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# Time-Course of Photoadaptation in the Photosynthesis-Irradiance Relationship of a Dinoflagellate Exhibiting Photosynthetic Periodicity

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## Abstract

Cultures of the marine dinoflagellate *Glenodinium* sp. were light-shifted and rates of photoadaptation determined by monitoring changes in cell volume, growth rate, pigmentation, parameters of the photosynthesis-irradiance (P-I) curves and respiration. To approximate physiological conditions of field populations, cells were cultured on an alternating light-dark cycle of 12hL:12hD, which introduced a daily periodicity of photosynthesis. One result of the present study was to demonstrate how specific parameters of the P-I relationship influenced by periodicity of the light:dark cycle are distinguished from photosynthetic parameters influenced by changes in light level. Under steady-state conditions, rates of both light-saturated ($P_{max}$) and light-limited photosynthesis changed in unison over the day; these changes were not related to pigmentation, and displayed their maxima midday. This close relationship between $P_{max}$ and the slope ($\alpha$) of the cellular P-I curves in steady-state conditions was quickly adjusted when growth illumination was altered. Rates of light-limited photosynthesis were increased under low light conditions and the periodicity of cellular photosynthesis was maintained. The short-term responses of the P-I relationship to changing light level was different, depending on (1) whether the light shift was from high to low light or *vice versa*, and (2) whether the high light levels were sufficient to promote maximal photosynthesis rates. Major increases in the photosynthetic carotenoid peridinin, associated with a single type of light-harvesting chromo protein in the chloroplast, was observed immediately upon shifting high light cultures to low light conditions. Following pigment synthesis, significant increases in rates of light-limited photosynthesis were observed in about one-tenth the generation time, while cellular photosynthetic potential was unaffected. It is suggested that general results were consistent with earlier reports that the major photoadaptive "strategy" of *Glenodinium* sp. is to alter photosynthetic unit (PSU) size. Photoadaptive response times to high light were light-dependent, but appeared to be slower than photoadaptive responses to low light. If light intensities were bright enough to maximize growth rates, photosynthetic response times were on the order of a generation period and pigmentation fell quickly as cells divided at a faster rate. If light-intensities were not sufficient to maximize growth rates, then pigment content did not decline, while rates of light-limited photosynthesis declined quickly. In all cases, photoadaptation was followed best by monitoring fast changes in half saturation constants for photosynthesis, rather than fluctuating changes in pigmentation. Results compared well with time-course phenomena reported for other groups of phytoplankton. Overall, results suggest phytoplankton can bring about photo-induced changes in photosynthesis very quickly and thus accommodate widely fluctuating light regimes over short periods of time.

## Introduction

During the last 3 yr, there have been a number of studies which have looked at the mechanisms underlying the photoadaptive strategies of major phytoplankton groups (Prézelin, 1976; Prézelin *et al.*, 1976; Prézelin and Sweeney, 1978, 1979; Falkowski and Owens, 1979; Meeson and Sweeney, 1979; Perry *et al.*, 1979; Marra, 1980). Like other researchers working with marine phytoplankton, we have consistently seen very large increases in cellular pigmentation associated with growth at low light intensities. Working with dinoflagellates, our research objectives have been to find out how these phytoplankton regulate pigmentation under low light conditions and to determine what effect these responses might have on the cell's ability to gather additional light energy and to convert it into photosynthetic potential, thereby optimizing growth rates under situations of environmental light stress. Actively growing dinoflagel-

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lates, like *Glenodinium* sp. and *Gonyaulax polyedra*, cultured at low light intensities, contain up to 5 times the pigment content of high light cells. Increased pigmentation was shown to reflect increased amounts of specific light-harvesting pigment-proteins at low light levels (Prézelin, 1976; Prézelin and Sweeney, 1978). Presumably as a result of significant increases in the amount of light-harvesting components (LHC) associated with the photosystems in these phytoplankton, the $P_{max}$ cell$^{-1}$ did not change over a wide range of growth illuminations, while the half-saturation constant for cellular photosynthesis ($I = \frac{1}{2} P_{max}$ cell$^{-1}$) steadily declined with decreased light levels. Thus changes in the photosynthesis-irradiance (P-I) relationship occurred when cells were grown at lower light levels, and reflected increases in the rates of light-limited photosynthesis. As a result, the photosynthetic performance (photosynthetic activity at *in situ* growth light levels) of low light cells were almost twice as high as what would have been predicted if no change in the P-I relationship had occurred (Prézelin, 1976; Prézelin and Sweeney, 1978). Thus it was suggested that increased photosynthetic antenna size was an important part of a photoadaptive mechanism that presumably optimized photosynthesis at low light levels and provided a means of maintaining significant growth rates of dinoflagellates under light-limiting conditions.

The photo-induced response outlined above did not appear to be ubiquitous among dinoflagellates or other phytoplankton, and subsequent studies suggested that while some phytoplankton photoadapt primarily through altered antenna size, others are capable of photoadaptation by altering the actual number of photosystems in the cell (Falkowski and Owens, 1979; Meeson and Sweeney, 1979; Perry *et al.*, 1979; Prézelin and Sweeney, 1979). However, all the studies on dinoflagellates to date suggest low light photoadaptive mechanisms involve major changes in the composition and activity of the light reactions of photosynthesis, rather than major changes in enzymatic activity (Prézelin and Alberts, 1978; Prézelin and Sweeney, 1979). Also, it is beginning to appear that the precise type of photoadaptive response evoked by specific dinoflagellate species may be closely related to the kinds of natural light environments to which these species have become accustomed.

The objective of the present study was to see how fast the changes in pigmentation and the photosynthesis-irradiance (P-I) relationship came about when dinoflagellates were moved into a new light environment. *Glenodinium* sp. was chosen as the first test species because the mechanism of its photoadaptation appeared the simplest of the dinoflagellates previously studied (Prézelin, 1976). Also, the effect of a light-dark cycle in the P-I relationship and pigmentation had been well defined and became important in understanding the results of the present experimental design (Prézelin *et al.*, 1977; Prézelin and Sweeney, 1977). In order to approximate physiological conditions of the field populations better, lab cultures were kept on an alternating light:dark schedule (12 h L:12 h D). To look at photo-induced responses of photosynthesis, the light intensity used during the light period was changed during the experiments and the time-course changes in photosynthesis followed. Thus photoadaptive responses were imposed on a phytoplankton population displaying natural photosynthetic periodicity. Thus one of our aims was to demonstrate how it was possible to distinguish specific parameters of the P-I relationship which are influenced directly by the periodicity of the light:dark schedule from those parameters exclusively influenced by changes in growth illumination.

## Methods and Materials

### Growth Conditions

*Glenodinium* sp. (L. Provasoli, M. Bernard isolate; UCSB code no. 5M29) was grown in unialgal batch cultures in 2.8 l Fernbach flasks containing 1.5 l of half-strength *f* medium (f/2) (Guillard and Rhyther, 1962). Cells were cultured on an alterating 12 h L:12 h D cycle at 18 °C ± 1C°, with illumination provided by banks of 110 W cool-white fluorescent lamps (General Electric F48P617-CW Power Groove) placed beneath glass shelves supporting the culture flasks. Irradiances of 500, 2500 and 5000 $\mu$W cm$^{-2}$ were obtained by placing different layers of cheese cloth between the lamps and the cultures. Irradiances were measured at the base of the flasks with a United Detector Technology Model 40A light meter. In experiments designed to determine the time course of photoadaptation, cultures were transferred from one light level to another at the beginning of the light period.

To insure adequate numbers of cells of equivalent physiological condition, several culture flasks were grown at each light level and individually monitored. Growth was assessed directly by cell counts made with an AO Bright Line Haemocytometer. Cell counts were made at the onset of each light period. If population densities had increased by more than 20% (doubling time of 5 d since inoculation), cells from the several flasks were combined, diluted with fresh medium back to cell densities normally indicative of mid-to-late-exponential populations in batch culture (0.8 to 1.4 x $10^5$ cells ml$^{-1}$) and redistributed into the culture flasks. This procedure allowed an estimate of daily growth rates, while minimizing effects of increasing cell densities on available light energy within the culture. Before experimentation was begun, several cell doublings were followed to allow adequate light acclimation. Packed cell volume measurements also were made, following standard procedures (Sorokin, 1973).

