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Photosynthetic parameters of arctic marine phytoplankton: Vertical variations and time scales of adaptation

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Abstract

In the eastern Canadian arctic the photosynthesis-irradiance curves of phytoplankton from the 50% and 1% light levels differ mainly in their susceptibility to photoinhibition. The photoinhibition parameters of deep populations and the intensity of the deep chlorophyll maximum were correlated with N^2, the bulk stratification parameter of the water column. Comparison of data from the same region in different periods suggests that the characteristic susceptibility to photoinhibition requires 2–6 weeks to develop once a population is isolated below a pycnocline.

Insensitivity to photoinhibition developed much more quickly when a population from the chlorophyll maximum was exposed to surface light. The threshold of photoinhibition increased rapidly, reaching surface intensities within 4–6 h. The adaptation is sufficiently rapid that phytoplankton from the chlorophyll maximum should be stressed only briefly when transported to the surface by a mixed-layer-deepening event.

It has been known for some time from both laboratory and field studies that marine phytoplankton demonstrate considerable flexibility in the curve relating their photosynthetic rate to light intensity (Steemann Nielsen and Hansen 1959; Ryther and Menzel 1959; Yentsch and Lee 1966). Various conditions in the growth environment of phytoplankton may alter their photosynthetic response to light, but most attention has been focused on the influence of available light, and the process has been called light-shade adaptation. In the field the adaptability of the photosynthesis-irradiance (*P-I*) response is manifested by vertical variations in the parameters characterizing the curve. Typically, for differences to be observed, samples must be separated by a pycnocline which provides an effective barrier to mixing (Ryther and Menzel 1959; Savidge 1979; Falkowski 1981; Platt et al. 1982).

Most studies of light-shade adaptation have emphasized the parameters of the *P-I* curve that determine the rate of photosynthesis at limiting and saturating intensities. Generally, growth at low light intensity results in a lower intensity needed to saturate photosynthesis (usually expressed as I_k, the intensity at which extrapolation of the initial slope of the *P-I* curve intersects the maximum rate: Talling 1957) and a lower rate of photosynthesis at saturating intensities (Yentsch and Lee 1966; Beardall and Morris 1976). More recently the physiological mechanisms by which these changes take place have been identified as adjustments in either the size or the numbers of photosynthetic units (Prézelin and Sweeney 1978; Falkowski and Owens 1980; Falkowski 1981; Perry et al. 1981); it has been shown that phytoplankton isolated in environments of low light availability maintain higher growth rates than would be possible if these changes did not take place (Falkowski 1980; Perry et al. 1981).

In a set of experiments from Baffin Bay of the eastern Canadian arctic, Platt et al. (1982) found that samples from the depths of penetration of 50% and 1% of the surface irradiance were virtually indistinguishable with respect to I_k. Average values of the maximum photosynthetic rate normalized to Chl *a* concentration, P_m^B, were lower for populations from the 1% light level, but ranges overlapped. The most pronounced and reproducible differences

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between populations from the two levels in this region were at the optimal intensity for photosynthesis and for susceptibility to inhibition at high irradiance (*see also* Ryther and Menzel 1959; Huntsman and Barber 1977). Deep populations were readily inhibited by near-surface light intensities, whereas shallow populations were virtually uninhibited by intensities as high as are likely to be found anywhere.

In a later cruise to the eastern Canadian arctic in summer 1980 we were interested in the temporal stability of the parameters characterizing the populations' response to optimal and supraoptimal light. In particular we wanted to know how long the susceptibility to photoinhibition takes to develop, and how quickly it is reversed. The questions are significant because transport of phytoplankton from the 1% light levels to surface conditions could transfer the organisms from the stress of light limitation to light inhibition. Any adverse effect on growth rate would then depend on how quickly the curve recovers after such a transfer.

We investigated the time scales for the parameter adjustments by two approaches: phytoplankton growing at either high light in the surface mixed layer or near the bottom of the euphotic zone below the pycnocline were transferred to the opposite light regimes in containers on the deck of the ship and *P-I* curves monitored at intervals following the transfers; and vertical variations in *P-I* parameters were examined in relation to the local density structure of the water column. The approaches are related because the vertical variations of the photosynthetic parameters depend on a balance between the rate at which phytoplankton respond to changes in their environment and the rate at which vertical mixing tends to redistribute the organisms.

Our results indicate that although the susceptibility to photoinhibition develops only slowly (time scale ≈ several weeks) it is reversed rapidly (time scale ≈ several hours). When considered in the context of physical processes that redistribute phytoplankton, we conclude that deep populations would be only briefly (if ever) stressed by transport to the surface.

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Methods

All samples were collected in 30-liter Niskin bottles. For time-course experiments, samples were collected from 10 m and within the surface mixed layer, or from below the pycnocline at the depth of penetration of 1% of surface irradiance as roughly indicated by Secchi depth reading, or from the deep chlorophyll maximum as revealed by in vivo fluorescence on a pumped sample. A subsample was used for initial biomass measurements, principally Chl *a*. The rest was put into several 10-liter Pyrex jars (either clear or made opaque with black polyethylene) sealed with silicone stoppers and placed in a tub of flowing seawater on the deck of the ship. In one experiment, a 10-liter portion of a deep sample was immediately exposed to surface light and an additional 10 liters of the same sample was held in darkness for 6 h before exposure to surface light. This was an attempt to separate diel, endogenous regulating processes that might depend on the time of day from effects of the imposed light-shift.

