Limnol. Oceanogr., 44(3), 1999, 597–607

Carbon fixation by phytoplankton in high Arctic lakes: Implications of low temperature for photosynthesis

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Abstract

Photosynthesis vs. irradiance relationships were determined for phytoplankton communities from seven lakes in the Canadian high Arctic, including ultraoligotrophic Char Lake, nutrient-enriched Meretta Lake, and two meromictic lakes. The derived photosynthetic parameters were low for all samples, with a mean (±SD) light-saturated photosynthetic rate (P_m^B) of 0.46 (±0.28) g C g^{-1} chlorophyll *a* (Chl *a*) h^{-1} and a mean α^B (light-limitation parameter) of 1.23 (±0.56) g C g^{-1} Chl *a* m^2 mol^{-1}. The saturation irradiance (E_k) ranged from 50 to 196 μmol quanta m^{-2} s^{-1} and was positively correlated with mean irradiance for the water column. Quantum yields for photosynthesis in the Arctic lake phytoplankton were also low (mostly <10 mmol C mol^{-1} quanta). An intersystem comparison of α^B and P_m^B values with literature data for algae from other cold environments showed that the photosynthetic parameters for phytoplankton in Arctic and Antarctic lakes are three- to sixfold lower than for marine algae, ice algae, and cultures over the same low-temperature range. This may be the result of more severe nutrient stress in high-latitude lakes relative to polar marine environments and to the persistence of nonactive pigments in cold freshwaters.

Photosynthetic carbon uptake by phytoplankton is regulated by the dynamic interplay between cellular physiology and the supply of resources. Phytoplankton can optimize growth rate by adjusting their photosynthetic apparatus to the prevailing conditions of light (Falkowski 1980; Prézelin 1981) and nutrients (Geider et al. 1993). However, although the combined effects of light plus nutrient stress have been investigated under laboratory conditions (Kolber et al. 1988), less is known about natural phytoplankton in this regard (Cullen et al. 1992). Temperature is a basic property of the environment that directly affects photosynthetic processes as well as the ability of algae to adjust their photosynthetic apparatus to changes in resource availability. Oligotrophic lakes in the high-latitude regions are characterized by low nutrients and cold water and are therefore likely to present an extreme set of adverse conditions for phytoplankton photosynthesis and growth.

The objective of the present study was to measure light absorption and photosynthetic performance of the phytoplankton in a broad range of Arctic lakes and to evaluate these measurements in the context of other low-temperature systems. Seven lakes were selected in the Canadian high Arctic as extreme types of pelagic systems with persistent low temperatures, low-nutrient concentrations, and, for some of the lakes, deep mixing. We hypothesized that the measured values would represent a lower limit for phytoplankton performance in situ, and we addressed this hypothesis by way of comparisons with literature data for other cold-water and ice environments. The seven lakes were chosen to represent optically contrasting systems and widely different mixing regimes. These measurements of photosynthetic performance should encompass most conditions found within lakes of the high Arctic.

Materials and methods

Sampling sites—Sampling was conducted in lakes on Cornwallis Island and Little Cornwallis Island in the Queen Elizabeth Archipelago, high Arctic Canada (73–75°N, 92–95°W). The area has a cold, desert climate with a mean annual temperature of −15°C and an annual precipitation of 136 mm (McCann et al. 1972). The lakes in the area are only ice free for 1–10 weeks in July–September, depending on the local climate around the lake and the summer temperature. Some lakes in this region do not thaw out completely every year (Schindler et al. 1974*b*). Low temperatures and the low incident radiation associated with increasing cloud cover in July and August mean that the lakes often remain unstratified during the ice-free period.

Seven lakes were investigated between 3 and 13 August 1995. Four were cold freshwater lakes with a mean depth of ≤10.5 m (Table 1) and situated in the vicinity of Resolute Bay, Cornwallis Island. The mean depth of the fifth freshwater lake, Eleanor Lake on the far eastern side of Cornwallis Island, is unknown, but it is likely comparable to that of nearby Lake Sophia, which is 22 m (maximum depth = 50 m). Two meromictic lakes were also sampled, Lake Garrow (Little Cornwallis Island) and Lake Sophia. These lakes have a freshwater layer of 12–13 m on top of a monimolimnion with a salinity two- to threefold higher than the salinity of seawater. Lake Garrow receives process water from a nearby zinc-lead mine and is therefore highly turbid.

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Acknowledgments

This research was funded by The Danish Science Research Council (grant 9400292) and by the Natural Sciences and Engineering Research Council (Canada). Logistic support was provided by the Polar Continental Shelf Project (this is PCSP publication 003998). Additional funding for instrumentation was provided by The Carlsberg Foundation, Denmark. We are grateful to the staff of Polar Continental Shelf Project for its help and to the Polaris Mine for permission to work on Lake Garrow.

Table 1. Background limnological data for the seven high Arctic lakes.

Lake	Area (km²)	Depth (m)				K_d (m⁻¹)
		Mean	Maximum	Mixing	Secchi	
Char Lake	0.5	10.2	27.5	10.2[a]	6.0	0.14
Eleanor Lake	6.0	nd*	nd	22*†	4.5	0.24
Meretta Lake	0.2‡	3.25[c]	9	3.25*‡	6.8	0.26
North Lake	0.7	5§	11.6‖	5*	4.3	0.29
Resolute Lake	1.3	7§	15.6‖	7*	6.8	0.16
Lake Sophia	3.4	22.4	50	4	8.0	0.18,¶ 0.13#
Lake Garrow	4.3	22.9	49	3	1.85	0.50,** 0.21#

* Mixing depth is assumed to be equal to the mean depth in the well-mixed lakes; *see text.*
† No data available; the mean depth is assumed to be equal to the mean depth of Lake Sophia; the two lakes are similar in size and shape, and both are situated in valleys on the east coast of Cornwallis Island.
‡ Applies only to the northern basin where samples were taken.
§ Estimated from air photos and 10–15 depth measurements.
‖ Deepest value observed.
¶ Value for the mixolimnion.
# Values for the pycnocline.
** Value for the upper part of the mixolimnion.