Pigments were extracted according to the methods of Jeffrey (1968). Details of extraction, TLC and extinction coefficients have been described previously (Prézelin, 1976).

Photosynthetic measurements were designed to provide a 12 to 15 point photosynthesis *vs* irradiance (P-I) curve within 2 h from the time cultures were

sampled. Freshly harvested cells (3 min 1300 rpm, room temperature, 22 °C) were suspended in a small volume of fresh f/2 medium supplemented with 10mM Na $HCO_3$ (pH 8). To minimize effects of self-shading, dilute suspensions of cells were used for $O_2$ production measurements which routinely contain less than 1 $\mu$g chl *a* $ml^{-1}$ sample. Prior to photosynthetic measurements, $O_2$ levels in the sample were reduced by passing $N_2$ gas over the surface of the cell suspension. Chilling effects of $N_2$ gas were reduced by keeping the sample immersed in an 18 °C water bath. The sample was then divided and each portion placed on 2 identically designed Delieu and Walker (1972) arrangements of the Clark-type $O_2$ electrode. Temperature was controlled in the reaction vessels at 18 °C by a constant temperature water bath (Forma Scientific). Collimated light was supplied from cooled 500 W tungsten bulks from Viewlex model V-25 slide projectors and was filtered through 5 cm of 1% cupric sulfate solution. The irradiance of the incident beam was varied by placing neutral density filters (Turner) between the lamp and the reaction chamber. Incident irradiance was measured with the UDT light meter. The maximum irradiance, without any neutral filters, was 8000 $\mu W\ cm^{-2}$.

Initial respiration rates were estimated from oxygen consumption rates monitored on the electrodes for at least 10 to 15 min before the onset of any illumination. Respiration rates were also calculated after cells were subsequently illuminated and the 2 sets of data are presented separately.

Using the oxygen production rates, P-I curves for *Glenodinium* sp. were constructed at different times after cultures were exposed to different light levels. From the P-I curves, calculations were made to estimate the light-limiting slope ($\alpha$) and the subsequent intensity at which the photosynthetic potential ($P_{max}$) was half-saturated ($I = \frac{1}{2} P_{max}$). To estimate $\alpha$, linear regression analyses of oxygen production rates of irradiances below 2800 $\mu W\ cm^{-2}$ were made. No intercept at zero was required in calculations carried out either on a Texas instruments TI-55 programmable calculator or a Hewlett Packard 9830 calculator equipped with an Infotek Systems FD-30A mass memory, a printer (HP 9866a) and an x-y plotter (HP 9682a).

## Results

Under nutrient-saturated steady-state conditions, the dinoflagellate *Glenodinium* sp. demonstrated a regular diel periodicity in light-saturated photosynthesis ($P_{max}$) which was independent of pigmentation and displayed its maximum midday (Fig. 1, Prézelin *et al.*, 1977). In

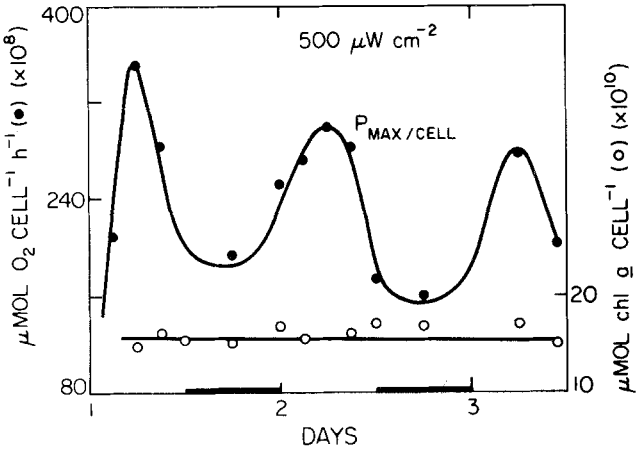


Fig. 1. *Glenodinium* sp. Periodicity of photosynthetic capacity expressed as $\mu$mol $O_2$ $cell^{-1}h^{-1}$ ($\times 10^8$) (closed circles). chl *a* concentrations measured over the day are expressed as $\mu$mol chl $cell^{-1}$ ($\times 10^{-10}$) (open circles). Light-dark cycle was 12 hL:12 hD and irradiance of light phase was 500 $\mu W\ cm^{-2}$. Dark periods are indicated by blackened bars and abscissa

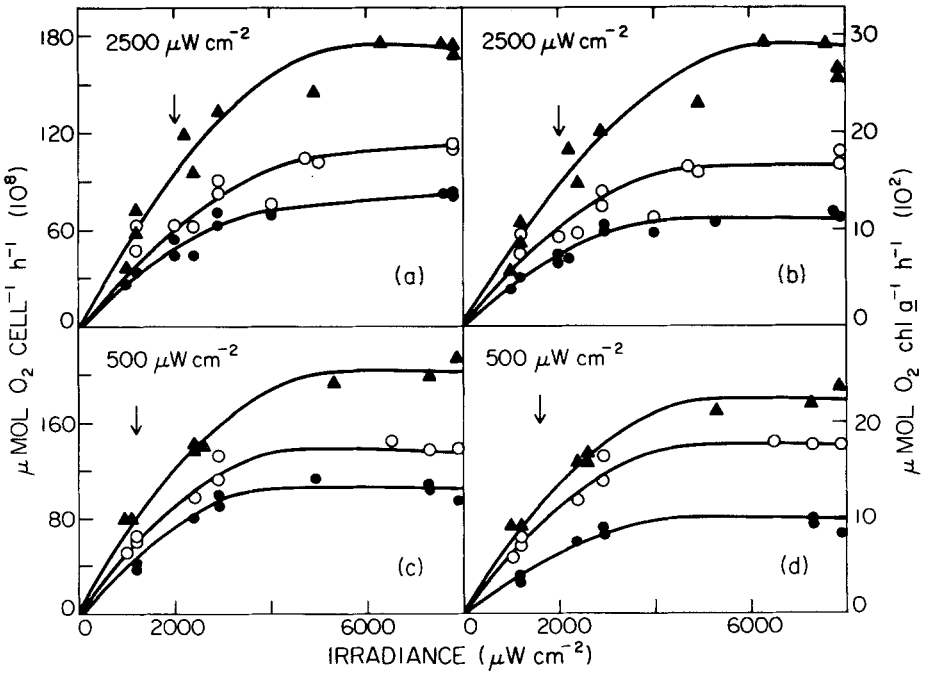


Fig. 2. *Glenodinium* sp. Comparison of P-I curves determined at different times of day. Open circles represent the onset of the light period, closed triangles represent midday, and closed circles represent the onset of the dark period. Arrow indicates light level at which photosynthesis was half-saturated. Cells were collected from cultures entrained to a 12 hL:12 hD cycle. (a) Irradiance of light period was 2500 $\mu W\ cm^{-2}$ and photosynthesis expressed as $\mu$mol $O_2$ $cell^{-1}\ h^{-1}$ ($10^8$). (b) Irradiance of light period was 2500 $\mu W\ cm^{-2}$ and photosynthesis expressed as $\mu$mol $O_2$ chl $a^{-1}h^{-1}$ ($10^2$); (c) Irradiance of light period was 500 $\mu W\ cm^{-2}$ and photosynthesis expressed as $\mu$mol $O_2$ $cell^{-1}h^{-1}$ ($10^8$); and (d) Irradiance of light period was 500 $\mu W\ cm^{-2}$ and photosynthesis expressed as $\mu$mol $O_2$ chl $a^{-1}h^{-1}$ ($10^2$)