At predetermined intervals, 4.6 liters were removed from the jars, 2.6 liters were used for photosynthesis measurements, and replicate subsamples of 750 ml were filtered on GF/C glass-fiber filters for chlorophyll determinations. Filters were stored frozen at −21°C for 1–5 d, then extracted in 85% acetone for 24 h in darkness at 4°C. Extracts were assayed aboard ship for Chl *a* by the fluorometric method of Yentsch and Menzel (1963).

For photosynthesis measurements, a portion of sample was inoculated with

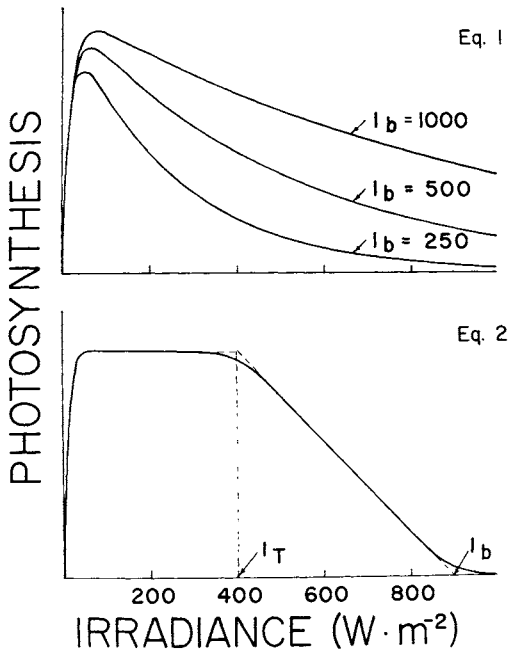

Fig. 1. Above: *P-I* curves described by Eq. 1 for three different values of photoinhibition parameter, $I_b \cdot P_S^B = 1.0$; $\alpha = 0.05$. Below: interpretation of threshold of photoinhibition, I_T, and photoinhibition parameter, I_b, for *P-I* curves described by Eq. 2. $P_S^B = 0.85$, $\alpha = 0.05$, $I'_b = 650$, $I'_T = 250$.

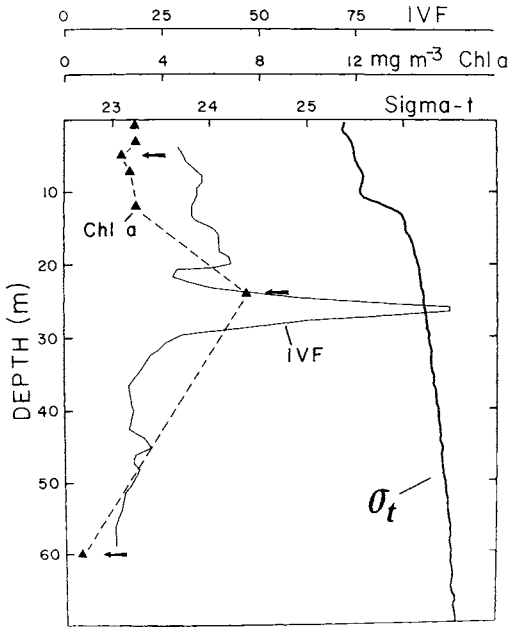

Fig. 2. Vertical profiles of extracted Chl *a*, in vivo fluorescence (IVF), and density (σ_t) at station 67 in Lancaster Sound. Arrows indicate depths at which *P-I* curves were measured.

$H^{14}CO_3^-$ to a concentration of about 0.05 μCi·ml^{-1}, and 100 ml was dispensed into each of a number of 125-ml Pyrex bottles; 22–26 bottles were used for time-course experiments, and 43 for depth profiles. The bottles were incubated for 2 h in linear incubators (Platt et al. 1980). Contents of the bottles were filtered onto 0.45-μm Millipore membrane filters and assayed for radioactivity (Platt et al. 1980).

Photosynthesis normalized to chlorophyll, P^B, was described by one of the following equations (Platt et al. 1980; Platt and Gallegos 1980)

$$P^B = P_S^B[1 - \exp(-\alpha I/P_S^B)] \cdot \exp(-\beta I/P_S^B) \quad (1)$$

or

$$P^B = (P_S^B/2)\tanh(\alpha I/P_S^B) \cdot \left\{1 - \frac{I - I'_b}{[(I - I'_b)^8 + I'^8_T]^{1/8}}\right\}. \quad (2)$$

Two equations are needed to accommodate the various shapes of curves encountered (Fig. 1). The parameter P_S^B(mg C·mg Chl a^{-1}·h^{-1}) sets the overall magnitude of the curve, α[mg C·mg Chl a^{-1}·h^{-1}·(W·m^{-2})$^{-1}$] is the initial slope, and β (same units as α) controls the strength of photoinhibition in Eq. 1. In Eq. 2, I'_b and I'_T (W·m^{-2}) are characteristic intensities that fix the onset and strength of photoinhibition. Procedures for discriminating between Eq. 1 and 2 and for estimating parameters are given by Gallegos and Platt (1981).