The lakes are located on bedrock, mainly dolomite, or on marine deposits, and alkalinity was above 1 meq liter^{-1} in all the waters (Table 2). A particular feature of polar desert catchments is their sparse vegetation cover and resultant low concentrations of chromophoric dissolved organic matter (dissolved organic carbon [DOC] levels of <2 mg C liter^{-1}, Vincent 1997). Plants are virtually absent from the Char Lake catchment and are sparsely distributed around the other lakes as patches of lichens, *Salix arctica,* moss, and low herbs. Only Meretta Lake has a relatively dense vegetation in part of the watershed around a creek that received sewage effluent from the airfield in the 1970s. Char and Meretta Lakes were major study sites for the International Biological Program (IBP) in the 1970s, and there is extensive background literature on their limnology, e.g., Kalff and Welch (1974); Schindler et al. (1974*a,b*); Welch and Kalff (1974). Nutrient data from these studies showed that total phosphorus (TP) concentrations were between 2 and 14 μg liter^{-1} with dissolved reactive phosphorus (DRP) from below detection (<0.2 μg liter^{-1}) to 2 μg liter^{-1}. Total nitrogen (TN) concentrations ranged from 40 to 80 μg N liter^{-1} in Char Lake and 170 μg N liter^{-1} in Meretta Lake. Nutrient data obtained for the surface waters of the lakes during August 1994 were similar to these earlier ranges and are likely to be a reasonable guide to the nutrient conditions at the time of sampling in August 1995: TP concentrations were 8.4 (Char), 7.3 (North), and 7.1 (Meretta) μg P liter^{-1}; DRP concentrations were <0.2 (Char), 0.2 (North), and 0.3 (Meretta) μg P liter^{-1}; and TN concentrations were 89 (Char), 54 (North), and 200 (Meretta) μg N liter^{-1}. Although there is extensive literature on the geology and chemistry of the two meromictic lakes (e.g., Stewart and Platford 1986; Ouellet et al. 1987, 1989), little is known about their biology.

Sample collection—Samples were collected from an inflatable boat or a float-equipped helicopter over the central or deepest part of the lakes. Profiles of temperature, conductivity, and dissolved oxygen were measured with a Cole-

Table 2. Environmental, light absorption, and photosynthetic characteristics at two depths in the upper water column of seven high Arctic lakes. Units: temperature, °C; alkalinity, meq liter^{-1}; Chl *a,* mg m^{-3}; P_m^B, g C g^{-1} Chl *a* h^{-1}; α^B, g C g^{-1} Chl *a* m^2 mol^{-1} quanta; E_k and E_{mean}, μmol quanta m^{-2} s^{-1}; $\hat{a}_{ph}^B$, m^2 g^{-1} Chl *a*; a_{436}/a_{676}, $\hat{a}_{ph}(436)/\hat{a}_{ph}(676)$; ϕ, mmol C mol^{-1} quanta; —, no data.

Lake	Depth	Temp.	Alk.	E_{mean}	Chl *a*	P_m^B	α^B	E_k	$\hat{a}_{ph}^B$	a_{436}/a_{676}	ϕ
Char Lake	0.5	4.7	1.6	53.4	0.46	0.40	1.30	85	22.6	2.19	4.4
	15	4.5	1.5	53.4	0.78	0.16	0.70	62	16.8	2.12	3.2
Eleanor Lake	0.5	2.0	1.1	16.2	0.97	0.24	1.37	48	14.6	1.38	7.3
	20	1.7	1.1	16.2	1.02	0.43	2.30	52	14.8	1.70	12.1
Meretta Lake	0.5	5.5	1.2	67.2	1.11	0.77	1.30	163	15.0	2.73	6.6
	6	7.2	1.1	67.2	0.96	0.62	1.06	162	13.2	2.94	6.1
North Lake	0.5	6.0	1.3	51.0	0.86	0.31	0.78	111	20.3	2.35	2.9
Resolute Lake	0.5	4.5	1.5	55.6	1.00	0.27	0.63	119	18.3	2.56	2.6
	12	5.5	1.2	55.6	1.06	0.18	0.53	96	18.2	2.95	2.2
Lake Sophia	0.5	6.0	1.2	79.0	0.31	0.62	1.03	167	17.3	1.40	4.6
	12	6.8	3.7	23.6	1.24	0.38	2.12	50	8.2	1.34	20.8
Lake Garrow	0.5	5.2	1.7	52.9	0.40	1.12	1.60	196	16.7	1.68	7.8
	12	1.6	2.3	3.6	0.04	—*	—*	—*	—†	—†	—*†

* Light counts were indistinguishable from dark counts.
† The absorption spectrum of particles showed only weak absorption by pigments.