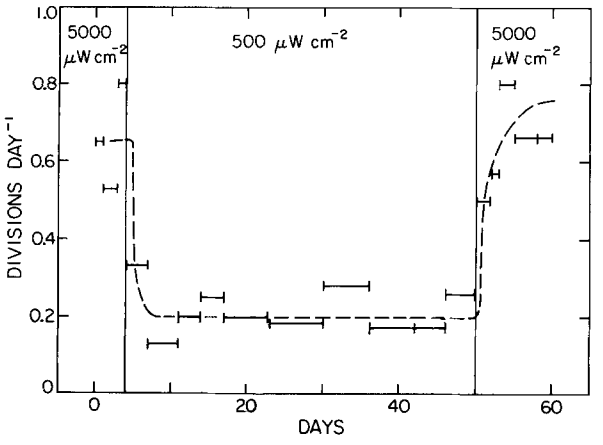


Fig. 3. *Glenodinium* sp. Exponential growth rates expressed as divisions $d^{-1}$, and plotted in relation to time at light-saturating (5000 $\mu W\ cm^{-2}$) and light-limiting (500 $\mu W\ cm^{-2}$) growth and photosynthesis illuminations. Cells were cultured on a 12 hL:12 hD cycle at 18 °C; vertical lines indicate time of change in growth illumination

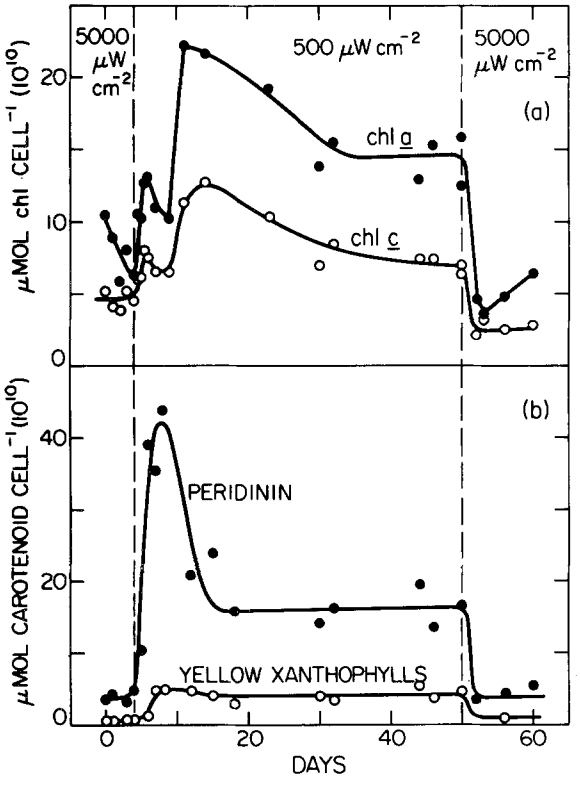


Fig. 4. *Glenodinium* sp. Whole cell pigment content of density-independent cultures in relation to duration of time at light-saturating (5000 $\mu W\ cm^{-2}$) and light limiting (500 $\mu W\ cm^{-2}$) growth illumination. Cells were cultured on a 12 hL:12 hD cycle at 18 °C; vertical dashed lines indicate time of change in growth illumination. (a) concentrations of chlorophyll *a* (closed circles) and chlorophyll *c* (open circles) are expressed as μmoles pigment $cell^{-1}$ ($10^{10}$). (b) concentrations of peridinin (closed circles) and yellow xanthophylls (open circles) are expressed as μmol pigment $cell^{-1}$ ($10^{10}$)

addition, the initial slope ($\alpha$) of the P-I curve was also a time-dependent parameter which oscillated in direct proportion to the change in $P_{max}$ (Fig. 2). Such a close relationship was shown to exist between $P_{max}$ and light-limited rates of photosynthesis in the P-I curves of *Glenodinium* sp. over the day, when steady-state culture conditions were maintained at any light level (Figs. 2 and 8). These observations were consistent with earlier work on the diurnal periodicity of photosynthesis in *Glenodinium* sp. and other dinoflagellates, where light-limited and light-saturated photosynthesis were shown to be regulated by a biological clock (Prézelin and Sweeney, 1977).

The daily change in light-saturated ($P_{max}$) and light-limited photosynthesis ($\alpha$), which persisted when cells were cultured at different light levels (Fig. 2), were not necessarily representative of growth rate changes observed. However, the half-saturation intensity for photo synthesis was not periodic over the day, but did change in response to changes in growth illumination (Fig. 2) and was believed to be indicative of the photo-adaptive state of the cells. Most important, since the effects of photoperiod on the photosynthetic characteristics of the P-I curves could be distinguished from effects of growth illumination on the P-I curves of *Glenodinium* sp., it was possible to set up experiments to look at the time-course of the photoadaptive changes in photosynthesis while keeping a photoperiod as part of the culture regime.

In the first study, cells of *Glenodinium* sp. were cultured at 5000 $\mu W\ cm^{-2}$ for several generations, keeping the cell densities at about $1.0 \pm 0.2 \times 10^5$ cells $ml^{-1}$. Cell density and culture turbidity were kept reasonably constant by making daily cell counts, diluting with fresh medium when necessary (every 2 to 3 d for high light cultures; every 7 to 10 d for low light cultures) and then redistributing the combined population into a series of Fernbach culture flasks. In this way, some estimates of daily growth could be made, while insuring that the population was nutrient-rich, received illumination unmodified by major changes in cell density, and that each batch culture flask was reasonably representative of the whole culture population. At 5000 $\mu W\ cm^{-2}$, the growth rate of *Glenodinium* was about $0.66 \pm .13$ divisions $d^{-1}$ (Fig. 3), which compares well with $0.68 \pm .04$ divisions $d^{-1}$ maximal growth rate, determined previously for this organism under conditions of nutrient saturation and optimal light intensities (Prézelin, 1976).

Once the growth rate and pigment content of 5000 $\mu W\ cm^{-2}$ cultures were determined, the growth illumination was lowered to 500 $\mu W\ cm^{-2}$ and the changes in growth rate and cellular amounts of photosynthetic pigments were followed (Figs. 3 and 4). Changes in growth illumination were made at the onset of the light period of the photoperiod. The growth rate of *Glenodinium* fell immediately upon transfer to an estimated $0.21 \pm .05$ divisions $d^{-1}$ within less than 2 d. While growth rate was lowered quickly to a new steady-state level, pigmentation fluctuations occurred over a period

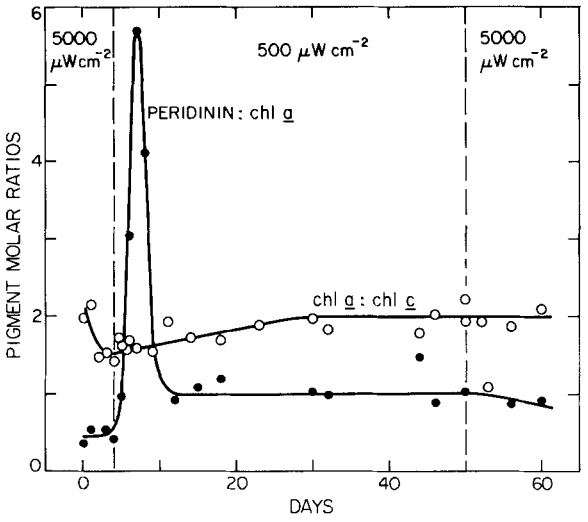


Fig. 5. *Glenodinium* sp. Pigment molar ratios of density-independent cultures in relation to duration of time at light-saturating (5000 $\mu$W cm$^{-2}$) and light-limiting (500 $\mu$W cm$^{-2}$) growth illumination. Cells were cultured on a 12 hL:12 hD cycle at 18 °C; vertical dashed lines indicate time of change in growth illumination. Ratios of peridinin:chl *a* (closed circles) and chl *a*:chl *c* (open circles) are expressed on a molar basis