Two derived parameters best characterize the susceptibility to photoinhibition: the minimum or threshold intensity, I_T, at which photoinhibition begins, and the intensity, I_b, at which extrapolation of initial slope of the inhibited portion of the curve intersects zero on the photosynthesis axis. Smaller values of I_b and I_T indicate greater susceptibility to photoinhibition (Fig. 1). In Eq. 1, photosynthesis is maximal at a unique irradiance; in this case the optimal irradiance is iden-

tical with I_T. Identities for calculating I_T and I_b from the primary parameters have been given (Platt et al. 1980; Platt and Gallegos 1980).

Results

Transfer from low to high light—In Lancaster Sound we encountered a well defined deep chlorophyll maximum (DCM) at a depth of 24 m, just below a sharp density discontinuity (Fig. 2). The depth of the DCM coincided approximately with the 1% light level as indicated by Secchi depth. Photosynthesis-irradiance curves of samples from above, within, and below the DCM measured immediately after sampling are illustrated in Fig. 3. Populations from the surface layer were only slightly susceptible to photoinhibition, as indicated by a value of $I_b > 1{,}000$ W·m^{-2} (Table 1), and populations from the DCM were strongly inhibited by surface light, $I_b < 300$ W·m^{-2} (Fig. 3, Table 1). The sample from the aphotic zone, 60 m, appeared to be highly stressed with $P_m{}^B < 0.25$ mg C·mg Chl^{-1}·h^{-1}.

At a nearby station we put a sample from 24 m into a 10-liter Pyrex bottle, exposed it to surface light, and determined *P-I* parameters at 2-h intervals for 6 h (Fig. 4A, Table 2). During that time both $P_m{}^B$ and I_T increased. After 4 h exposure to surface light I_T was as high as the median of the range of intensities received on the deck of the ship. As a consequence, photosynthetic performance (i.e. photosynthetic rate at surface intensities) inferred from the *P-I* curves increased linearly with time (Fig. 4B); at the end of 6 h, photosynthetic performance was more than double its initial value, even though $P_m{}^B$ only increased 35%.

A sample held in darkness during this time was then exposed to surface light for another 6 h, with *P-I* curves determined initially and at 2-h intervals. The maximum photosynthetic rate again increased, as did the threshold intensity for photoinhibition and the photosynthetic performance at surface intensities (Table 2). The increases were less pronounced than during the first 6 h, possibly due to

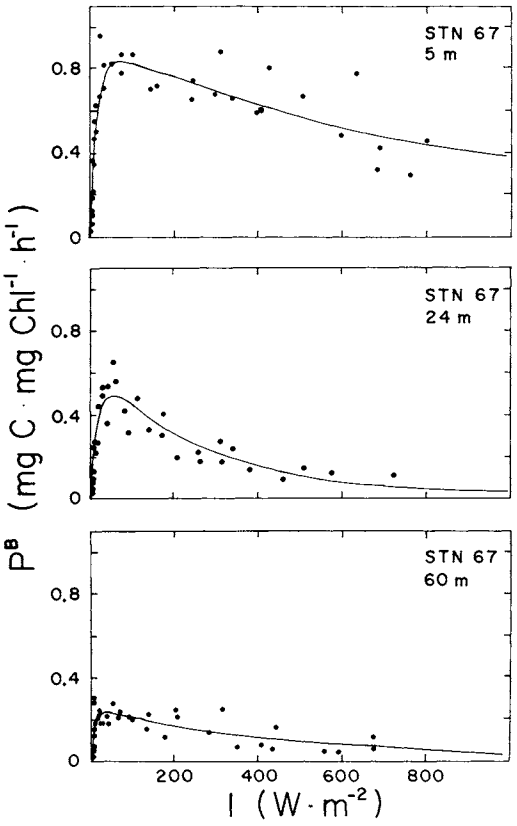

Fig. 3. Photosynthesis-irradiance curves of phytoplankton from three depths at station 67 in Lancaster Sound.

the prolonged containment; but also the range of irradiances during the second 6 h was considerably lower than during the first 6 h. The difference between the curves for samples held 6 h in the dark and 6 h at surface light (Fig. 4A) indicate that the changes during the first 6 h of exposure were induced by the light shift and were not due to a diurnal rhythm independent of the recent light history of the phytoplankton.

Transfer from high to low light—At a station in Baffin Bay (station 22: Table 1) a sample from 10 m was placed in an opaque container and *P-I* curves determined after 12, 24, and 48 h (Fig. 5, Table 1). The pronounced susceptibility to photoinhibition did not develop during that time. Light-saturated photosynthetic rates, while higher than the initial maxi-

Table 1. Vertical variations in extracted Chl *a* and photosynthetic parameters for stations in Lancaster Sound, Baffin Bay, Jones Sound, and Kane Basin (z_m—mixed layer depth; z_s—sampling depth).

