Prézelin 1988). It is usually believed that the diel oscillations in photosynthetic properties are due to an endogenous mechanism (circadian clock) which is entrained by changes in environmental factors (Enright 1970, Stross et al. 1973).

When considering variations in primary production, it is difficult to separate the effect of diel rhythms in the photosynthetic parameters α and P_{max} (Platt & Jassby

1976), and photoadaptive responses often encountered among algal cells exposed to different light intensities (Harding et al. 1983). Such adaptations depend upon the degree of vertical mixing and turbidity. Under conditions of low vertical mixing, 'light-adapted' and 'shade-adapted' cells may be found near the surface and at the bottom of the euphotic zone, respectively. The shade-adapted cells are characterized by either increased size of the photosynthetic unit (PSU) or increased number of PSUs (reviews: Falkowski 1980, Prézelin 1981), which is considered to improve their photosynthetic capacity. Marra (1978), on the other hand, found no depressed photosynthesis in a wind-mixed water column compared with that of a well-stratified water column. The same result emerged from an investigation by Quéguiner & Legendre (1986), who found that phytoplankton could adapt their photosynthetic characteristics to a rapidly fluctuating light regime.

Here we report on diel rhythms of photosynthesis of natural phytoplankton at different depths (0.5, 5 and 10 m) studied during 5 consecutive 24 h periods during midsummer in Lindåspollene. This land-locked fjord has restricted tidal water exchange and a stable water column with a relatively marked density gradient extending almost from the surface to about 20 m (e.g. Skjoldal & Wassmann 1986). Apart from the upper few meters, vertical mixing is therefore very restricted. By comparing 3 depths, our approach was to describe diel rhythms for phytoplankton experiencing different light intensities in a stable physical environment, which would allow adaptation to occur. More information on the vertical structure of the environment and the phytoplankton community will be given in another paper (Skjoldal & Erga unpubl.).

MATERIALS AND METHODS

All sampling and experiments were conducted from an anchored wooden raft (water depth 40 m), situated at the northern part of Spjeldnesosen, the mid-basin of Lindåspollene. For a description of the sampling area and information on the topography see Dahl et al. (1973).

Samples were obtained through 3 nontoxic polyethylene tubes ending at 0.5, 5 and 10 m, by using a vacuum pump connected to 5 l reservoir flasks. Additional samples were taken from 21 m by a 5 l Ruttner water bottle. Special care was taken to protect samples against strong light. On 33 occasions, from 15:30 h local time on 7 June to 16:30 h local time on 12 June, samples were collected for analyses of salinity, temperature, pH, ^{14}C -assimilation, *in vivo* fluorescence, chlorophyll *a*, and phytoplankton abundance and

composition. Samples for analysis of particulate organic carbon, nitrogen, and phosphorus were also taken, but these results are not reported here. The samples were taken at 3 h intervals during the first day and at 4 h intervals during the subsequent 4 d. In order to reduce the effect of grazing during incubation, and the effect of zooplankton on phytoplankton biomass estimates, all samples were prescreened (60 μm) upon transfer from the reservoir flasks to 5 l plastic carboys. This could be done due to the predominance of small phytoplankton forms during summer. Samples of chlorophyll *a* and ^{14}C -assimilation were filtered onto Whatman GF/C filters and stored frozen prior to analysis.

Primary production was measured according to the ^{14}C -method (Steemann Nielsen 1952). Incubations were conducted in a temperature-controlled incubator equipped with a fluorescent light bank (Philips TL 20 W/33). The incubation bottles (25 ml borosilicate-glass) were mounted on a rotating wheel and exposed to 7 different light intensities ranging from 16 to 900 $\mu\text{E m}^{-2} \text{s}^{-1}$ (400 to 700 nm). The light gradient was achieved by neutral density filters, with the maximum value being obtained by a reflector mounted behind the bottle. The incubation time was 2 h which is reported to give rates approaching gross photosynthesis (Dring & Jewson 1982). Calculations of ^{14}C -uptake rates were as described by Erga & Heimdal (1984) and no corrections were made to compensate for excretion of photosynthesized products during incubation (see Erga 1989b). Data on *in situ* primary production measurements are taken from Skjoldal & Erga (unpubl.).

At each sampling, the *P* vs *I* relationship was determined for samples from 0.5 and 10 m. The photosynthetic parameters α^{B} (initial slope of the light saturation curve), $I_{\text{K}} = P_{\text{max}}/\alpha$ (irradiance at which the prolongation of the initial and horizontal parts of the photosynthesis curve intersect) and $P_{\text{max}}^{\text{B}}$ (specific production rate at optimal light intensity) were derived from the equation of optimal curve adaptation as presented by Platt et al. (1980). Samples from 5 and 21 m were incubated at 550 $\mu\text{E m}^{-2} \text{s}^{-1}$ only, and the photosynthetic rate was assumed to represent $P_{\text{max}}^{\text{B}}$. For the shade-adapted cells at 21 m, however, this light intensity was probably higher than optimum, and $P_{\text{max}}^{\text{B}}$, therefore, may be underestimated due to photoinhibition.

In vivo fluorescence of the water samples was determined using a Turner Designs fluorometer. Chlorophyll *a* was analyzed fluorometrically with methanol as solvent (Holm-Hansen & Riemann 1978). Light measurements and light conversion factors were as given by Erga (1989a). Salinity was measured by an Autolab Salinometer. Phytoplankton abundance was determined according to Utermöhl (1931), using neutralized formalin as preservative.

RESULTS

Light and hydrography

The weather was clear and sunny throughout the period of investigation. The maximum surface irradiance at noon was $1550 \mu\text{E m}^{-2} \text{s}^{-1}$ and the natural light:dark (L:D) cycle was 19:5 h (cf. Fig. 1). The turbidity of the water was nearly constant from 7 to 12 June (Fig. 1), and the 1% light depth was ca 20 m.