Palmer water analyzer probe. Profiles of downwelling spectral irradiance were measured with a Li-Cor model 1800 underwater spectroradiometer (*see* Li-Cor 1984). Samples for photosynthetic experiments and particulate light absorption were taken with a van Dorn bottle at the surface and close to the bottom (20 m in Eleanor Lake) or just below the pycnocline in the meromictic lakes. Samples were transferred to rinsed polyethylene bottles and kept in the dark at in situ temperatures until the initiation of the photosynthesis incubations, usually <2 h after sampling. Samples for chlorophyll were collected at 5-m intervals. Transparency was measured with a standard 30-cm Secchi disk.

Laboratory measurements—Photosynthetic rates (P) were measured as a function of irradiance (E) by the ^{14}C technique (Steemann-Nielsen 1952) in a linear incubator (*see below*). The temperature of the incubator was controlled to the value measured in the lake at the time of sampling. Light was provided by a combination of halogen lamps and fluorescent tubes to provide a spectrum resembling surface daylight conditions. A 2.1-liter sample was placed in a bottle on a magnetic stirrer and inoculated with 140 μCi liter^{-1} of ^{14}C-bicarbonate, mixed, and then subsampled for specific activity. Aliquots were dispensed into two sets of 14 bottles (62 ml), including 12 light bottles and two dark bottles. The bottles were incubated for 90 min in the incubator, and the contents of each bottle were then filtered through a 25-mm-diameter GF/F filter. The filters were stored frozen and later transferred to vials where 100 μl of 1 M HCl was added. After 24 h, scintillation cocktail (Beckman Ready Safe) was added, and the vials were counted in a Beckman 6500 scintillation counter after chemiluminescence had ceased. Vials with blank filters were used for background counts, which were subtracted and the resultant values converted to disintegrations per minute using an internal quench curve. Dark uptake rates were subtracted from the light uptake to obtain the photosynthetic carbon uptake.

Light absorption by seston was measured by the filter technique (Yentsch 1962). Subsamples of water were filtered through GF/F filters, and the transmission of light through the filter was measured in an integrating sphere connected to the Li-Cor 1800 spectroradiometer via a fiber-optic cable. The total particulate absorption was corrected to account for the increase of the light path in the filter and was then partitioned into the component due to algal pigments and that due to background absorbance. This was done by the procedure of Bricaud and Stramski (1990), which assumes that the background absorption increases exponentially with decreasing wavelength and that the ratio of absorption by pigments is 0.99 from 505 to 380 nm and 0.92 from 580 to 692.5 nm.

Dissolved inorganic carbon concentrations were calculated from pH and alkalinity determined by Gran-titration. Samples for Chl *a* were filtered through GF/F filters, and the filters were kept frozen at −20°C until they were extracted with 90% acetone and analyzed fluorometrically (Strickland and Parsons 1972), with acid correction, using a Shimadzu RF5000 spectrofluorometer. The latter instrument was calibrated with Chl *a* from *Anacystis nidulans* (Sigma Chemical).

Linear incubator—The incubator for the P vs. E determinations consisted of an inner part made of black Perspex with nine slots, each capable of holding 16 flat 62-ml tissue-culture bottles stacked together (Jassby and Platt 1976; Frenette et al. 1993) within a box with a glass front. Temperature control was maintained by a continuous flow of water running from the bottle closest to the lamp and back again. Light was provided from a combination of a horizontal series of nine 12-V tungsten halogen lamps and a vertical series of four fluorescent tubes (Fig. 1). The fluorescence tubes were a combination of two blue (Philips TLD18), one green (Philips TLD17), and one cool-white tube (Philips TLD33). This combination provided a light field with higher maximum irradiance than is possible with fluorescent tubes alone and with a more even spectrum in the photosynthetically available radiation (PAR) region than is possible with tungsten halogen lamps alone (Fig. 2). The desired irradiance gradient was obtained by placing pieces of black nylon screen between the bottles and in front of the first bottle in the series. Irradiance inside the bottles was measured with a Biospherical quantum meter (4π-sensor) for each combination of screens.

Calculations—The diffuse light-attenuation coefficient for downwelling PAR (K_d) was calculated by fitting the parameters in the equation $E(z) = E_{0-} \exp(-z\ K_d)$, where $E(z)$ is the irradiance between 400 and 700 nm at depth z, and E_{0-} the irradiance just below the surface, to the observed data by nonlinear regression (SAS 1990). Wavelength specific values for $K_d(\lambda)$ were calculated in the same way.

The mean irradiance experienced by the plankton community (E_{mean}) was calculated for each sample. For the nonstratified lakes, the mean percent surface irradiance (%SI) for the phytoplankton in a mixing water column was calculated from the mean depth and K_d according to Riley (1957) and was assumed to be equal for the surface sample and the deep samples. For the two meromictic lakes, the values for the surface samples were calculated from z_{mix} (Table 1) and K_d for that zone, whereas the values for the deep samples were the observed irradiance at that depth. In all cases, E_{mean} was calculated from $E_{\text{mean}} = 0.9\ E_o$ %SI/100, where E_o is the 24-h mean of hourly values for surface irradiance in the sampling period (3–13 August 1995), and 0.9 corrects for reflection at the surface.

Photosynthetic parameters were obtained from the nonlinear regression fit of the P vs. E data to a saturating exponential model (Webb et al. 1974), modified by the inclusion of an offset (c):

$$P^B = P_{\text{est}}(1 - \exp(-\alpha^B\ E/P_{\text{est}})) - c \qquad (1)$$

where α^B is the light-limitation parameter (g C g^{-1} Chl *a* m^2 mol^{-1}), and P^B_m, the light-saturated photosynthetic rate (in g C g^{-1} Chl *a* h^{-1}), was calculated as $P_{\text{est}} + c$. The offset (c) was incorporated to allow the alpha region of the curve to pass through the origin; this adjustment was equivalent to 2–10% of P^B_m. Photoinhibition was observed only at the highest irradiances, and zero to three data points in this region of the curve were excluded from the saturating exponential fit. The saturation irradiance (E_k) was calculated as P^B_m/α^B.