of at least 30 d before a new equilibrium in cellular content was approached (Fig. 4). The content of 4 pigments was monitored, as they are unequally distributed in the various chromoproteins of the PSU of *Glenodinium* sp. (Prézelin and Alberte, 1978; Prézelin and Boczar, 1980). Thus, differences in their time-course response to changing light levels should be indicative of differential rates of synthesis and/or degradation of these chromoproteins (Prézelin, 1976; Prézelin and Sweeney, 1978). For example, peridinin is the major photosynthetic carotenoid in all dinoflagellates and is believed to be located exclusively in a discrete peridinin-chl *a*-protein complex, PCP, surrounding the reaction centers of the PSU (Prézelin and Haxo, 1976; Prézelin and Alberte, 1978; Prézelin and Sweeney, 1978). Upon the transfer of cells to 500 $\mu$W cm$^{-2}$, the perdinin content of *Glenodinium* cells increased 11-fold within 5 d, from 4.1 ± 0.67 to about 44.0 × $10^{-9}$ $\mu$mol peridinin cell$^{-1}$, and then decreased at a rate of about 3.5 × $10^{-9}$ $\mu$mol peridinin cell$^{-1}$ d$^{-1}$ to a steady state level of 16 ± 1.9 × $10^{-9}$ $\mu$mol peridinin cell$^{-1}$ about 12 d after the light change (Fig. 4b). As a result, the molar ratio of peridinin: chl *a* also climbed 11-fold, from about 0.5 to 5.5 within 3 d of lowering the growth illumination (Fig. 5). As the peridinin content of the cell fell and the chl *a* content began to rise, the peridinin: chl *a* ratio fell. Within 8 d of the light shift, the ratio had come to a steady-state value of about 1.0 peridinin chl $a^{-1}$ in *Glenodinium*.

Unlike peridinin, the increase of the other pigments during the first 5 d of transfer was more modest. In the case of the chlorophylls, secondary increases in cellular content were noted after 5 d and before an eventual decline to steady-state values more than 30 d after the initial light-shift (Fig. 4). Chl *a*, which is present in all the chromoproteins of the PSU of *Glenodinium* sp. (Prézelin and Alberte, 1978; Boczar *et al.*, 1979; Prézelin and Boczar, 1980), almost doubled in cellular content during the first 2 d after transfer, from about 7 to about 13 × $10^{-9}$ $\mu$mol chl *a* cell$^{-1}$. This initial rise was followed by a small decline between 2 to 5 d after transfer, falling to about 10 × $10^{-9}$ $\mu$mol chl *a* cell$^{-1}$ (Fig. 4a). A second doubling of the chl *a* content occurred between d 5 and 7, with values as high as 22 × $10^{-9}$ $\mu$mol chl *a* cell$^{-1}$ being recorded. The second increase in chl *a* was followed by a gradual decline to steady-state values of about 14.8 ± 1.3 × $10^{-9}$ $\mu$mol chl *a* cell$^{-1}$ (Fig. 4a).

Chl *c* appears to be located predominantly in a chl *a*-chl *c* light-harvesting protein complex (Boczar *et al.*, 1979; Prézelin and Boczar, 1980). Chl *a* showed a similar time-course response to lowered growth illumination as was observed with chl *a*. The amount of chl *c* in the cells of *Glenodinium* increased by about 50% during the first 2 d, from about 5 to 7.5 × $10^{-9}$ $\mu$mol chl *c* cell$^{-1}$, and then roughly doubled between 5 and 10 d after transfer to a high value of 12.5 × $10^{-9}$ $\mu$mol chl *c* cell$^{-1}$ (Fig. 4a). Like chl *a*, the chl *c* content declined to a steady state value within 30 d of transfer, to about 7.7 ± .67 × $10^{-9}$ $\mu$mol chl *c* cell$^{-1}$. The increase in chl *a* and chl *c* were similar, but not exact. The chl *a*:chl *c* molar ratio of *Glenodinium* increased from 1.5 to 2.0 during the first 30 d of the shift to lower growth illumination (Fig. 5).

Also monitored was the effect of the light shift on the combined xanthophyll content of *Glenodinium* sp. The xanthophylls are dominated by diadinoxanthin, whose largely increased concentrations are usually associated with bright light photoinhibition responses, and dinoxanthin, the probable synthetic precursor to peridinin (Mandelli, 1972; Johansen *et al.*, 1974). The combined xanthophyll content increased slightly within 3 d of low light transfer (Fig. 4b). However, no comment can be made whether this reflected generalized increases in photosynthetic membranes or an accumulation of peridinin precursors as peridinin synthesis is slowed.

After steady-state pigmentation was reached in both growth rate and pigment content of cells at 500 $\mu$W cm$^{-2}$, illumination was increased once again to 5000 $\mu$W cm$^{-2}$. Growth rate rose immediately, but the maximal growth rate potential of the cells, approximately 0.7 divisions d$^{-1}$, was not reached until 5 d after the light shift. Pigment content, however, declined immediately at a rate proportional to cell division to values originally measured in steady-state cultures grown at 5000 $\mu$W cm$^{-2}$ (Fig. 4). Chl *a* fell almost 3-fold within 3 d, from about 15 to 5 × $10^{-9}$ $\mu$mol cell$^{-1}$. Similarly, the chl *c*, peridinin, and combined xanthophyll content fell 3-fold within the first 3 d, to respective values of about 2.5, 4.5, and 1 × $10^{-9}$ $\mu$mol pigment cell$^{-1}$ (Fig. 4). This fairly uniform decrease in all pigmentation is reflected in the minimum changes in peridinin:chl *a* and chl *a*:chl *a* ratios during the first 10 d of increased growth illumination, and may simply reflect a partitioning of existing chloroplast membranes among actively dividing cells.

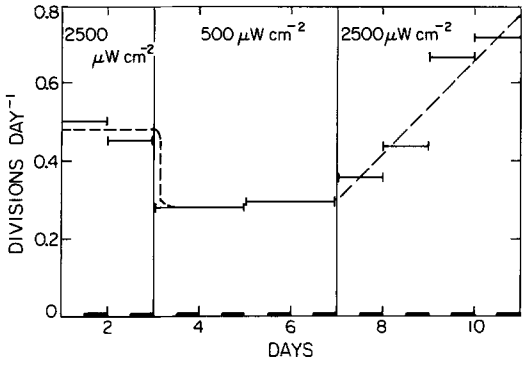


**Fig. 6.** *Glenodinium* sp. Exponential growth rates expressed as divisions $d^{-1}$, and plotted in relation to time at different light levels. A 2500 $\mu$W $cm^{-2}$, growth was light-saturated but photosynthesis was light-limited. At 500 $\mu$W $cm^{-2}$, both growth and photosynthesis are light-limited