Surface salinities changed markedly from 8 to 9 June (Fig. 2). This probably had nothing to do with fresh-water runoff since there was no precipitation in June prior to our investigation. No consistency was found between the salinity variations of the upper 5 m of the water column and the semidiurnal tidal cycle (Fig. 2). The very low tidal amplitude in Lindåspollene indicates that tidal forces are of little importance in this context. Most likely, the observed changes in salinity were associated with wind-driven currents. Relatively

strong winds from the south on 7 June were followed by northerly winds on 8 June. This probably resulted in an accumulation of less saline surface water at the site of the raft (northern end of Lindåspollene) on 7 June, while on 8 June more saline water was vertically advected to compensate for a south-flowing surface layer. These exchange processes were, however, restricted to the upper 10 m of the water column as revealed by the unchanged salinity at 10 m (Fig. 2).

The salinity of the surface layer was about 29.5 and the temperature was around 15°C . Salinity and temperature changed with depth to about 31 and 5°C , respectively, at 20 m. Inorganic nutrients were uniformly low down to 15 m (Skjoldal & Erga unpubl.).

Diel variations in photosynthetic activity

Rates of carbon assimilation showed a clear diel pattern, with maximum values in the morning period

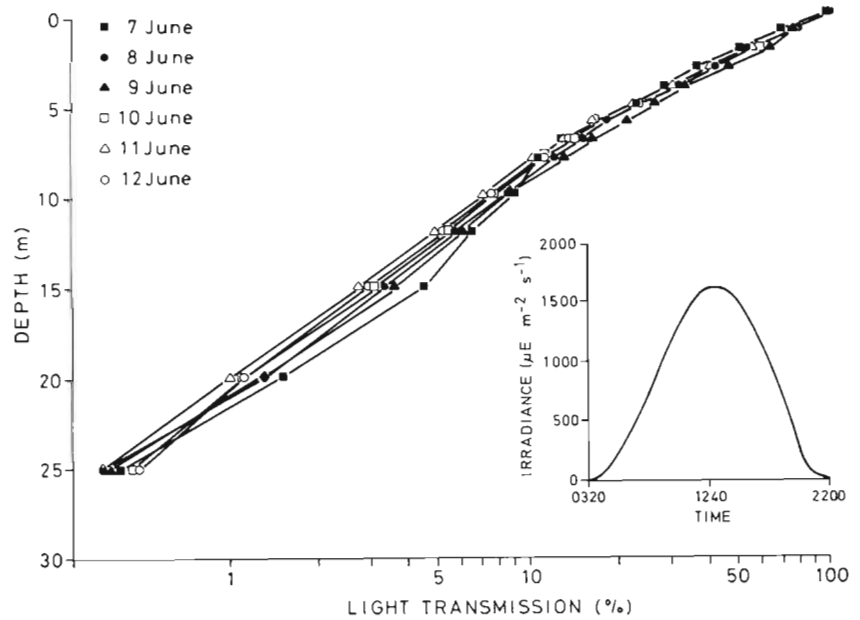


Fig. 1. Light attenuation for the upper 25 m of the water column in Lindåspollene during the period 7 to 12 June 1982. Surface irradiance throughout the day are given in the inset

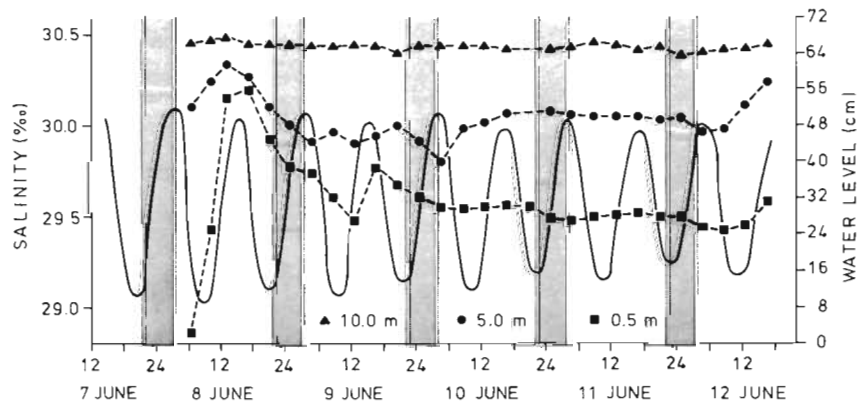


Fig. 2. Salinities at 0.5, 5 and 10 m (broken line) and tidal water level variations (continuous line) during the period 7 to 12 June 1982 in Lindåspollene. Shaded columns show periods of darkness

and minimum values in late evening (Fig. 3). The ratio of in vivo fluorescence to chlorophyll *a* (IVF/chl *a*) appeared to vary inversely with carbon assimilation, showing low values in the morning and high values in the evening (Fig. 4). This pattern, however, was less consistent with respect to a diel rhythm than that of the carbon assimilation. There was no clear evidence of a diel pattern in the variations of chlorophyll *a* (Fig. 4). Low concentrations at 0.5 m and high concentrations at 10 m during the day seemed, however, to be recurrent events.

The maximal carbon assimilation rate (P_{\max}) showed a general increase with depth (Table 1). The high P_{\max} values at 21 m were apparently not due to higher biomass, as concentrations of particulate organic carbon, nitrogen, and phosphorus were lower there than in the upper layer (Skjoldal & Erga unpubl.). They

reflected, on the other hand, increased cellular levels of chlorophyll *a* in the deeper layer (Fig. 5).

The P vs I curve parameters, P_{\max}^B , α^B and I_K (Platt et al. 1980), revealed pronounced diel patterns (Figs. 6 and 7). Due to the relatively small temporal variations in chlorophyll *a* (Fig. 4), the pattern of changes in P_{\max}^B (normalized to chlorophyll *a*) was not much different from that of P_{\max} (Fig. 3). Both the lowest and highest P_{\max}^B values were found at 0.5 m (Table 1). The amplitude of the diel oscillations in P_{\max}^B seemed to decrease with increasing depth whereas the mean P_{\max}^B values changed little.