Location	z_m	% I_0	z_s	Chl *a*	P_S^B*	α†	$10^3\beta$‡	I'_b‡	I'_T‡	P_m^B*	I_T‡	I_b‡
Lancaster Sound												
Station 67		38	5	2.43	0.90	0.036	0.80			0.81	59	1,128
74°26.3′N, 86°3′W	11	1	24	9.51	0.66	0.029	2.56			0.49	58	260
		0.001	60	0.68	0.24	0.056	0.45			0.23	20.5	532
Station 82		—	5	8.13	0.80	0.054		639	298	0.80	341	937
74°3′N, 93°39′W	2	—	10	8.92	0.95	0.053	1.16			0.86	69	821
		—	25	15.02	1.09	0.054	1.91			0.93	68	570
Station 103		30	10	0.62	0.83	0.033		731	304	0.83	427	1,035
73°37.6′N, 74°54.9′W	6	9	20	3.22	0.66	0.048	2.87			0.52	39	230
		1	40	2.39	0.55	0.044	2.56			0.44	36	215
Baffin Bay												
Station 4		46	5	0.51	1.50	0.038	0.806			1.36	153	1,870
67°22′N, 56°26′W	§	0.5	35	1.19	1.50	0.052	3.01			1.20	84	500
		0.01	64	0.19	0.15	0.004	0.400			0.11	93	387
Station 7		30	8	0.44	2.42	0.109		659	310	2.41	349	969
74°55′N, 65°52.5′W	§	2	25	0.43	1.13	0.102	1.79			1.04	45	634
		0.2	40	0.34	1.58	0.140	0.985			1.52	56	1,609
Station 22		30	10	0.45	0.76	0.030	0.451			0.70	105	1,670
75°54′N, 68°4′W	15	5	20	0.68	0.80	0.028	1.06			0.68	95	754
		0.01	60	0.26	0.47	0.027	3.82			0.31	36	124
Station 52		6	20	0.66	0.66	0.070		636	283	0.66	353	919
73°52.6′N, 81°47.5′W	4	2	30	0.62	0.76	0.029		692	260	0.76	432	952
		0.02	60	0.26	0.35	0.043	0.736			0.32	33	469
Jones Sound/Kane Basin												
Station 148		18	10	3.02	0.67	0.040		750	328	0.67	421	1,078
78°19.3′N, 74°54.9′W	23	1	30	2.60	0.85	0.040		708	465	0.85	243	1,173
		0.1	40	2.02	0.94	0.044	1.65			0.81	74	590
Station 156		15	10	4.98	0.76	0.062	0.896			0.70	52	843
79°46.9′N, 69°29.5′W	15	0.3	30	3.36	0.62	0.037	1.02			0.54	60	606
		0.05	40	0.60	0.36	0.060	0.584			0.34	28	609

* Units, mg C mg Chl $a^{-1}\cdot h^{-1}$.
† Units, mg C·mg Chl $a^{-1}\cdot(W\cdot m^{-2})^{-1}\cdot h^{-1}$.
‡ Units, $W\cdot m^{-2}$.
§ CTD not available.

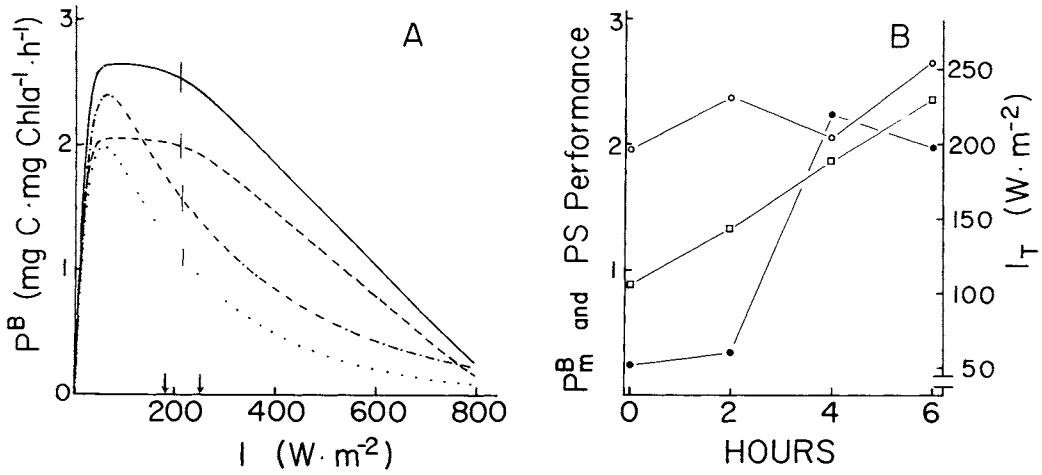

Fig. 4. A: Photosynthesis-irradiance curves of phytoplankton from 24 m in Lancaster Sound held 6 h in darkness (· · · · ·), and after 2 (– · – · –), 4 (– – –), and 6 (———) h at surface light. Arrows on abscissa show range of irradiance during exposure. Error bars are ±2 SE. B: Time-course of variations in P_m^B (○), photosynthetic (PS) performance (□), and I_T (●) for curves in panel A.

mum rate, did not change after the first 12 h. The difference between the initial P_m^B and all subsequent curves is probably due to a difference in temperature. For the initial curve the sample was incubated close to its in situ temperature at the time of sampling (sample temp, 0.9°C; incubation temp, 0.3°C). Subsequent curves were determined at the temperature of the ship's seawater system (≈3°C), which was also used for regulating the temperature of the sample during containment.