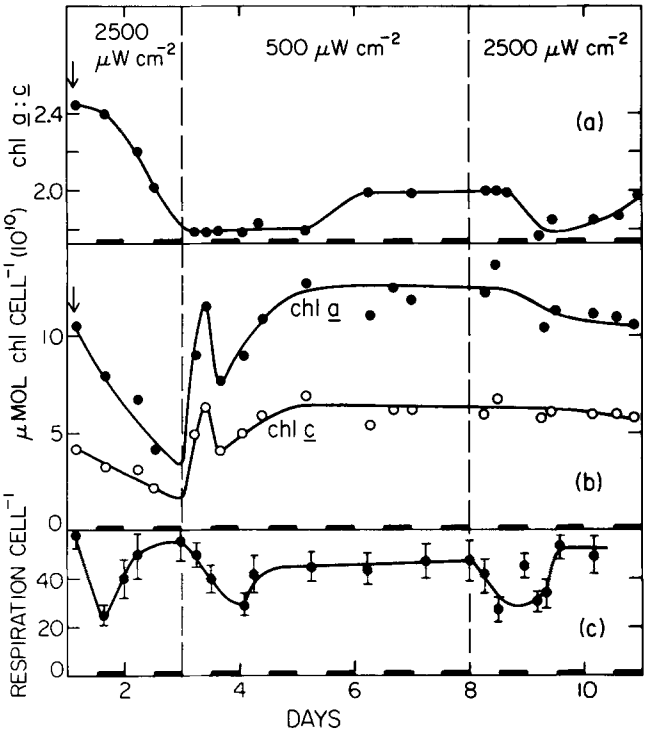


**Fig. 7.** *Glenodinium* sp. Comparison of changes in pigment molar ratios, whole cell pigmentation and cellular respiration in relation to time spent at 2500 and 500 $\mu$W $cm^{-2}$. Cells were cultured on a 12 hL:12 hD cycle at 18 °C; vertical dashed lines indicate time of change in growth illumination, and arrow indicates time of major dilution of population to a steady-state concentration of 0.968 ± .028 × $10^4$ cells $ml^{-1}$. (a) Ratios of chl *a*:chl *c* (closed circles) are expressed on a molar basis; (b) Concentrations of chl *a* (closed circles) and chl *c* (open circles) are expressed as $\mu$mol pigment $cell^{-1}$ ($10^{10}$); (c) Respiration $cell^{-1}$ were measured after illumination of dark-adapted cells and expressed as $\mu$mol $O_2$ $cell^{-1}h^{-1}$ ($10^8$). The vertical bars represent one standard deviation

Since the major changes in growth rate occurred within the first few days of light shift, a study was undertaken to examine the accompanying changes in photosynthetic activity over the same short period of time. In the second study, however, steady-state cultures were shifted back and forth between 2500 $\mu$W $cm^{-2}$ and 500 $\mu$W $cm^{-2}$. At 2500 $\mu$W $cm^{-2}$, *Glenodinium* sp. is moderately light-limited in growth, with division rates of about .48 divisions $d^{-1}$ (Fig. 6), when cell densities were maintained at about 0.968 ± 0.28 × $10^4$ cells $ml^{-1}$. Upon transfer from 2500 to 500 $\mu$W $cm^{-2}$, growth rates declined to about 0.3 divisions $d^{-1}$ within the first day. After 4 d at 500 $\mu$W $cm^{-2}$, growth illumination again was raised to 2500 $\mu$W $cm^{-2}$. Growth rate appeared to increase linearly over the next 4 d to reach a maximal 0.72 divisions $d^{-2}$.

Just before the study was begun, it was determined that the steady-state cell density was too high and some additional light-limitation may have been imposed on the population. The population was diluted from about 2 × $10^5$ cells $ml^{-1}$ to about $10^5$ cells $ml^{-1}$. When cell densities were lowered by half, but growth illumination kept constant at 2500 $\mu$W $cm^{-2}$, the chlorophyll content of the cells decreased about two-fold within 2 d to a steady-state value of about 4 × $10^{-9}$ $\mu$mol chl *a* $cell^{-1}$ and about 2 × $10^{-9}$ $\mu$mol chl *c* $cell^{-1}$ (Fig. 7b). The effect was to decrease the chl *a*: chl *c* molar ratio to 1.8 (Fig. 7a).

When 2500 $\mu$W $cm^{-2}$ cultures were shifted to a lower illumination of 500 $\mu$W $cm^{-2}$, a biphasic increase in chl *a* and chl *c* again was observed. Again pigmentation increases were detected within the first 6 h of the light shift, chlorophyll content more than doubling within the first 12 h, followed by a brief decline during the first dark period, and then gradually increasing to apparent steady-state values of about 10 and 6.5 × $10^{-9}$ $\mu$mol $cell^{-1}$ of chl *a* and chl *c*, respectively, during the next 4 d at 500 $\mu$W $cm^{-2}$ (Fig. 7b). Secondary decreases in chl content were not observed during the following 5 d that the cells were kept at 500 $\mu$W $cm^{-2}$. Chl *a*:chl *c* molar ratios did not change during the first 2 d of lower illumination, but increased slightly from 1.8 ± .02 to 2.0 ± .09 during the next 3 d (Fig. 7a).

When growth illuminations were restored to 2500 $\mu$W $cm^{-2}$, pigmentation declined very slowly. Chl *a* declined only by about 25% during the first 3 d, while chl *c* values changed little if at all (Fig. 7b). As a result, Chl *a*:chl *c* ratios declined initially, as chl *a* content presumably fell sooner than chl *c*, and then began to rise again as chl *c* content began to fall by the end of the third day. Thus changes in chl *a* and chl *c* could occur independently of each other, suggesting changes in concentrations of specific chromoproteins in the photosynthetic membranes.

Associated with the light-induced changes in pigmentation, transient effects on cell respiration rates also were noted (Fig. 7c). If monitored as rates of oxygen consumption per cell after any period of illumination, respiration rates showed transients when cell cultures were significantly diluted (thereby increasing the light intensity within the population) or after presumably steady-state cultures were light-shifted to higher or lower growth illuminations (Fig. 7c). Respiration increases were correlated with times when either pigment

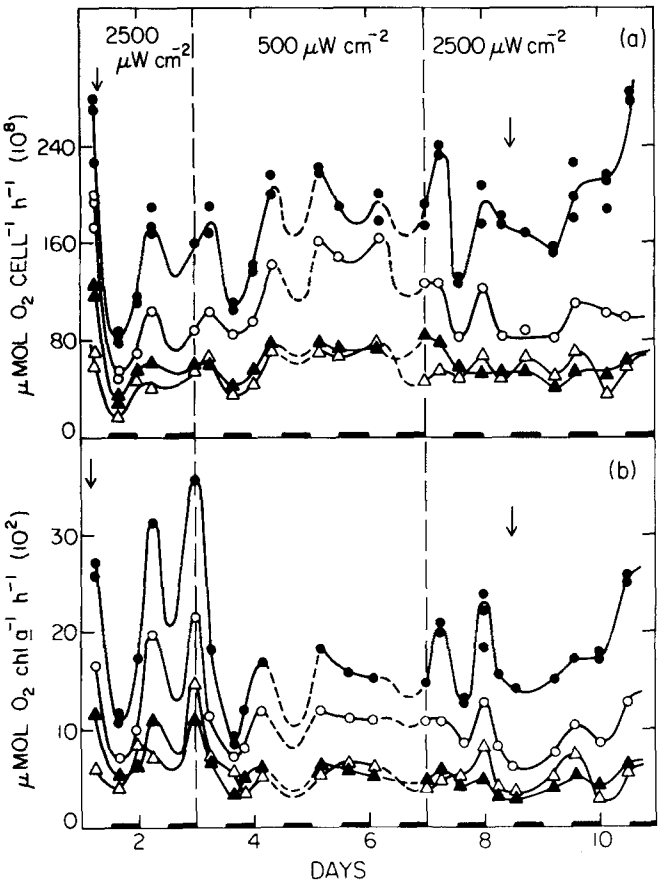


Fig. 8. *Glenodinium* sp. Periodicity of photosynthesis in relation to time spent at growth illuminations of 2500 and 500 $\mu$W cm$^{-2}$. Cells were cultured on a 12 hL:12 hD cycle at 18 °C; vertical dashed lines indicate time of change of growth illumination, and arrow indicates time of major dilution of population to steady-state concentration of 0.968 ± 0.28 X $10^4$ cells ml$^{-1}$. Photosynthesis rates measured at 6000 $\mu$W cm$^{-2}$ (closed circles), 2300 $\mu$W cm$^{-2}$ (open circles), and 1100 $\mu$W cm$^{-2}$ (closed triangles) are presented for comparison. Respiration rates, measured before any illumination of dark-adapted cells, are presented (open triangles). (a) Rates of photosynthesis and respiration expressed as $\mu$mol $O_2$ cell$^{-1}$h$^{-1}$ ($10^8$); (b) Rates of photosynthesis and respiration expressed as moles $O_2$ $\mu$mol chl $a^{-1}$h$^{-1}$ ($10^2$)

synthesis or rates of cell division were increased significantly.