The total light absorption by the phytoplankton per unit

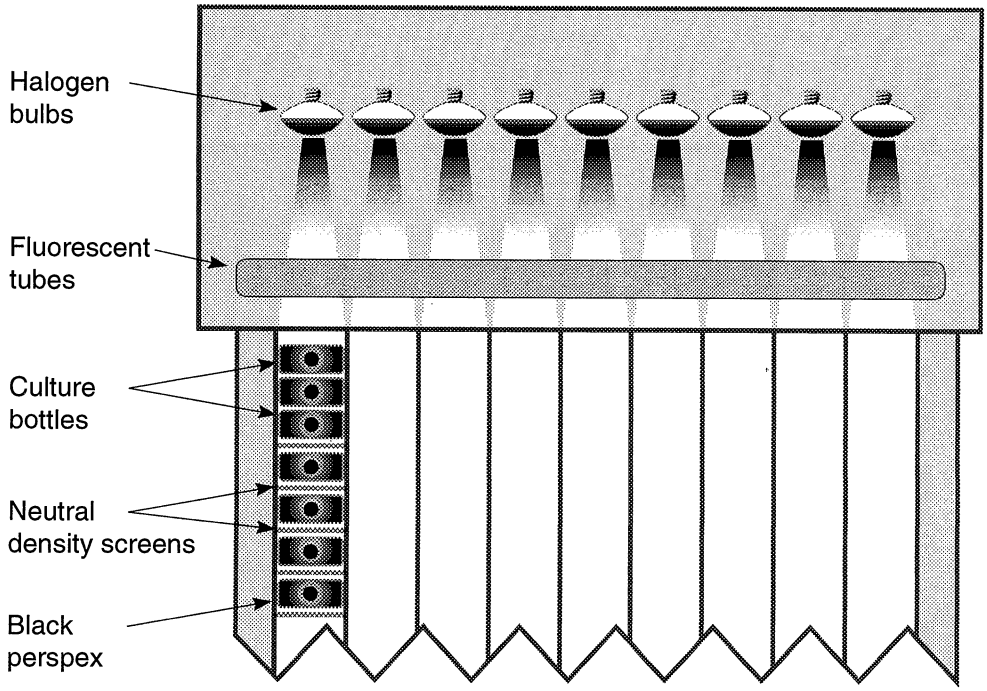

Fig. 1. Plan view diagram of the transportable linear incubator equipped with a combination of stacked fluorescent tubes (*see text*) and 12-V tungsten halogen lamps. The spectral output of the lamps is shown in Fig. 2. The stacking of the bottles and the temperature control is as shown in Babin et al. (1994).

Chl *a* (E_a) was calculated from the spectral light-absorption coefficients per unit Chl *a* ($a^B_{ph}(\lambda)$) and the spectral irradiance in the incubator ($E(\lambda)$), both measured at 1-nm intervals:

$$E_a = \Sigma\, a^B_{ph}(\lambda) \cdot E(\lambda) \quad (2)$$

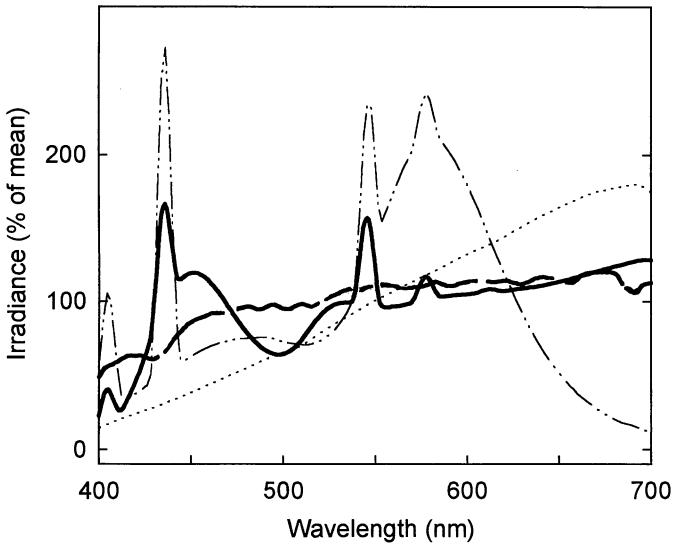

Fig. 2. Spectrum of the lamp system used in the *P* vs. *E* determinations (solid line). Also shown is an incident irradiance spectrum for the Resolute area at the time of sampling (dashed line) and the component lamps used in the incubator: a Sanyo cool-white fluorescent tube FL40SS (dot and dash line) and an Osram 12-V, 50-W tungsten halogen lamp (dotted line).

The mean absorption coefficient ($\hat{a}^B_{ph}$) was calculated as $E_a / \Sigma\, E(\lambda)$. Quantum yield ($\phi$ in mmol C fixed per mol of photons absorbed) was then calculated as $\alpha/(0.012\ E_a)$, where the factor 0.012 is for the conversion of units for carbon.