Depth profiles of photosynthetic parameters—Consideration of the depth-dependent differences in photosynthetic parameters in relation to the local stratification and chlorophyll structure may give some indirect information concerning the time scale for the formation of the pronounced susceptibility to photoinhibition by deep populations. The contrast between the *P-I* curves of populations from 5 and 24 m at station 67 in Lancaster Sound (Fig. 3) is typical of depth-related differences observed previously and ubiquitous in Baffin Bay in 1978 (Platt et al. 1982). On this cruise we surveyed a wider geographic region earlier during the arctic summer (24 July–26 August 1980, opposed to 26 August–14 September 1978); the depth profiles of photosynthetic parameters were more varied than observed before. For example, at station 52 in Baffin Bay at the mouth of Lancaster Sound (Fig. 6) we found a shallow mixed layer (≈5 m), below which was a weak fluorescence gradient, with a maximum at 30 m, which did not parallel the more uniform profile of extracted Chl *a* (Fig. 6). The *P-I* curves of populations from 20 and 30 m (Fig. 7) were not significantly different from each other (Table 2) and had characteristics of surface populations: $I_T \gtrsim 300$ W·m^{-2}, $I_b \geqslant 900$ W·m^{-2}. At this station we also did a time-course experiment on the sample from 30 m, such as was done at station 67 (Table 2). The threshold of photoinhibition, I_T, remained roughly constant above 300 W·m^{-2} during the first 4–6 h at surface light and declined to about 220 W·m^{-2} between 6 and 8 h, but I_T was greater than surface incident irradiance at all times during the exposure (Table 2). The maximum photosynthetic rate varied only slightly with time, and since surface irradiance was saturating but not inhibiting, photosynthetic performance was likewise constant and identical with P_m^B.

Table 2. Time-course of variations in photosynthetic parameters for samples exposed to surface light or kept in darkness (I_0—range of irradiance experienced during exposure).

Location	z_e	I_0*	Hours after exp	Chl a	P_S†	α‡	$10^3\beta$‡	I'_b*	I'_T*	$P_m{}^B$†	I_T*	I_b*
Lancaster Sound			2	5.0	3.16	0.14	1.05			2.39	62	300
Station 65	25	120–260	4	5.31	2.05	0.11		528	308	2.05	220	816
74°21.2′N, 86°9.5′W			6	4.83	2.65	0.13		526	328	2.65	198	854
			6 h dark	4.78	2.75	0.12	11.9			1.97	55	231
			+2	5.17	2.86	0.08	8.99			1.99	82	318
	25	18–188	+4	5.38	2.53	0.14	6.07			2.42	56	417
			+6	5.38	2.98	0.12	7.11			2.38	70	419
Baffin Bay			0	0.45	0.76	0.030	0.451			0.70	105	1,670
Station 22			12	0.42	1.08	0.045	0.0			1.08	§	§
	10	Dark	24	0.42	1.10	0.062	0.0			1.10	§	§
			48	0.34	1.00	0.044	0.0			1.00	§	§
			0	0.62	0.76	0.029		692	260	0.76	432	952
Baffin Bay			2	0.62	0.81	0.052		660	309	0.81	351	969
Station 52	30	106–261	4	0.58	1.03	0.068		696	317	1.03	379	1,013
			6	0.67	0.85	0.079		757	452	0.85	305	1,209
			8	0.67	0.66	0.032		579	353	0.66	226	932

* Units, $W \cdot m^{-2}$.
† Units, mg C·mg Chl $a^{-1} \cdot h^{-1}$.
‡ Units, mg C·mg Chl $a^{-1} \cdot (W \cdot m^{-2})^{-1} \cdot h^{-1}$.
§ Undefined when $\beta = 0$.

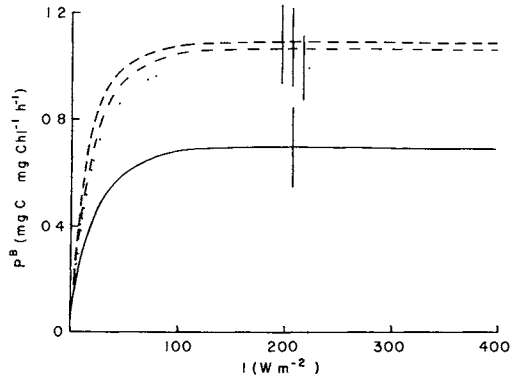

Fig. 5. Photosynthesis-irradiance curves of phytoplankton from 10 m in Baffin Bay immediately after sampling (———) (T = 0.3°C), and after 12 (–·–·–), 24 (– – –), and 48 (· · · · ·) h of darkness (T = 3.5°C, *see text*).