There were also major changes in specific photosynthetic parameters associated with light shifts and changes in population densities. One apparent effect of changes in growth illumination was on the expression of daily periodicities in photosynthesis (Fig. 8). When photosynthesis was expressed on the basis of oxygen production per cell (Fig. 8a), light-saturated photosynthesis rates determined midday were about the same after shifts to low light and after shifts back to higher light levels. The same was generally true for measured rates of light-limited photosynthesis compared at similar times of the day. By contrast, the periodicity of $P_{max}$/chl *a* was dampened noticeably by the lowering of growth illumination to 500 $\mu$W cm$^{-2}$ (Fig. 8b) and was presumably related to fluctuation in cellular pigmentation occurring at this time. The amplitude of daily periodicity in photosynthesis declined form 2 to 3-fold changes at 2500 $\mu$W cm$^{-2}$ to less than 1.5 after transfer to 500 $\mu$W cm$^{-2}$, and the rhythm appeared to lose much of its regularity. Transfer of the cultures back to 2500 $\mu$W cm$^{-2}$ did not induce regular periodicity of photosynthesis even after 4 d (Fig. 8b).

Since growth is affected immediately by a change in illumination, but pigmentation changes may occur over widely varying time periods after a light shift, it became interesting to try to estimate how long it took before photoadaptive responses in pigmentation were translated into effective changes in the photosynthesis-irradiance relationship. In Fig. 9 the P-I curve determined midday on the day prior to a light shift is compared with the P-I curves measured midday on subsequent days after the shift in illumination. Within the first 6 h of the shift to lower light levels, during which time the pigment content of the cells already had increased noticeably, $P_{max}$ chl *a* cell$^{-1}$ (Fig. 9) declined by a third to a level that was maintained through subsequent days at this light level. In contrast, $P_{max}$ cell$^{-1}$ never changed significantly in response to the shift to lower light (Fig.

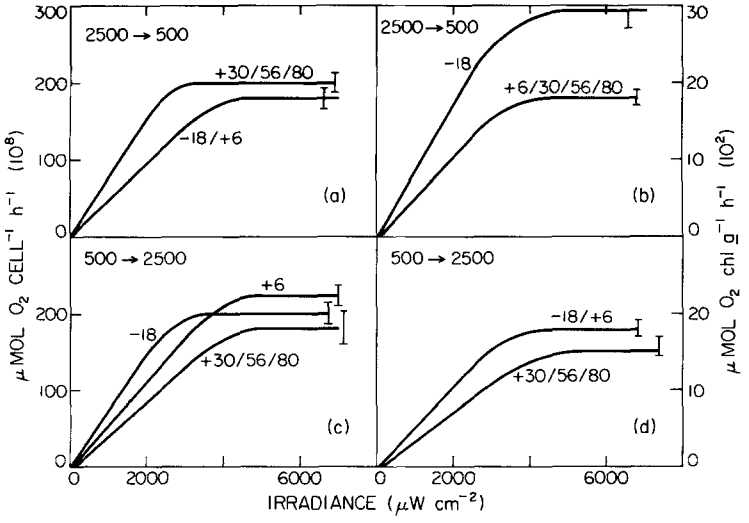


Fig. 9. *Glenodinium* sp. Comparison of P-I curves determined at midday at different time intervals before and after a shift to a different growth irradiance. (a) P-I curves determined midday 18 h before (−18) and 6, 30, 56, and 80 h after cultures were shifted from a growth irradiance of 2500 to 500 $\mu$W cm$^{-2}$. Photosynthesis rates are expressed as $\mu$mol $O_2$ cell$^{-1}$h$^{-1}$ ($10^8$) and vertical bars indicate one standard deviation; (b) Same photosynthesis data as in Fig. 9a, but expressed at $\mu$moles $O_2$ $\mu$mol chl $a^{-1}$h$^{-1}$ ($10^2$); (c) P-I curves determined midday 18 h before (−18) and 6, 30, 56 and 80 h after cultures were shifted from a growth irradiance of 500 to 2500 $\mu$W cm$^{-2}$. Photosynthesis rates are expressed as $\mu$mol $O_2$ cell$^{-1}$h$^{-1}$ ($10^8$) and vertical bars indicate one standard deviation; (d) Same photosynthesis data as in Fig. 9c, but expressed as $\mu$mol chl $a^{-1}$h$^{-1}$ ($10^2$)

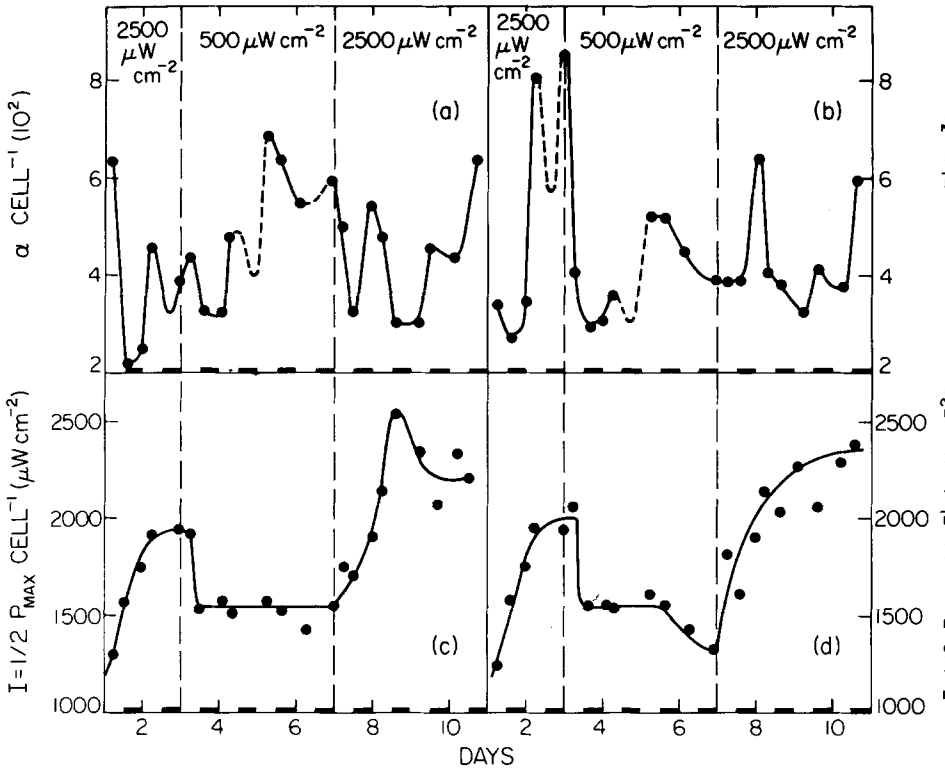


Fig. 10. *Glenodinium* sp. Comparison of relationship of slope parameters of P-I curves to time spent at growth illumination of 2500 and 500 $\mu$W cm$^{-2}$. Vertical dashed lines indicate changes in growth illumination. (a) Periodic changes in the light-limited slope of P-I cell$^{-1}$ curves, expressed as $\alpha$ cell$^{-1}$ ($10^2$); (b) Periodic changes in the light-limited slope of P-I chl $a^{-1}$ curves, expressed as $\alpha$ chl $a^{-1}$ ($10^3$); (c) Effect of growth irradiance on the half-saturation constants of P-I chl $a^{-1}$ curves, expressed as I = $P_{max}$ cell$^{-1}$ in $\mu$W cm$^{-2}$; (d) Effect of growth irradiance on the half-saturation constants of P-I chl $a^{-1}$ curves, expressed as I = $P_{max}$ chl $a^{-1}$ in $\mu$W cm$^{-2}$