There was a diel covariation of α^B and P_{\max}^B (Fig. 6). Maximum and minimum values occurred in the morning and evening periods, respectively. The range of α^B values changed little from 0.5 to 10 m depth (Table 1).

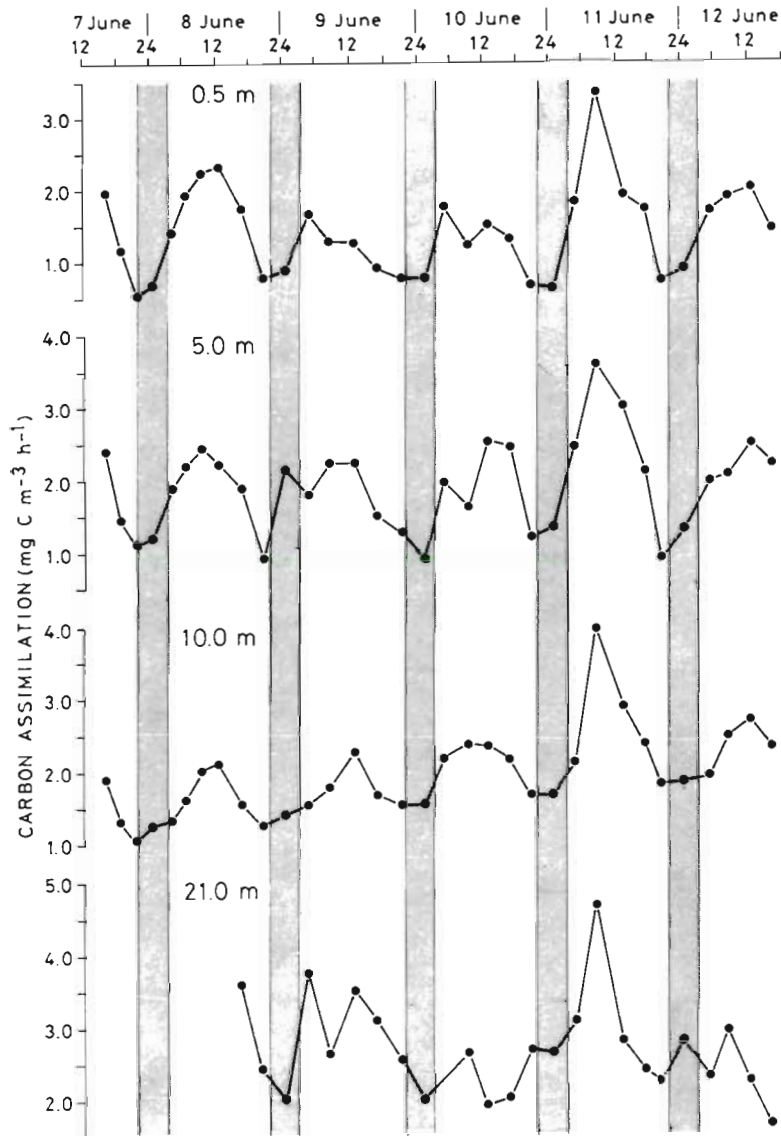


Fig. 3. Diel changes in carbon assimilation at 0.5, 5, 10 and 21 m from 7 to 12 June 1982 in Lindåspollene. Shaded columns show periods of darkness

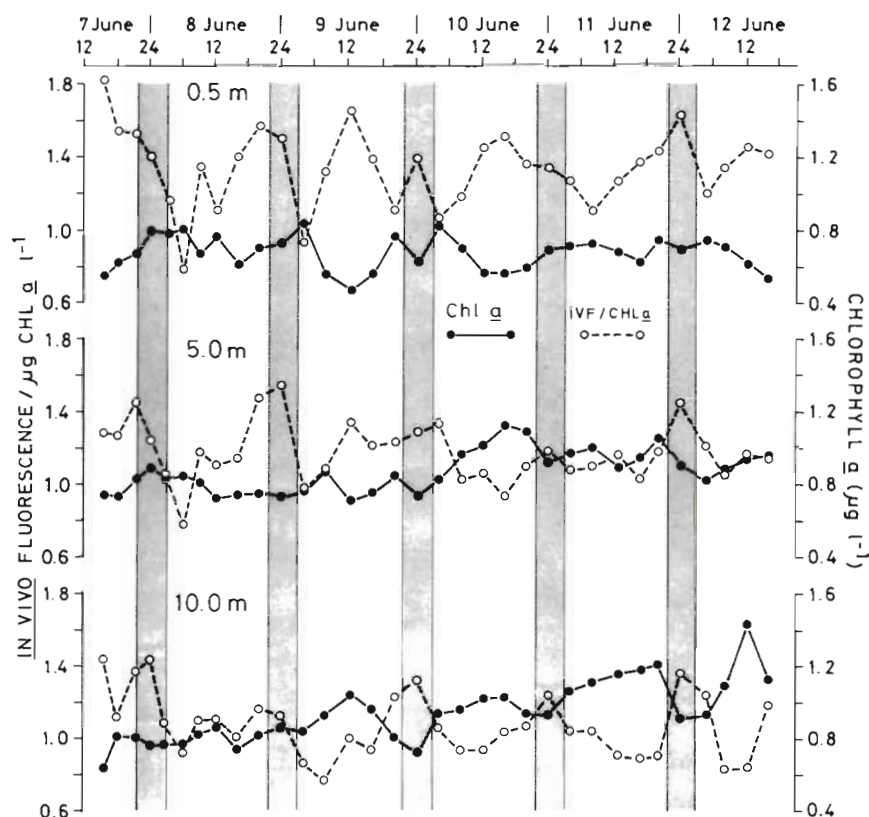


Fig. 4. Diel variations in chlorophyll *a* concentrations and in vivo fluorescence/chlorophyll *a* ratios at 0.5, 5 and 10 m during the period 7 to 12 June 1982 in Lindåspollene. Shaded columns show periods of darkness