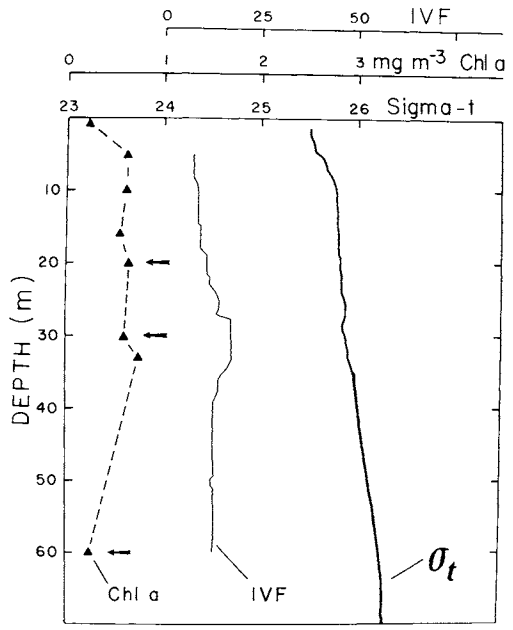

Fig. 6. As Fig. 2, but at station 52 in Baffin Bay.

At station 52 both the initial profile of photosynthetic parameters and the time-course of variations after a shift in irradiance indicate that the population from 30 m was fully adapted to surface conditions, even though isolated below a pycnocline. Although we cannot estimate the time since the population at 30 m was isolated, the intensity of vertical stratification is an index of that time. In this region the pycnocline is established soon after the breakup of ice; stratification intensifies with time as melting and surface warming continue. In Fig. 8 is plotted the index of susceptibility to photoinhibition, I_b, for samples from 20–30 m, as a function of N^2—the bulk stratification (or buoyancy) parameter; N^2 was computed as $(g/\rho) \times (\Delta\rho/\Delta z)$, where $\Delta\rho/\Delta z$ is the mean density gradient across the primary interface. The least susceptibility to photoinhibition among deep populations occurs at stations with the weakest density stratification (smallest N^2) and susceptibility to photoinhibition increases as stratification intensifies. The data of Platt et al. (1982; open circles, Fig. 8) occur as a continuation of this trend, with deep populations highly susceptible to photoinhibition ($I_b < 400$ W·m^{-2}) and stratification intense ($N^2 > 2.5 \times 10^{-3}$·s^{-2}). Also plotted as a function of N^2 in Fig. 8 is the ratio of the mean chlorophyll concentration in the mixed layer to the chlorophyll concentration at the 1% light level. The relationship of the chlorophyll ratio to the bulk N^2 is very similar to the relationship between I_b and N^2. This suggests that the time scale for development of the DCM is similar to that of susceptibility to photoinhibition among populations at the 1% light level.

Discussion

We cannot determine with precision the length of time required for the vertical patterns of photosynthetic parameters to develop. From the time-course experiments in which surface populations were contained in darkness (Fig. 5) we determine a lower bound of 2 days. Talling (1957) found that in a culture of *Asterionella* susceptibility to photoinhibition developed after 6 days of dark containment. Platt et al. (1982) estimated that populations at the 1% light level in Baffin Bay during the first week in September had been isolated below the pycnocline

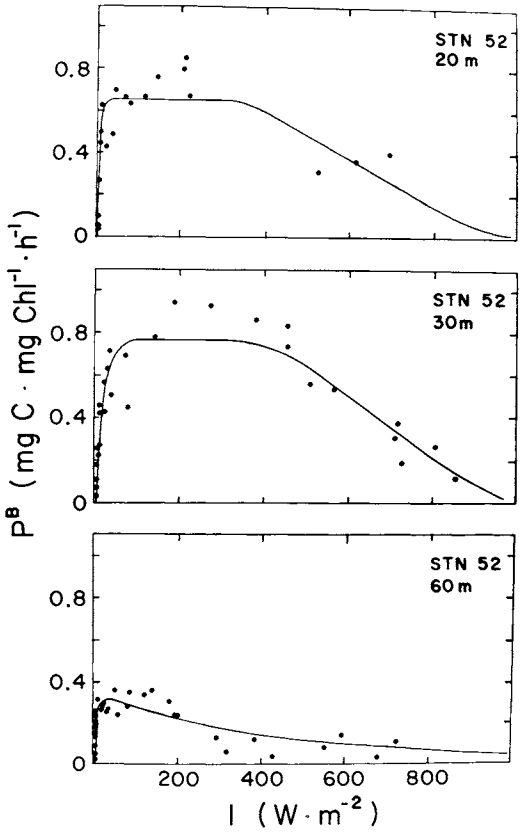

Fig. 7. As Fig. 3, but at station 52 in Baffin Bay.