9b). Interestingly, and presumably related to increased pigmentation, the slope of the photosynthesis cell$^{-1}$ increased (Fig. 9a) sometime between 6 and 30 h after transfer, while the slope of the P-I chl $a^{-1}$ decreased within the first 6 h of transfer, effectively driving half-saturation constants for photosynthesis in both cases from about 2000 $\mu$W cm$^{-2}$ to about 1500 $\mu$W cm$^{-2}$. In other words, the increased slope of the P-I cell$^{-1}$ curve resulted in a lower half-saturation constant for cellular photosynthesis. In the case of P-I chl $a^{-1}$, $P_{max}$ chl $a^{-1}$ was more severely reduced than the $\alpha$ chl $a^{-1}$ and also resulted in a lower calculated half-saturation constant. The changes in these photosynthetic parameters are not considered independent of one another. On the contrary, they can be most simply explained by a sizeable increase in the photosynthetic antenna size gathering light energy for a relatively fixed number of photosynthetic reaction centers. It would explain the specific increase in certain pigments, the drop in $P_{max}$ chl $a^{-1}$ in proportion to increase chl $a$ content, and the lack of change in $P_{max}$ cell$^{-1}$. It would also explain the increase in light-limited cellular photosynthesis as larger photosynthetic units would gather light over a larger area and should show higher rates of photosynthesis than smaller photosynthetic units at the same light intensity. The lower $\alpha$ chl $a^{-1}$ would thus reflect the increased pigmentation in the cells. Although such changes had the effect of returning the half-saturation constants for photosynthesis to previous higher values, it was "not" by a simple reversal of the mechanism allowing cells to respond to low light intensities (Fig. 9b). A simple interpretation of the latter results is not yet possible.

From this study, it has become apparent (Fig. 10a, b) that the light-limited slopes ($\alpha$) of the P-I curves of dinoflagellates were sensitive to both changes in growth illumination and time of day (i.e., circadian regulation). Thus, they could not be selected as a reliable indicator of the photoadaptive state of these phytoplankton populations, although they might be useful in determining photoperiodicity effects on photosynthesis *in situ* (Prézelin and Ley, 1980). Previous studies (Prézelin, 1976; Prézelin and Sweeney, 1978, 1979), however, had suggested that the half-saturation constants of P-I curves of those dinoflagellates which photoadapt by altering the size of PSU are very sensitive indicators of the photoadaptive state of the cell. This assumption also seems to be valid in the present study and is confirmed in Fig. 10c, d. The half-saturation constant I = 1/2 $P_{max}$ cell$^{-1}$ (Fig. 10c) showed a quick response to changes in cell density (i.e., the increase observed when the high-light population was diluted) and changes in growth illumination to either higher or lower light levels and, in addition, is unaffected by the time of day the measurements are made (i.e. circadian regulation). The half-saturation constant, I = 1/2 $P_{max}$ chl $a^{-1}$, also responded to changes in cell density and growth illumination and was not sensitive to regulation by a biological clock. In addition, changes in these half-saturation constants do generally follow the growth potential of the organism (compare Figs. 6, 10c) when populations of similar cell densities at steady-state are compared.

## Discussion

In the present study, experiments were designed to follow the time course of changes which occurred in the photosynthesis-irradiance (P-I) relationship of a typical marine dinoflagellate *Glenodinium* sp. when the light intensity of the growth environment was significantly altered. However, in order to more closely approximate physiological conditions of field populations, cultures were maintained on an alternating light-dark cycle of 12 h L:12 h D. Therefore, it was important to distinguish parameters of the photosynthesis-irradiance relationship which were influenced by the presence of a light-dark cycle from those parameters which were most strongly influenced by changes in light intensity.

Previous work with *Glenodinium* sp. (Prézelin, 1976), maintained for several months in constant illumination of differing light intensities, showed no daily periodicity in photosynthetic potential ($P_{max}$). Under these steady-state conditions, major differences were noted in the shape of the P-I curves as a function of growth irradiance. The major differences were related to changes in cellular pigmentation, resulting from alterations in the size of the light-harvesting component (LHC) associated with a fixed number of photosynthetic units (PSU) per cell. These photoadaptive responses were most easily characterized in steady-state cultures by monitoring changes in pigmentation and the half-saturation constants for photosynthesis per cell ($I = P_{max}{}^{-2}\,cell^{-1}$), i.e. the light level at which half the maximal photosynthetic potential per cell is reached (Prézelin, 1976). The photoadaptive response of the P-I curves outlined for *Glenodinium* also were shown to be characteristic of the low light-induced responses of the red tide dinoflagellate, *Gonyaulax polyedra* (Prézelin and Sweeney, 1978).

In comparison to light intensity studies, when *Glenodinium* sp. was cultured at a constant light level but on a light-dark cycle, daily periodicities in $P_{max}$ $cell^{-1}$ and $P_{max}$ chl $a^{-1}$ were observed. Under these steady-state conditions the pigmentation per cell, including chl *a*, chl *c*, and peridinin, did not change. These characteristics are identical for a growing number of phytoplankters whose daily periodicity of photosynthesis is regulated by a biological clock (Prézelin *et al.*, 1977; Harding *et al.*, 1980; Prézelin and Ley, 1980). Furthermore, present studies with *Glenodinium* sp. have indicated light-limited photosynthesis also changed over the day in direct proportion to light-saturated photosynthesis. Therefore, in *Glenodinium* sp. the photosynthetic potential, expressed either as $P_{max}$ $cell^{-1}$ or $P_{max}$ chl $a^{-1}$, changed over the day in direct relationship to the light-limited slope ($\alpha$) of the P-I curves, expressed either as $\alpha$ $cell^{-1}$ or $\alpha$ chl $a^{-1}$. These 2 parameters, $P_{max}$ and $\alpha$, taken together provide predictable indicators of diurnal regulation of photosynthesis in these phytoplankters. A similar relationship already has been documented for *G. polyedra* and suggested in mixed field samples of phytoplankton (Prézelin and Sweeney, 1978; Prézelin and Ley, 1980). A biological basis of this close relationship in dinoflagellates has been proposed (Prézelin and Sweeney, 1977) and regulatory aspects examined in some detail (Govindjee *et al.*, 1979; Sweeney *et al.*, 1979). What is important in the present study is that, because of the close relationship between $P_{max}$ and $\alpha$ over the day in such steady-state populations, there is no periodic effect on the light intensity at which photosynthesis is half-saturated (Fig. 2). Thus any observed changes in half-saturation constants of the P-I curves of these organisms cannot be explained by the light-dark cycle itself, and in the present study, was shown to respond quickly to changes variable in growth illumination.

One of the most interesting results of the present study was the observation that the time-course of photoadaptation and the nature of the short-term responses of the photosynthesis-irradiance relationship was different, depending on 1) whether the light shift was from high to low or *vice versa* and 2) whether the high light levels were sufficient to promote maximal photosynthesis rates.

"High to low" light photoadaption occurred quickly. Full photosynthetic response occurred within 12 h of the light shift, much faster than the estimated 5 d generation time at low light levels. Within 3 h the pigment content of the cell began to increase rapidly. However, it was the rapid increase in a single type of light-harvesting component, PCP, that is the cause for the large increase in pigment content and enhanced cell absorption (Figs. 4 and 5). For example, the amount of PCP in the cells in one experiment rose 11-fold in 5 d and then fell to a steady-state level 4-fold higher than high light concentrations. By comparison, the increases in chl *a* and chl *c* were much slower, more modest in amount, and fluctuated up and down over a 30 d period before reaching a steady-state level about 1.5 to 2.0-fold higher than in high light cells. Thus, chl *a* values would not be a good indicator of the photoadaptive state of these types of phytoplankton.