Table 1. Maximum (max), minimum (min) and mean values (\bar{x}) of chlorophyll *a* (Chl *a*), maximal carbon assimilation rate (P_{\max} , mg C $m^{-3} h^{-1}$), photosynthetic capacity (P_{\max}^B , mg C mg chl $a^{-1} h^{-1}$), light utilization efficiency (α^B , mg C mg chl $a^{-1} \mu E^{-1} m^2 s$) and light-saturation intensity (I_K , $\mu E m^{-2} s^{-1}$) at 0.5, 5 and 10 m depth for the period 7 to 12 June 1982 in Lindåspollene. At 5 m, α^B and I_K were not measured. P_{\max} was also measured at 21 m. n: number of samples, SD: standard deviation

Parameters	0.5 m				5 m				10 m				21 m ^a			
	\bar{x}	max min	SD	n	\bar{x}	max min	SD	n	\bar{x}	max min	SD	n	\bar{x}	max min	SD	n
Chl <i>a</i>	0.67	0.84 0.47	0.09	33	0.87	1.12 0.71	0.11	33	0.94	1.83 0.64	0.17	33	—	—	—	—
P_{\max}	1.45	3.37 0.54	0.62	33	1.91	3.51 0.91	0.63	33	1.97	3.97 1.10	0.57	33	2.70	4.65 1.66	0.68	24
P_{\max}^B	2.26	4.62 0.85	1.06	33	2.22	3.58 1.10	0.72	33	2.07	3.58 1.36	0.47	33	—	—	—	—
$\alpha^B \times 10^{-3}$	10.1	18.7 6.3	2.9	33	—	—	—	—	10.4	20.8 7.0	3.2	33	—	—	—	—
I_K	215	311 96	61.9	33	—	—	—	—	202	282 149	27.5	33	—	—	—	—

^a Values are probably too low due to photoinhibition caused by the relatively high incubation light-intensity

At 0.5 m, I_K showed a pronounced diel variation with values being high during the midday hours and decreasing to minimum in late evening or early night (Fig. 6). In contrast, no clear diel rhythm was found at 10 m. Mean values of I_K did not change significantly from 0.5 to 10 m

depth (Table 1). α^B and P_{\max}^B were significantly correlated at both 0.5 and 10 m (Table 2). The relationship was apparently linear, but differed between the 2 depths (Fig. 8) (see 'Discussion' for further comments). P_{\max}^B showed a significant positive correlation with I_K at 0.5 m,

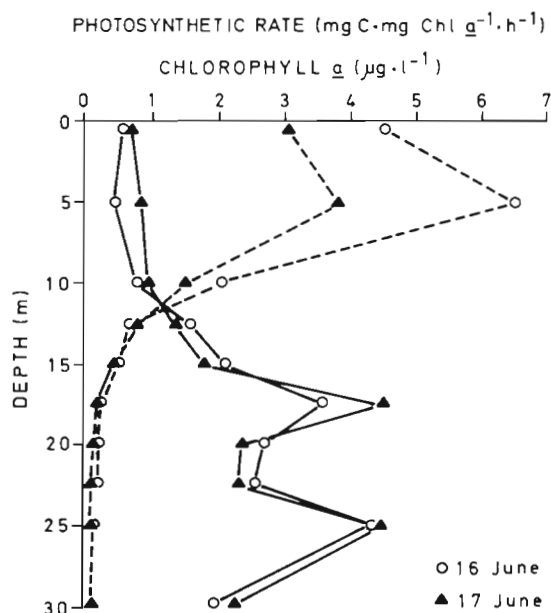


Fig. 5. Vertical profiles of chlorophyll a concentration (continuous line) and photosynthetic rate (broken line) on 16 and 17 June 1982 in Lindåspollene

but not at 10 m (Table 2) since no diel rhythm in I_K was found at this depth. α^B and I_K were not significantly correlated at any depth (Table 2).

There were no strong indications of photoinhibition at irradiances up to $900 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 7). The in situ primary production measurements (Fig. 5) suggest, however, that photoinhibition probably occurred for surface phytoplankton at irradiances exceeding $1000 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 1). Harris (1980) concluded that this value represents a threshold value concerning photoinhibition for natural phytoplankton.

Species composition and abundance

Phytoplankton were enumerated for 4 major categories: coccolithophorids, diatoms, dinoflagellates, and unidentified ultraplankton ($< 5 \mu\text{m}$) flagellates. Coccolithophorids and ultraplankton flagellates dominated at 0.5 and 5 m depths in terms of both cell numbers (Fig. 9) and biomass. Diatoms at these depths appeared to be in poor physiological condition as judged from low content of protoplasm and frustules covered by bacteria. The high cell numbers of diatoms in the surface layer on 8 June coincided with the intrusion of more saline water (Fig. 2). The number of coccolithophorids decreased strongly from 5 to 10 m, while for the other groups the differences were relatively small (Fig. 9). At 21 m (about 1% light depth) centric diatoms and silicoflagellates were the most important groups.

Emiliania huxleyi and *Rhizosolenia delicatula* were totally dominant among coccolithophorids and diatoms, respectively, in the upper 10 m of the water column. *E. huxleyi* seemed to grow under conditions of low nutrients, high irradiance and relatively high temperatures. This reflects a competitive advantage of this species under such circumstances (Berge 1962, Eppley et al. 1969, Erga & Heimdal 1984). Okada & Honjo (1973) concluded that coccolithophorids are particularly successful in oligotrophic environments. Further details on the vertical structure and species composition of the phytoplankton community will be given elsewhere (Skjoldal & Erga unpubl.).