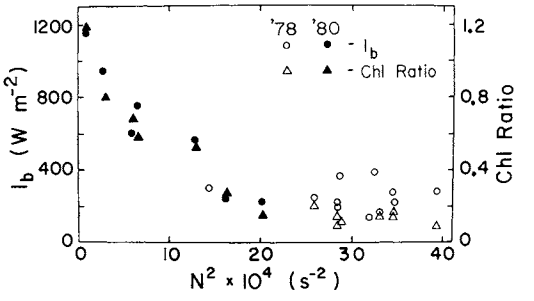

Fig. 8. Photoinhibition parameter, I_b, of samples from below the pycnocline, and the ratio (Chl ratio) of average chlorophyll concentration in the mixed layer : chlorophyll concentration at the 1% light level (an index of the intensity of the DCM) as a function of the bulk stratification parameter, N^2.

for a period ≳6 weeks. The consistent observation of vertical stratification in I_T and I_b in 1978 suggests 6 weeks for a probable upper limit for the development. We visited the region about 4 weeks earlier in 1980 and found that I_b and the presence of a DCM depended strongly on the water column stratification parameter (Fig. 8). Stratification was most intense (and hence I_b of deep populations was smallest) in Lancaster Sound. Ice charts for 1980 (Ice Forecasting Central, Ottawa) show that stations in Lancaster Sound had been free of ice for about 50 days before occupation, whereas stations in Baffin Bay had been free of ice for 7–30 days. Thus 3–6 weeks seems a more likely range of the time scale for development of the vertical variations in photosynthetic parameters.

Correlations between photosynthetic parameters and water column stability have been noted before. Harris et al. (1980) found that $P_m{}^B$ and I_k of phytoplankton in Hamilton Harbour increased with an index of water column stability at a lag of about 1 week. Demers and Legendre (1982) found that $P_m{}^B$ correlated with the density difference between 5 and 35 m in the St. Lawrence estuary. Those results were for shallow populations. Our results are for deep populations and suggest that the stratification, photosynthetic parameters, and chlorophyll structure coevolve in this region so that the correlation in Fig. 8 may not apply in other regions.

Although the time scale for development of the vertical structure is rather poorly defined, it is clearly longer than the time scale at which phytoplankton from the chlorophyll maximum adapt to high irradiance when exposed to the surface (Fig. 4). The substantially longer time for this characteristic to develop and its dependence on the intensity of stratification suggest that the ability by deep populations to photosynthesize at maximal rate at surface intensities is lost only slowly as the populations double at in situ light levels. Using growth rates reported in Harrison et al. (1982), Platt et al. (1982) estimated that populations from the 1% light level in Baffin Bay had been isolated below the pycnocline for ≈15 generations. Using the 3–6-week time scale estimated above, we find that ≈7–15 gen-

erations are required for phytoplankton at the 1% light level to develop the pronounced susceptibility to photoinhibition at surface intensities.

In contrast, $\ll 1$ generation time is required to eliminate the susceptibility to photoinhibition when populations from the chlorophyll maximum are exposed to the surface. A possible mechanism for the adaptation of the inhibition parameters could be the synthesis of carotenoid pigments which can quench the triplet excited state of chlorophyll and thereby protect the pigment against photooxidation (Junge 1977). Herron and Mauzerall (1972) measured a half-rise time of 13.5 h for carotenoid synthesis in a greening mutant of *Chlorella*. Although this is longer than the time required for I_T to equal surface intensities, it is possible that we truncated the measurements before the adaptation process had reached completion. Indeed, some values of I_T in Table 1 are >400 $W \cdot m^{-2}$, well in excess of irradiance levels ever experienced at these latitudes. The time needed for developing the capacity to utilize irradiance levels greater than those actually received is evidently >6 h.

The ecological significance of the parameter variations depends on the magnitude of time scales of physical processes that could result in such a shift in growth intensities relative to that of biological processes responsible for photoinhibition. In the samples from a strong chlorophyll maximum, photosynthesis was described by Eq. 1 and I_T was low, indicating the onset of photoinhibition at slightly greater than saturating intensities. These characteristics suggest that the time scales of the processes responsible for photoinhibition in these populations are short relative to incubation time. The process could be photochemical (e.g. Krinsky 1979), operating at fractions of a second, or physiological (e.g. chloroplast conformational changes: Kiefer 1973, or reversible inactivation of P700: Gerber and Burris 1981), with time scales of minutes to several hours.

The physical process most likely to transport significant quantities of phytoplankton to surface waters is a mixed-layer-deepening event. In the eastern Canadian arctic, the mixed layer penetration would have to reach a depth of ≈25 m to entrain organisms growing in the chlorophyll maximum. The time scale, T, of mixing is given by

$$T = h^2/2K_z$$

(where h is the mixed layer depth and K_z is a coefficient of vertical eddy diffusivity). For T to be comparable to the adaptation time scale, i.e. 4 h, with $h = 25$ m would require $K_z \approx 200$ $cm^2 \cdot s^{-1}$. The mixed layer model of Kundu (1980) with surface wave flux included and a surface stress of 1.5 $dyn \cdot cm^{-2}$ gives eddy coefficients of ≈300 $cm^2 \cdot s^{-1}$ near the surface, decreasing to molecular values below the density interface. Thus the rate at which the organisms are exposed to surface conditions could be comparable to, but not much shorter than, the rate at which they adapt to those conditions. Furthermore, these large eddy coefficients near the surface imply that the light regime to which entrained cells would be exposed is highly variable because of rapid motions in the vertical light gradient. This variable light might partially alleviate photoinhibition arising from processes acting at physiological (minutes to several hours) time scales (Harris 1978; Gallegos and Platt 1982). The duration of any stress incurred by photochemical effects would then be governed by the adaptation of I_T (Fig. 4) and thus should not greatly exceed about 6 h.