Second, the increase in PCP most likely represented an increase in the antenna pigments associated with a fixed number of photosynthetic units in the cells, as shown in earlier studies on *Glenodinium* sp. cultures at different light levels (Prézelin, 1976; Prézelin *et al*, 1976; Prézelin and Albeite, 1978). This increase in antenna size can be related to the rapid decline in $P_{max}$ chl $a^{-1}$ (within 6 h after the increased synthesis of PCP), a maintenance of $P_{max}$ $cell^{-1}$, an increase in the light-limited slope ($\alpha$) of the P-I/cell (within 12 h), and a decrease in the light-limited slope of the P-I chl $a^{-1}$ (within 6 h) as the increased pigment content lowered the apparent relative quantum yield of photosynthesis (Fig. 9a, b). In contrast, earlier studies comparing cultures grown for some time at different light intensities showed $\alpha$ chl $a^{-1}$ to be the same in all samples (Prézelin, 1976). This observation suggests that the initial changes in $\alpha$ chl $a^{-1}$ seen in the present study, and presumably a direct result of immediate synthesis of PCP and increased photon capture, are eventually reversed by some additional photoadaptive mechanism which keeps the relative quantum yield of photosynthesis about the same over widely varying light

regimes. It is the changes in the light-limited slope $\alpha$ cell$^{-1}$ which determines the light-limited rates of cellular photosynthesis and the optimal light-limited growth rates of the cells. Thus, it can be appreciated how important a fast response to maximize light-limited photosynthesis may be to the survival of dinoflagellates in natural low light habitats.

"Low to high" transfer however is not a simple and fast reversal of mechanisms outlined above, although the transition to the prior high light P-I relationship is eventually made (Prézelin, 1976). First, pigment content immediately fell only if the high light level was high enough to light-saturate photosynthesis (*i.e.* 5000 $\mu$W cm$^2$). In this case, pigment content of the cells declined at a rate proportional to the growth rate, suggesting pigment synthesis slowed and pigment content was reduced by dilution as cells divided. If increased light levels were not sufficient to light-saturate photosynthesis completely (*i.e.* 2500 $\mu$W cm$^2$), then the pigment content fell much more slowly than rates of increased growth.

In both cases of transfer back to high light, optimal growth rates were not established until several days after transfer. Thus the rate of pigment synthesis, and in this case presumably the size of the PSU, were very closely tied to the degree of photosynthetic light-limitation the cells were experiencing. Also, it was apparent that the specific parameters of the P-I curves did not simply reverse either (Fig. 9). For instance, we expected $P_{max}$ chl $a^{-1}$ to increase in high light, because we expected pigmentation to decline but it stayed the same during the first 80 h at higher growth illumination. However, $\alpha$ cell$^{-1}$ did fall back to lower values within 1 d, as we would have predicted (Fig. 9c), while $\alpha$ chl $a^{-1}$, which should have increased, actually declined further (Fig. 9d). The surprising effect was to reverse the values for the half-saturation constants (Fig. 10) to previous high light values, but "not" by a simple reversal of the low light response. The mechanisms underlying these initial responses are not yet fully understood and are the subject of additional experimentation.

Finally, a predictable indicator of the photoadaptive state of dinoflagellates, unaffected by periodicity of light:dark cycles, is suggested. Since the photoadaptive capabilities of dinoflagellates is dependent on abilities to optimize light-limited photosynthesis, a strong indicator should be some parameter of the light-limited portion of the P-I curve. However, $\alpha$ cell$^{-1}$ and $\alpha$ chl $a^{-1}$ are subject to periodicity over the day (Fig. 10) and thus subject to regulation by a circadian biological clock (Prézelin *et al.*, 1977; Prézelin and Sweeney, 1977; Prézelin and Ley, 1980). But the half-saturation constants for photosynthesis, I = 1/2 $P_{max}$ cell$^{-1}$ and I = 1/2 $P_{max}$ chl $a^{-1}$ are *not* influenced by the light:dark cycle (Fig. 10) and prove to be reliable indicators of photoadaptive state of some types of phytoplankton. Since the photosynthetic physiology of the dinoflagellate *Gonyaulax polyedra* with regard to periodicity and light intensity is so similar to *Glenodinium* sp., it might be predicted that *G. polyedra* and other phytoplankton which photoadapt similarly should also respond quickly and similarly to changes in growth illumination.

Few studies on the rates of photoadaptive responses have previously been completed. Steeman-Nielson (1962) looked at photoadaptation phenomen in *Chlorella vulgaris* and found that high light cells exposed to low light conditions did not increase pigmentation within the first 48 h. However, the recalculated half-saturation constant for photosynthesis, I = ½ $P_{max}$ cell$^{-1}$, did show a shift gradually from about 8 to 2.5 klux over a 17 h period. Obviously, the mechanisms for accommodation to low light levels in *C. vulgaris* was different, but only a little slower in response time, when compared to *Glenodinium* sp. Since $P_{max}$ cell$^{-1}$ and $P_{max}$ chl $a^{-1}$ did not shift appreciably within the first 48 h, but light-limited slopes increased slowly, mechanisms involving turnover times, rather than increased size or density of PSU, were probably involved in initial photoadaptive responses of *C. vulgaris*. Therefore it is difficult to compare the time-course results directly with the present study. It is known that low light *C. vulgaris* cells eventually did accumulate large amounts of pigments. But, since these low light cells were larger in size, it is likely that increased pigmentation was a result of reduced cell division rather than increased rates of pigment synthesis (Steeman-Nielson, 1962).

Brooks (1964) looked extensively at the rates of photoadaptation in 2 marine phytoplankton species, the green alga *Dunaliella tertiolecta* and the diatom *Skeletonema costatum*. Values for $P_{max}$ cell$^{-1}$, $P_{max}$ chl $a^{-1}$, pigment content and pigment ratios, and values for the Tallings constant, $I_k$, were presented and expressed on a per cell basis. The results for both organisms were quite similar, showing fast pigmentation and photosynthetic responses to both increasing and decreasing light levels. When light levels were altered significantly there was an immediate change in pigment content and pigment molar ratios of chl *a*:carotenoid, which appeared to stabilize over a long period of from 30 to more than 100 h later. Also, there was an observed change in $P_{max}$ chl $a^{-1}$. that was in direct proportion to the change in chl *a* concentration and no change at all in $P_{max}$ cell$^{-1}$. In addition, the $I_k$ values fell when light levels increased, and *vice versa*; and the time course for $I_k$ changes were much less than those for pigmentation changes. These results were interesting as they were identical to the kinds of photoadaptive responses seen in *Glenodinium* sp. It suggested that *D. tertiolecta* and *S. costatum* may also photoadapt by altering the size and composition of existing numbers of PSU, and that such phytoplankton can bring about photoinduced changes in photosynthesis very quickly and thus accommodate widely fluctuating light regimes. It should be noted that a recent note by Falkowski and Owens (1979) suggested that *S. costatum* photoadapted by increasing PSU size. This is consistent with the earlier study of Brooks (1964), and ongoing studes suggest the

photoadaptive response time of *S. costatum* may be much faster than previously reported (Prézelin *et al.*, in preparation). A fast photoadaptation time response on the order of a generation time (10 h) has also been reported for *Lauderia borealis* (Marra, 1980).

Overall, some interesting insights have been gained into how light level induces changes in the photosynthetic apparatus of a typical marine dinoflagellate, how quickly such changes come about, and what effect these changes have on the overall P-I relationship and growth potential of these phytoplankton populations. Tentatively, these responses appear to occur in members of different phytoplankton groups which display a similar photoadaptive "strategy". What is not known is how widespread this particular photoadaptive "strategy" is in the phytoplankton populations, and whether phytoplankton suspected of photoadapting by alternative mechanisms (*i.e.* changing PSU number altering relative quantum efficiencies, changing photosynthetic turnover times) can do so quickly. Also it is important to note that the time course for such responses do appear to depend on whether light levels are limiting or saturating in intensity for photosynthesis. The ecological significance of such studies appears important, providing information on how fast and by what means phytoplankton quickly alter photosynthetic potentials to favor optimum growth over a wide range of light levels. Furthermore, identification of photosynthetic parameters sensitive to the photoadaptive state of the cell, and independent of modification by the light-dark cycle, may prove useful in future attempts to determine light status of *in situ* phytoplankton populations.

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