Results

Profiles—The profiles for Eleanor and North Lakes showed that values for oxygen, temperature, and conductivity were constant with depth, indicating a recently mixed water column and the absence of a seasonal thermocline (Fig. 3). Profiles from the other three monomictic lakes were not available because of an instrument failure, but the temperature and alkalinity values were approximately equal in the surface sample and the deep sample, and surface temperatures for these lakes ranged from 4.5 to 7.2°C (Table 2) where the density change for water with temperature is low. Thus, we assumed that these lakes also were mixed or only weakly stratified, consistent with previous summer data from these sites (Schindler et al. 1974*b*, unpubl. data). There was a small increase in temperature and oxygen close to the surface in North Lake, probably associated with a diurnal stratification on the sampling day, which was calm and sunny. The lower surface temperature in Eleanor Lake (Table 2) reflects the partial ice coverage of this lake on the sampling date, whereas the other lakes were ice free.

The profiles from the two meromictic lakes are more complex and reflect the changes in density generated by the salinity gradients. Conductivity increased from 3.3 and 8.7 mS cm^{-1} at the surface to 78.1 and 91.7 mS cm^{-1} in the moni-

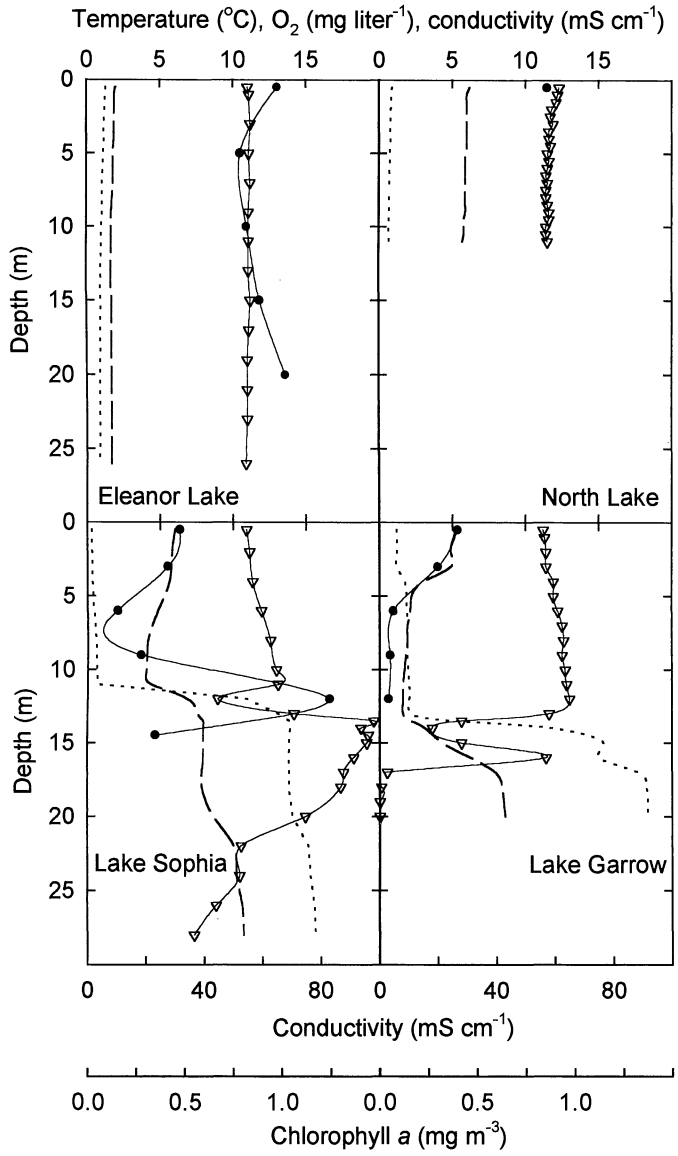

Fig. 3. Profiles of temperature (dashed line), conductivity (dotted line), oxygen (triangles), and Chl *a* (closed circles) for four lakes in the vicinity of Resolute Bay, high Arctic Canada. Note the shift in the scale for conductivity between the two cold monomictic lakes (upper panels) and the two meromictic lakes (lower panels).

molimnion for Lakes Sophia and Garrow, respectively (Fig. 3). The pycnocline was situated at 11.5 m in Lake Sophia and at 13.5 m in Lake Garrow. Temperature increased with depth under the pycnocline in both lakes, but it also increased toward the surface, such that the lowest temperatures recorded were just above the pycnocline in both lakes. The oxygen concentrations showed a well-defined minimum in the pycnocline and then declined with depth in the monimolimnion. The concentrations in the monimolimnion were higher in Lake Sophia, up to 165% of saturation, than in Lake Garrow (Fig. 3), probably reflecting the adequate penetration of light for photosynthesis in the former only. The fraction of the surface irradiance at the pycnocline was 20.2 and 0.7% in Lakes Sophia and Garrow, respectively.

Light attenuation—Light-attenuation coefficients for PAR were lowest in Lakes Char and Sophia (ca. 0.13 m^{-1}), intermediate in Resolute Lake, and higher in the other lakes, up to a maximum of 0.50 m^{-1} in the upper mixolimnion in Lake Garrow (Table 1). No significant changes in K_d with depth were observed in the cold monomictic lakes. In the two meromictic lakes, K_d was higher near the surface and in the pycnocline than in the lower part of the mixolimnion. This difference could not be explained by differences in chlorophyll concentration, because changes in Chl *a* with depth were much less than those of K_d and were most likely due to inorganic particles. This is in agreement with subsequent calculations, which show that nonchlorophyllous particles were important for light absorption in the two meromictic lakes, accounting for 40 and 21% of the total light absorption in Lakes Garrow and Sophia, respectively. Phytoplankton contributed little to light absorption, from 3.2% in Lake Garrow to 13.8% in Resolute Lake, and water was a major component of the light attenuation in all lakes. Mean irradiances (E_{mean}) were similar (59 ± 8 μmol quanta m^{-2} s^{-1}) for most of the lakes (Table 2), with a somewhat higher value (79 μmol quanta m^{-2} s^{-1}) in the epilimnion of Lake Sophia. Lowest values were found for Eleanor Lake, due the deep mixing in this lake, and at the pycnocline of the two meromictic lakes.