The standing stocks of the different groups of phytoplankton did not change significantly during the period of investigation (Fig. 9). In most cases diel variations in cell numbers were within the counting error (Fig. 9). One exception was the peak in diatom abundance at the beginning of the investigation. The maximum at 0.5 m was followed 11 and 35 h later by peaks at 5 and 10 m, respectively. This could have been due to sinking. The delay in the diatom peak from 5 to 10 m corresponds to an apparent sinking rate of 5 m d^{-1} , which is in good agreement with the maximum values given by Lännergren (1979) for natural populations of marine phytoplankton.

DISCUSSION

Environmental conditions

Environments with stable conditions over relatively long periods (days to weeks) are useful in studying diel rhythms in the photosynthetic activity of natural phytoplankton. Polls (land-locked fjords) are unique in this context due to very restricted exchange processes with the fjords outside (Matthews & Heimdal 1980). A stratified water column is typically found in Lindåspollene in June (Aure 1972, Skjoldal et al. 1983, Skjoldal & Erga unpubl.). It is characterized by low nutrient content and moderately low phytoplankton biomass in the upper 10 m (Lännergren 1976, Skjoldal et al. 1983). As a rule, the main peak in zooplankton biomass ($> 60 \mu\text{m}$, dominated by small copepods) is situated around 10 m, and little vertical migration is found among the predominant species (Lie et al. 1983, Aksnes & Magnesen 1988, Magnesen et al. 1989). It is therefore unlikely that the diel patterns in photosynthetic activity observed in the upper 10 m of the water column in Lindåspollene were due to grazing by zooplankton. This is also supported by the fact that no pronounced diel pattern in chlorophyll a concentrations was found (Fig. 4). Litaker et al. (1988), on the other hand, found that grazing by microzooplankton

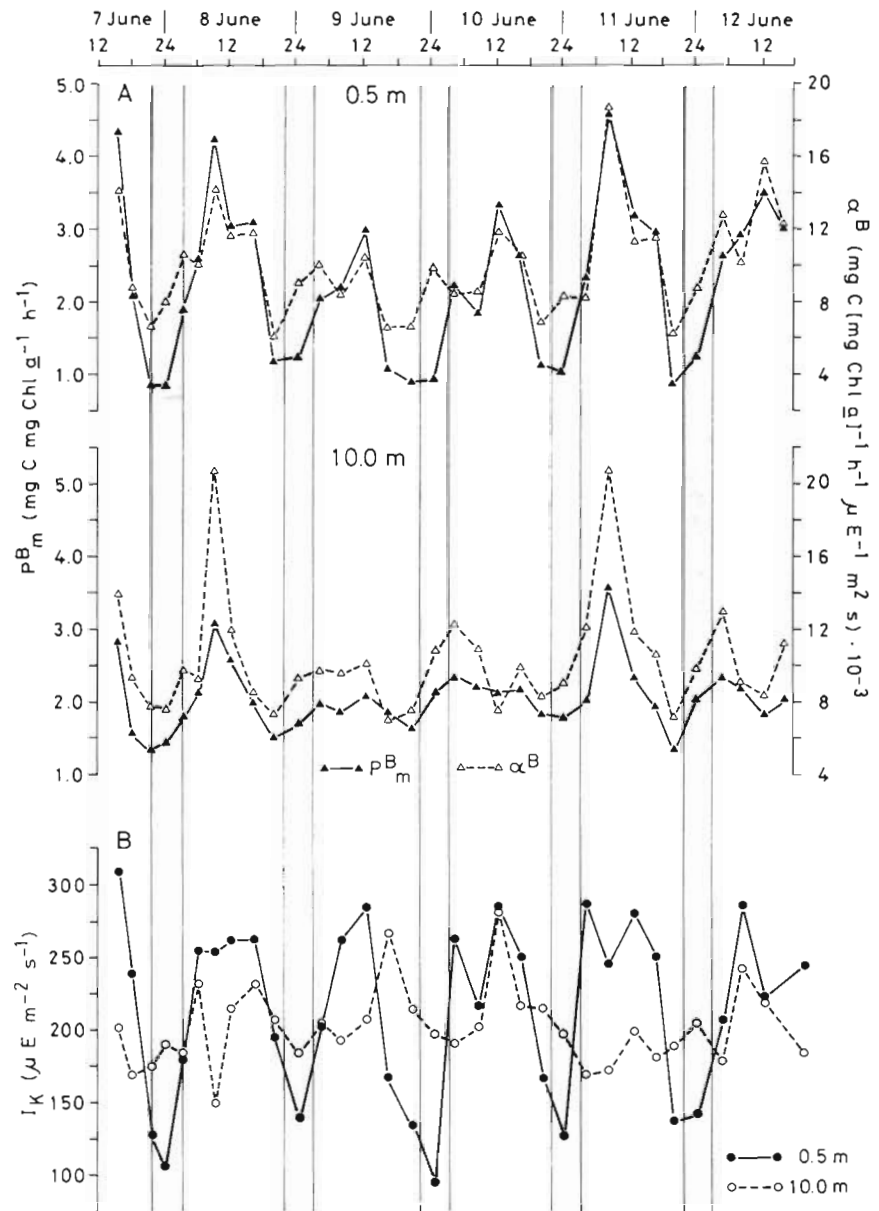


Fig. 6. Diel variations (A) in α^B (broken line) and P^B_{max} (P^B_m , continuous line) at 0.5 and 10 m, and (B) in I_K at 0.5 and 10 m, during the period 7 to 12 June 1982 in Lindåspollene. Shaded columns show periods of darkness

contributed substantially to diel changes in phytoplankton biomass (chlorophyll *a*) in Newport River Estuary, North Carolina (USA).