References

BEARDALL, J., AND I. MORRIS. 1976. The concept of light intensity adaptation in marine phytoplankton: Some experiments with *Phaeodactylum tricornutum*. Mar. Biol. **37:** 377–387.

DEMERS, S., AND L. LEGENDRE. 1982. Water column stability and photosynthetic capacity of estuarine phytoplankton: Long-term relationships. Mar. Ecol. Prog. Ser. **7:** 337–340.

FALKOWSKI, P. G. 1980. Light-shade adaptation in marine phytoplankton. Brookhaven Symp. Biol. **31:** 99–119. Plenum.

———. 1981. Light-shade adaptation and assimilation numbers. J. Plankton Res. **3:** 203–216.

———, AND T. G. OWENS. 1980. Light-shade adaptation: Two strategies in marine phytoplankton. Plant Physiol. **66:** 592–595.

GALLEGOS, C. L., AND T. PLATT. 1981. Photosynthesis measurements on natural populations of phytoplankton: Numerical analysis, p. 103–112. *In* Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210.

———, AND ———. 1982. Phytoplankton production and water motion in surface mixed layers. Deep-Sea Res. **29:** 65–76.

GERBER, D. W., AND J. E. BURRIS. 1981. Photoinhibition and P700 in the marine diatom *Amphora* sp. Plant Physiol. **68:** 699–702.

HARRIS, G. P. 1978. Photosynthesis, productivity and growth: The physiological ecology of phytoplankton. Ergeb. Limnol. **10:** 171 p.

———, G. D. HAFFNER, AND B. B. PICCININ. 1980. Physical variability and phytoplankton communities. 2. Primary productivity by phytoplankton in a physically variable environment. Arch. Hydrobiol. **88:** 393–425.

HARRISON, W. G., B. IRWIN, AND T. PLATT. 1982. Primary production and nutrient assimilation by natural phytoplankton populations of the eastern Canadian arctic. Can. J. Fish. Aquat. Sci. **39:** 335–345.

HERRON, H. A., AND D. MAUZERALL. 1972. The development of phytosynthesis in a greening mutant of *Chlorella* and an analysis of the light saturation curve. Plant Physiol. **50:** 141–148.

HUNTSMAN, S. A., AND R. T. BARBER. 1977. Primary production off northwest Africa: The relationship to wind and nutrient conditions. Deep-Sea Res. **24:** 25–34.

JUNGE, W. 1977. Aspects of light harvesting, electron transport and electrochemical potential generation in photosynthesis of green plants, p. 59–93. *In* Encyclopedia of plant physiology, v. 5. Springer.

KIEFER, D. A. 1973. Chlorophyll *a* fluorescence in marine centric diatoms: Responses of chloroplasts to light and nutrient stress. Mar. Biol. **23:** 39–46.

KRINSKY, N. I. 1979. Carotenoid pigments: Multiple mechanisms for coping with the stress of photosensitized oxidations, p. 163–187. *In* Strategies of microbial life in extreme environments, v. 13. Fisher.

KUNDU, P. K. 1980. A numerical investigation of mixed-layer dynamics. J. Phys. Oceanogr. **10:** 220–236.

PERRY, M. J., M. C. TALBOT, AND R. S. ALBERTE. 1981. Photoadaptation in marine phytoplankton: Response of the photosynthetic unit. Mar. Biol. **62:** 91–101.

PLATT, T., AND C. L. GALLEGOS. 1980. Modelling primary production. Brookhaven Symp. Biol. **31:** 339–362. Plenum.

———, ———, AND W. G. HARRISON. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J. Mar. Res. **38:** 687–701.

———, W. G. HARRISON, B. IRWIN, E. P. HORNE, AND C. L. GALLEGOS. 1982. Photosynthesis and photoadaptation of marine phytoplankton in the arctic. Deep-Sea Res. **29:** 1159–1170.

PRÉZELIN, B. B., AND B. M. SWEENEY. 1978. Photoadaptation of photosynthesis in *Gonyaulax polyedra*. Mar. Biol. **48:** 27–36.

RYTHER, J. H., AND D. W. MENZEL. 1959. Light adaptation by marine phytoplankton. Limnol. Oceanogr. **4:** 492–497.

SAVIDGE, G. 1979. Photosynthetic characteristics of marine phytoplankton from contrasting physical environments. Mar. Biol. **53:** 1–12.

STEEMANN NIELSEN, E., AND V. K. HANSEN. 1959. Light adaptation in marine phytoplankton populations and its interrelationship with temperature. Physiol. Plant. **12:** 353–370.

TALLING, J. F. 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. New Phytol. **56:** 29–50.

YENTSCH, C. S., AND R. W. LEE. 1966. A study of the photosynthetic light reactions, and a new interpretation of sun and shade phytoplankton. J. Mar. Res. **24:** 319–337.

———, AND D. W. MENZEL. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res. **10:** 221–231.

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