Chl a *and light absorption*—Chl *a* concentrations varied from 0.04 to 1.24 μg $liter^{-1}$. The lowest values were recorded in the mixolimnion in Lakes Garrow and Sophia (0.04–0.27 μg $liter^{-1}$), and the highest value was at the pycnocline in Lake Sophia. Values for the mixed lakes were from 0.46 to 1.1 μg $liter^{-1}$ and showed only small differences between surface and deep samples, except for Char Lake (Table 2). Light absorption per unit Chl *a* ($\hat{a}^B_{ph}$) varied little between depths and among lakes, with the exception of an anomalously low value for the deep sample in Lake Sophia. The ratio $a_{ph}(436)/a_{ph}(676)$, a measure of undegraded Chl *a* relative to the total chlorophyllous pigment concentration (Cleveland et al. 1989), ranged from 1.3 to 2.9, with more than half of the values above 2.0 (Table 2).

Photosynthesis—The photosynthesis–irradiance data were closely fit by Eq. 1, providing that P values at $E > 1{,}000$ μmol quanta m^{-2} s^{-1} were removed from the analysis for those curves where there was evidence of photoinhibition (Fig. 4). The maximum photosynthetic rate normalized to chlorophyll (P^B_m) varied sevenfold from 0.16 to 1.12 g C g^{-1} Chl *a* h^{-1}, but most values were below 0.5 g C g^{-1} Chl *a* h^{-1} (Table 2). There was no significant relationship between the P^B_m and E_{mean} (Table 3), but surface values of P^B_m were higher than values from the deep samples except in Eleanor Lake. The initial slope of the *P-E* curve normalized to chlorophyll (α^B) ranged from 0.53 to 2.3 g C g^{-1} Chl *a* m^2 mol^{-1} quanta and was negatively correlated with E_{mean} (Table 3). However, this relationship was due to the two high values (>2 g C g^{-1} Chl *a* m^2 mol^{-1} quanta) for the deep samples from Lakes Eleanor and Sophia. The other values were ca. 1 g C g^{-1} Chl *a* m^2 mol^{-1} quanta, with only small differences between surface and deep samples. The E_k values were between 48 and 196 μmol quanta m^{-2} s^{-1} (Table 2) and were

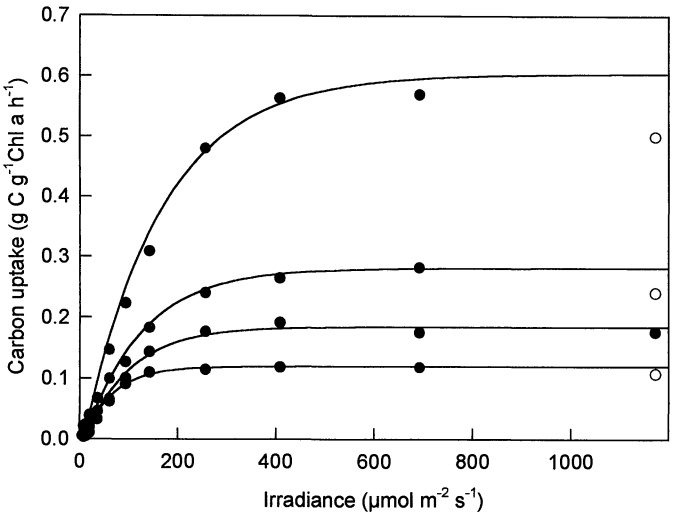

Fig. 4. Representative P vs. E curves for the Arctic lake phytoplankton. The curves are for samples from the following lakes and depths, from top to bottom at high irradiance: Meretta Lake at 6 m, North Lake at 0.5 m, Char Lake at 0.5 m, and Char Lake at 15 m. The open symbols were values considered to be influenced by photoinhibition and were therefore excluded from the P vs. E curve fits.

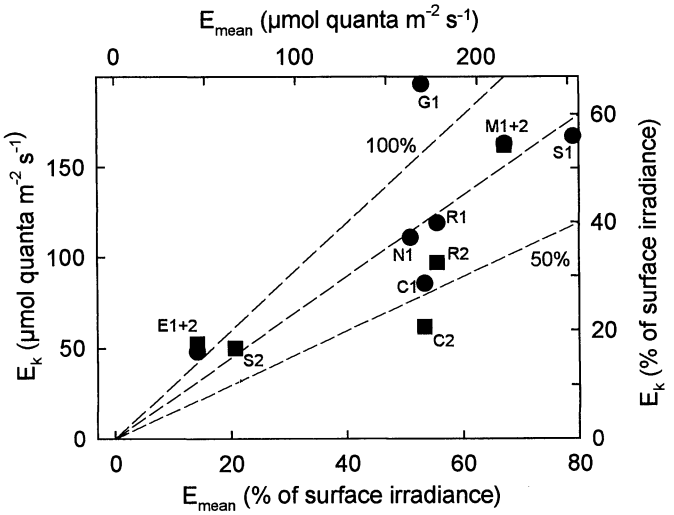

Fig. 5. Irradiance for the light saturation of photosynthesis (E_k) vs. the mean daily incident irradiance experienced by the phytoplankton (E_{mean}, *see text*). The dashed lines show E_k values equal to 50, 75, and 100% of E_{mean}. (C) Char Lake. (E) Eleanor Lake. (G) Lake Garrow. (M) Meretta Lake. (N) North Lake. (R) Resolute Lake. (S) Lake Sophia. The numbers indicate surface (1) or deep samples (2).

positively correlated with E_{mean} (Table 3). A plot of E_k vs. E_{mean} (Fig. 5) suggests that most of the phytoplankton communities were acclimated to an irradiance of 50–75% of the 24-h daily mean.