Another characteristic feature of the environmental conditions in Lindåspollene during the period of investigation was the very high surface irradiance, 1550 μE m $^{-2}$ s $^{-1}$, around noon, and a natural L:D cycle of 19:5 h (see 'Results'). The irradiance around noon decreased from between 300 and 350 μE m $^{-2}$ s $^{-1}$ at 5 m depth to between 100 and 140 μE m $^{-2}$ s $^{-1}$ at 10 m. Paasche (1967) reported 140 μE m $^{-2}$ s $^{-1}$ to be the lower irradiance for optimal growth of *Emiliania huxleyi*, and this is identical to the maximum irradiance at 10 m. Cell numbers of *E. huxleyi* decreased considerably

below 5 m depth in Lindåspollene (Fig. 9). As judged from cell counts at 5 m depth, *E. huxleyi* was dividing both in the light and in the dark. This is supported by the results of Nelson & Brand (1979), while Paasche (1967) found that another clone of the species divided only in the dark.

Factors controlling the diel rhythm of photosynthesis

A clear diel rhythm was found in the rate of photosynthesis, in terms of α^B and P^B_{max} , of the summer phytoplankton in Lindåspollene. A pattern of increasing rates of α^B and P^B_{max} in the early morning with

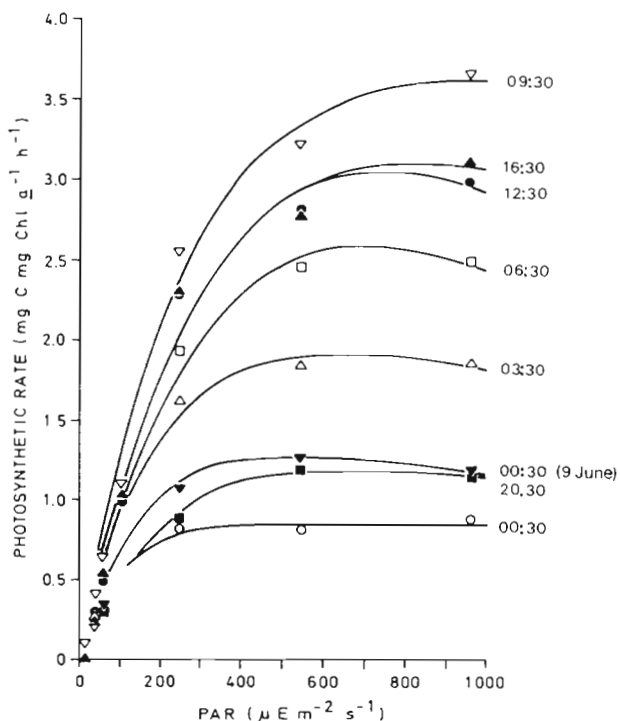


Fig. 7. Diel change in the photosynthesis vs irradiance relationship for phytoplankton taken from 0.5 m depth on 8 June 1982 in Lindåspollene

maximum values occurring before noon, and decreasing rates during the afternoon, was a persistent feature (Figs. 6 and 7). This is a common pattern that has been documented for several species of phytoplankton (Lorenzen 1963, McAllister 1963, Harding et al. 1981a,

Table 2. Linear regression analysis (Ricker 1973) of the relationships between photosynthetic capacity (P_{max}^B), light utilization efficiency (α^B), and light saturation intensity (I_K) at 0.5 and 10 m depth during the period 7 to 12 June 1982 in Lindåspollene. $n = 33$, r^2 = coefficient of determination, p = significance level

Variables	Depth (m)	Regression ($y = vx + u$)			
		v	u	r^2	p
P_{max}^B	0.5	370.8	-1.49	0.77	0.01
	10	147.3	0.54	0.79	0.01
P_{max}^B	0.5	0.0144	-0.84	0.71	0.01
	10	-0.0021	2.49	0.01	-
α^B	0.5	2.3×10^{-5}	0.01	0.25	0.01
	10	-6.0×10^{-5}	0.02	0.28	0.01

Marra & Heinemann 1982, Prézelin et al. 1986, Rivkin & Putt 1988). Malone (1971) and Paerl & Mackenzie (1977) emphasized a difference between nano (< 22 μm) and netplankton (> 22 μm) in this context. They found that nan- and netplankton had their maximal photosynthetic activities in the morning and afternoon, respectively. Our findings do not contradict this generalization since nanoplankton were predominant in the upper 10 m of the water column in Lindåspollene. For a spring bloom of the colony forming haptophycean *Phaeocystis pouchetii* in Balsfjorden and Skjomen, northern Norway, the highest photosynthetic rates occurred in the afternoon (Eilertsen & Taasen 1981). In their study the maximum photosynthetic rate was about 2 times the minimum value, as opposed to 4 to 5 times in our study.

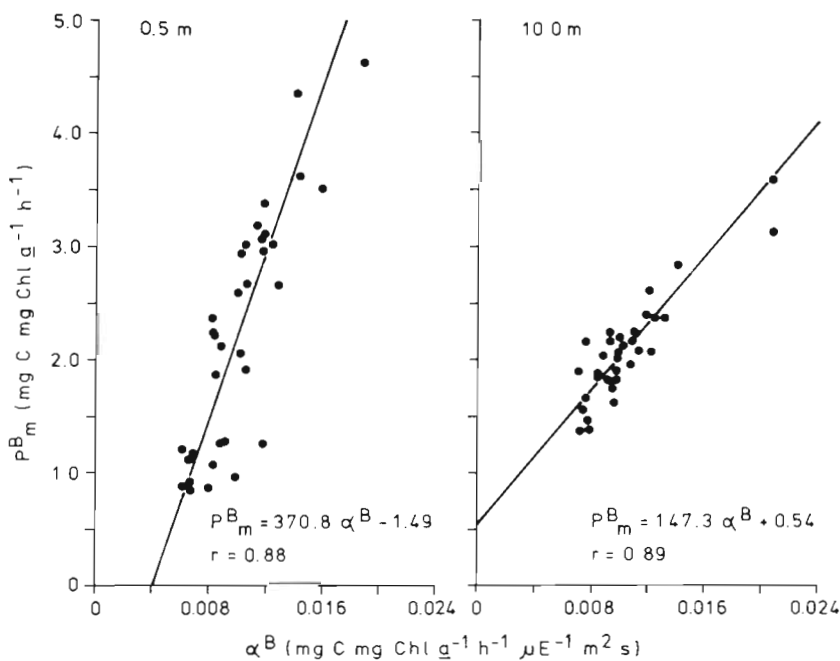


Fig. 8. Relationships between α^B and P_{max}^B (P_{m}^B) at 0.5 and 10 m in Lindåspollene for the period 7 to 12 June 1982. The functional regression lines are calculated according to Ricker (1973); $n = 33$; r : correlation coefficient