Quantum yield (ϕ) was low in all samples, with most values in the range of 2–8 mmol C mol^{-1} quanta (Table 2). Only the deep samples from Lakes Sophia and Eleanor showed higher values, 20.8 and 12.1 mmol C mol^{-1} quanta, respectively. There was an overall decrease in ϕ with increasing E_{mean}, but the relationship was not significant ($r = -0.46$, $p = 0.13$). Quantum yield values were negatively correlated with $\hat{a}^B_{ph}$ and the pigment ratio $a_{ph}(436)/a_{ph}(676)$.

Discussion

Limnological properties—These observations from the Canadian Arctic Archipelago illustrate the wide range of lake ecosystem types in the north polar region. These diverse bio-optical (clear, DOC-influenced, and turbid) and hydrodynamic (mixed, weakly stratified, or meromictic) conditions provide an excellent spread of environments for developing light-absorption and photosynthesis models. Much of what we know about high Arctic lakes is derived from the IBP program at ultraoligotrophic Char Lake. The comparisons made here suggest that Char Lake represents only one end of a wide bio-optical and trophic spectrum of lakes even in the Resolute Bay region, and results from the IBP study should be generalized with caution to other Arctic systems. Several features of Char Lake, however, were common to lakes throughout the region, specifically low temperature and the low Chl *a* biomass, reflecting a nutrient-poor chemical environment.

Photosynthetic parameters—The variation in the photosynthetic parameters among the lakes follow the pattern expected for acclimation to high or low irradiance. Higher mean irradiance (E_{mean}) was accompanied by lower values for α^B (significant negative correlation), which caused E_k to increase significantly (Table 3). The values for E_k were usually between 50 and 75% of the daily mean value of E_{mean} (Fig. 5), indicating that the phytoplankton community had acclimated to a light level somewhat lower than the mean

Table 3. Spearman correlation coefficients for the correlations among parameters for photosynthesis, light absorption, and E_{mean}.

	E_k	P^B_m	$\hat{a}^B_{ph}$	Chl *a*	E_{mean}	a_{436}/a_{676}
α^B	−0.27	0.51	−0.59*	0.11	−0.58*	−0.64*
ϕ	−0.29	0.53	−0.79**	0.18	−0.46	−0.65*
E_k		0.65*	0.24	−0.42	0.72**	0.36
P^B_m			−0.27	−0.18	0.27	0.04
$\hat{a}^B_{ph}$				−0.12	0.41	0.38
Chl *a*					0.06	0.20
E_{mean}						0.55

* $p<0.05$, ** $p<0.01$.

light level they were exposed to. Thus, for a major part of the 24-h continuous light cycle at this latitude, the phytoplankton are exposed to irradiances that allow a photosynthetic rate at or close to P_m. The high E_k values, relative to the daily mean of E_{mean} for Lakes Garrow and Eleanor, can be explained by a recent decline in E_{mean} associated with increased turbulent mixing after ice-out. Eleanor Lake was still partially (ca. 50%) covered with ice at the time of sampling. In Lake Garrow, the effect of increased turbulence after ice-out was compounded by suspended inorganic particles from the mine, which probably sediment out when the lake is covered by ice.

Nutrient supply is likely to be an important factor influencing photosynthetic performance in the range of high Arctic lakes sampled in the present study. The lakes with the highest values of photosynthetic parameters were Meretta, Sophia, and Garrow, which are likely to have the highest nutrient supply. The deep samples from Lakes Eleanor and Sophia displayed low values for P_m^B and high values for α^B as expected for low light-acclimated communities with access to nutrients. Samples from Char Lake, Resolute Lake, and the surface of North and Eleanor Lakes all showed low values for both α^B and P_m^B.

The pattern described above for the variation in photosynthetic parameters from lake to lake is consistent with a combined influence of light and nutrients. More striking, however, is the low absolute values of both α^B as well as P_m^B in all seven lakes. Both parameters are 10–50-fold below maximum values reported elsewhere (e.g., Harris 1978) and are among the lowest values in the literature. For P_m^B, an obvious explanation could be the low ambient temperatures, because P_m^B is primarily determined by enzymatic processes. For α^B, however, cold temperatures alone should not cause low values, because α^B is regulated by photochemical processes and should be temperature independent (Rabinowitch 1956), although some evidence to the contrary has been presented by Tilzer et al. (1986) for the Southern Ocean.