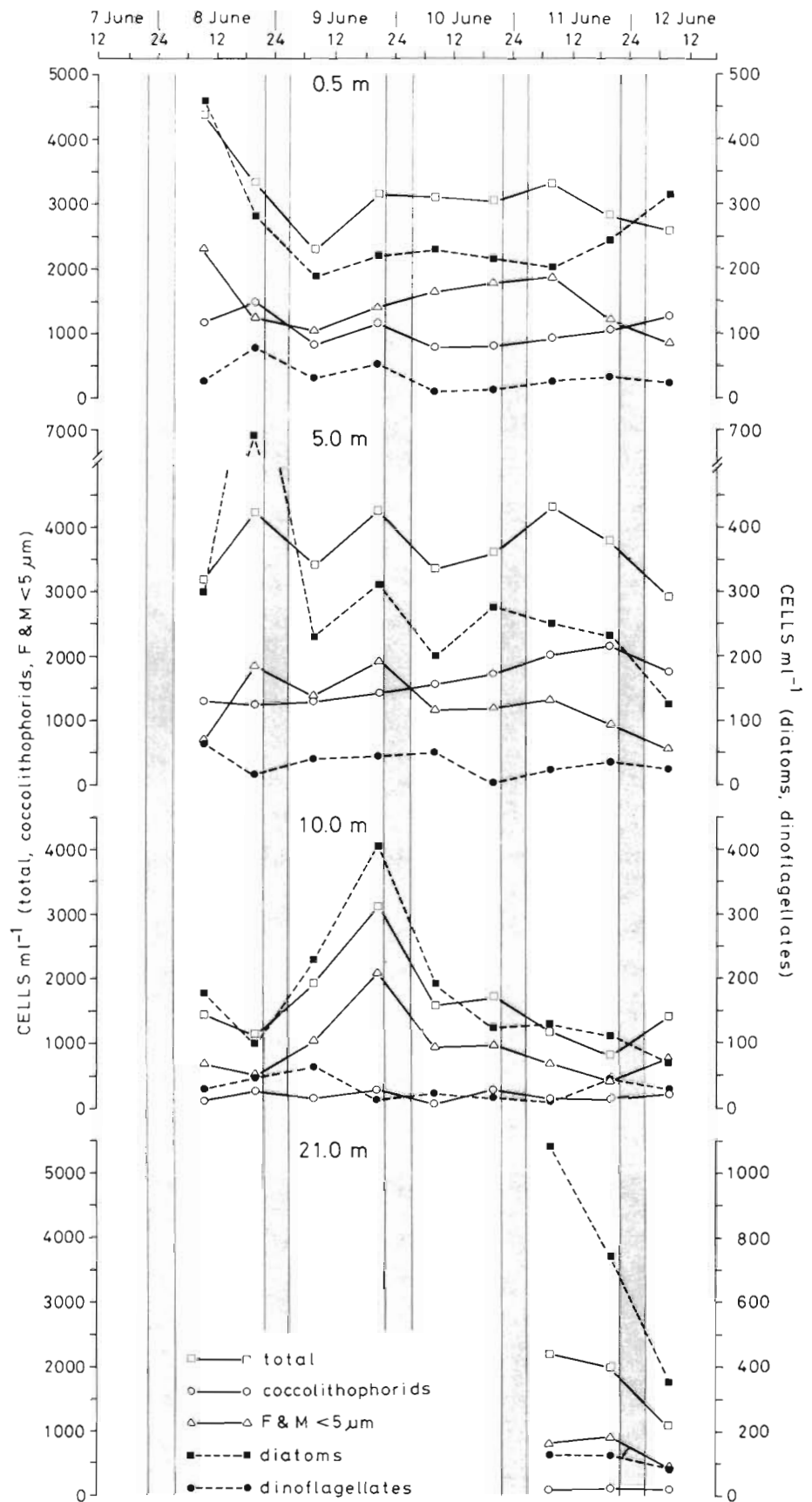


Fig. 9. Diel variations in phytoplankton cell numbers at 0.5, 5, and 10 m during the period 7 to 12 June 1982 in Lindåspollene and at 21 m from 11 to 12 June. The scale for the total fraction, coccolithophorids and flagellates & monads < 5 μm is to the left, while the scale for diatoms and dinoflagellates is to the right. Note the difference in scale. Shaded columns show periods of darkness

The IVF/chl *a* ratio tended to increase during the day from low values early in the morning to high values in the afternoon or night (Fig. 4). A tendency towards low values of this ratio at high light intensities and high values at low light intensities has been found in previous studies (Kiefer 1973a, Karabashev & Solovyev 1977, Prézelin & Sweeney 1977, Setser et al. 1982, Fuhrman et al. 1985, Pingree & Harris 1988). This suggests that chlorophyll *a* fluorescence is highly influenced by light (Vincent 1979). Other factors that may play a role are the physiological state of the cells, the species composition and the cell size (Kiefer 1973b, Setser et al. 1982, Alpine & Cloern 1985, Falkowski & Kiefer 1985).

In Lindåspollene the diel variations in photosynthetic capacity and chlorophyll *a* fluorescence seemed to be opposite (Figs. 4 and 6). This may indicate that the underlying mechanism of the diel rhythm in photosynthesis is closely connected with energy transfer processes in the thylakoid membrane (Prézelin & Sweeney 1977). According to Vincent (1979) high light intensities could lead to a transfer of excitation energy from the highly fluorescent photosystem II to the weakly fluorescent photosystem I, thereby reducing the chlorophyll *a* fluorescence dramatically. From this one may hypothesize that such a mechanism could save energy for the dark reactions of photosynthesis. Samuelsson et al. (1983) found that the diel rhythm in photosynthesis of the dinoflagellate *Gonyaulax polyedra* was mainly regulated by photosystem II.

Mean values of chlorophyll *a* were 40% higher at 10 m than at 0.5 m, while light utilization efficiency (α^B) did not change with depth (Table 1). Investigations on the vertical distribution of phytoplankton revealed that cell carbon and species composition remained unchanged down to 10 m (Skjoldal & Erga unpubl.). Such a response could therefore be indicative of shade adaptation of the algal cells.

Platt & Jassby (1976) suggested that α^B and P_{max}^B are uncoupled physiologically. Thus, the initial slope of the *P* vs *I* curve (α^B) is mainly a function of the photochemical processes of photosynthesis (Côté & Platt 1983), depending upon the pigment content of the cell and on the absorption characteristics of these pigments (Harris 1980). Photosynthetic capacity expressed per unit chlorophyll (P_{max}^B) is also sensitive to light variations, but in addition, is a function of the enzymatic processes in the dark reactions of photosynthesis. Therefore, it is also dependent upon other environmental factors such as nutrients and temperature (Harris 1980, Côté & Platt 1983). Nitrate and orthophosphate concentrations in the uppermost 10 m in Lindåspollene were not above 0.1 μ M (Skjoldal & Erga unpubl.). A moderate nutrient stress may thus be assumed for the phytoplankton of these strata. According to this, the observed morning

peak in photosynthetic activity could be a response to accumulation of nutrients in the cell during the night. This increased nutrient pool may enable the phytoplankton cells to metabolize the endproducts of the dark reactions of photosynthesis, thereby speeding up the photochemical processes. In accordance with this, Raimbault & Mingazzini (1987) found a strong diurnal pattern in nitrate storage for N-limited marine diatoms, with maximum accumulation occurring in the morning.

The photosynthetic parameters α^B and P_{max}^B were linearly correlated at both 0.5 and 10 m in Lindåspollene (Fig. 8, Table 2). This indicates a phased diel periodicity in α^B and P_{max}^B . Similar relationships have been described for natural phytoplankton off California, USA (Harding et al. 1982a), in Bedford Basin, Canada (Côté & Platt 1983), in Chesapeake Bay, USA (Harding et al. 1985, Harding & Jones 1988), on the Pacific coast of Canada (Forbes et al. 1986), in the Gulf of Maine, USA (Legendre et al. 1988) and in McMurdo Sound, Antarctica (Rivkin & Putt 1988). MacCaull & Platt (1977) and Putt & Prézelin (1985) found no diel rhythm in α^B , but only in P_{max}^B , for natural phytoplankton during summer in Bedford Basin (Canada) and in Santa Barbara Channel (USA), respectively.

The difference between 0.5 and 10 m in our study reflected a basic difference between the diel cycles of P_{max}^B and α^B at the 2 depths. α^B showed similar cycles with almost identical means and standard deviations at 0.5 and 10 m (Table 1, Fig. 6). P_{max}^B , in contrast, showed much more pronounced variation at 0.5 than at 10 m (Table 1, Fig. 6). Probably this has to do with light adaptation (i.e. increased activity of the enzymatic processes in the dark reactions of photosynthesis). This was reflected in a much steeper linear relationship between P_{max}^B and α^B at 0.5 than at 10 m (Fig. 8). Such a pattern has also been described by Harding et al. (1987). I_K is derived as the ratio between P_{max}^B and α^B . Due to the relatively greater diel variation in P_{max}^B than in α^B at 0.5 m, I_K changed by a factor of 2 to 3 (Fig. 6). Therefore the slope of the regression (linear) describing the relationship between P_{max}^B and α^B (Fig. 8) cannot be defined as an overall mean value of I_K at 0.5 m. This disparity was less pronounced at 10 m due to a more similar pattern of variation in α^B and P_{max}^B . I_K was only weakly correlated with α^B at both depths (Table 2). An uncorrelated relationship between I_K and α^B has been taken to infer that the photochemical and dark processes of photosynthesis are uncoupled physiologically (Platt & Jassby 1976). This interpretation may not be that straightforward, however, since I_K is derived from both α^B and P_{max}^B . Thus, the highly phased and correlated relationship between α^B and P_{max}^B suggests the opposite, i.e. closely coupled processes.

For cultures of marine phytoplankton a phased periodicity in α^B and P_{max}^B has been widely

documented (Prézelin & Sweeney 1977, Prézelin & Matlick 1980, Harding et al. 1981a, b, 1983, 1987, Putt & Prézelin 1988). In Lindåspollene the diel rhythm in photosynthesis (Figs. 6 and 7) was not accompanied by a similar periodicity in chlorophyll *a* concentrations (Fig. 4). This is also consistent with the findings of Prézelin et al. (1977), Prézelin & Matlick (1980), Harding et al. (1981a, 1982a) and Legendre et al. (1988). The independence of chlorophyll *a* concentrations and P-I periodicity has been interpreted as reflecting an endogenous rhythm regulating diel oscillations in photosynthesis (Harding et al. 1982a, Legendre et al. 1988). Other authors also lend support to the hypothesis that the circadian rhythm of photosynthesis is controlled by an endogenous component (Sournia 1974, Prézelin & Sweeney 1977, Prézelin et al. 1977, Harding et al. 1981a, Côté & Platt 1983). Such an endogenous mechanism is believed to be entrained by environmental factors (Enright 1970, Stross et al. 1973). Among these, nutrient deficiency and nutrient availability, and light:dark cycles were probably the most important in Lindåspollene.

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