Intersystem comparison—To examine whether the unusually low photosynthetic rates found in the present study represent a general response in cold waters, we compared our values with a compilation of data from the literature encompassing a total of 256 observations of P_m^B and α^B for phytoplankton and ice algae at temperatures from −2 to +6°C. The frequency distribution of P_m^B is shown in Fig. 6 with statistical information in Table 4. P_m^B values for freshwater phytoplankton are significantly lower than P_m^B values from other cold systems ($p < 0.0001$, t-test). The difference is sixfold when freshwater values are compared to values from marine systems and three- to fourfold when compared to ice-algae communities and cultures (Table 4). Freshwater values were all below 1.6 g C g^{-1} Chl *a* h^{-1}, while several values for marine phytoplankton and ice algae were above 2 g C g^{-1} Chl *a* h^{-1}. Several of the values in each group were obtained from algal communities acclimated to low light, ≤5–15 μmol quanta m^{-2} s^{-1}. The low values for ice algae, compared to marine phytoplankton, and the difference between the data from Resolute and certain other freshwater values (for example, the values from permanently ice-covered lakes in Antarctica) probably reflect differences in the

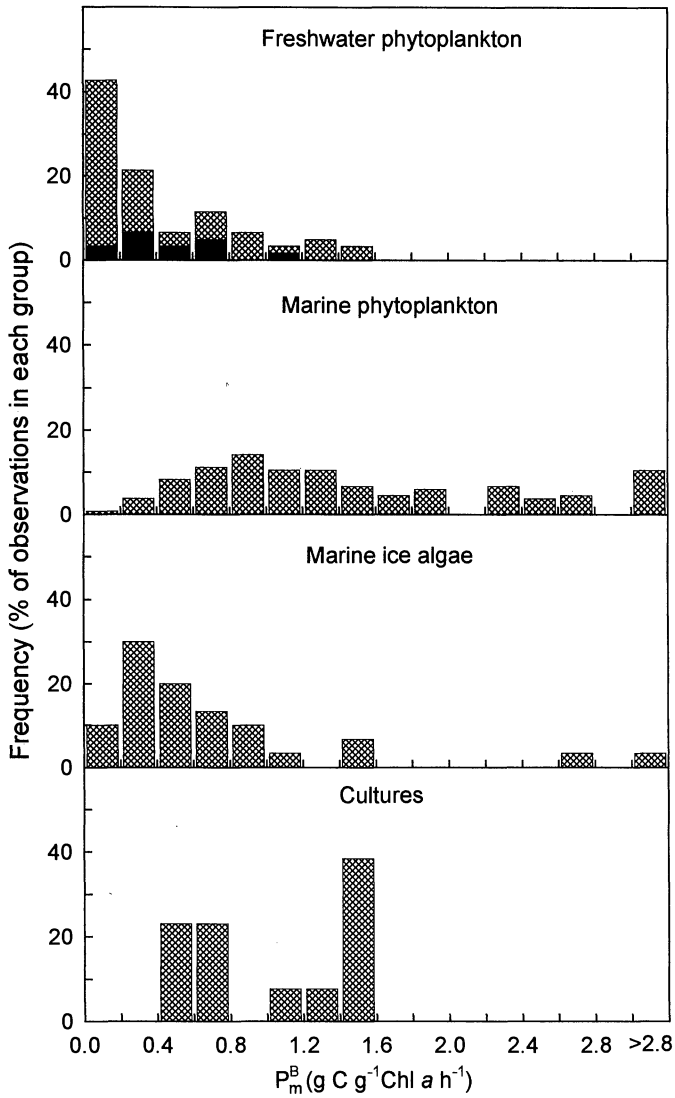

Fig. 6. Frequency distribution of P_m^B values from the literature at temperatures between −2 and +6°C. Filled bars represent the values from this study. The other high-latitude lake data (n = 61) were from Fee et al. (1988), Lizotte and Priscu (1992, 1994), and Milot-Roy and Vincent (1994); marine phytoplankton data (n = 134) were from Platt et al. (1982, 1987), Gallegos et al. (1983), Sakshaug and Holm-Hansen (1986), Tilzer et al. (1986), Beeler SooHoo et al. (1987), Rivkin and Putt (1987), Brightman and Smith (1989), and Gleitz and Kirst (1991); sea-ice data (n = 30) were from Palmisano et al. (1985, 1987); and culture data (n = 13) were from Thomas et al. (1992) and Smith et al. (1994).

light level the algae are acclimated to. However, nutrient concentrations are also likely to be an important factor contributing to the differences between freshwater and marine populations. Nutrient concentrations are much higher in most cold-water marine systems than in the lakes around Resolute. For example, about half of the data in Fig. 6 are from the Southern Ocean, in which nitrate values are typically >420 μg N liter^{-1}, and DRP values are >60 μg P liter^{-1} (Vincent 1988). Nutrient concentrations are also often high in the concentrated brine channel environment inhab-

Table 4. Statistics for the frequency distribution of α^B and P_m^B for literature values for microalgae between −2 and +6°C.

	α^B (g C g^{-1} Chl *a* m^2 mol^{-1} quanta)					P_m^B (g C g^{-1} Chl *a* h^{-1})				
	Freshwater plankton	Resolute plankton	Marine plankton	Ice algae	Cultures	Freshwater plankton	Resolute plankton	Marine plankton	Ice algae	Cultures
Mean ± SD	1.52±1.25	1.23±0.56	6.12±4.8	6.36±4.1	18.2±14.	0.22±0.22	0.45±0.28	1.38±0.89	0.66±0.62	1.62±1.11
Range	0.27–5.6	0.53–2.30	0.24–35.6	1.56–20.7	5.56–43.6	0.028–1.12	0.16–1.12	0.11–5.12	0.096–2.64	0.49–4.4
C.V.	0.81	0.46	0.78	0.64	0.81	0.97	0.62	0.64	0.93	0.68
Factor of variation	20.0	4.3	146	13.3	7.8	40	7.1	46.5	27.5	9.0
n	44	12	134	34	13	44	12	134	30	14

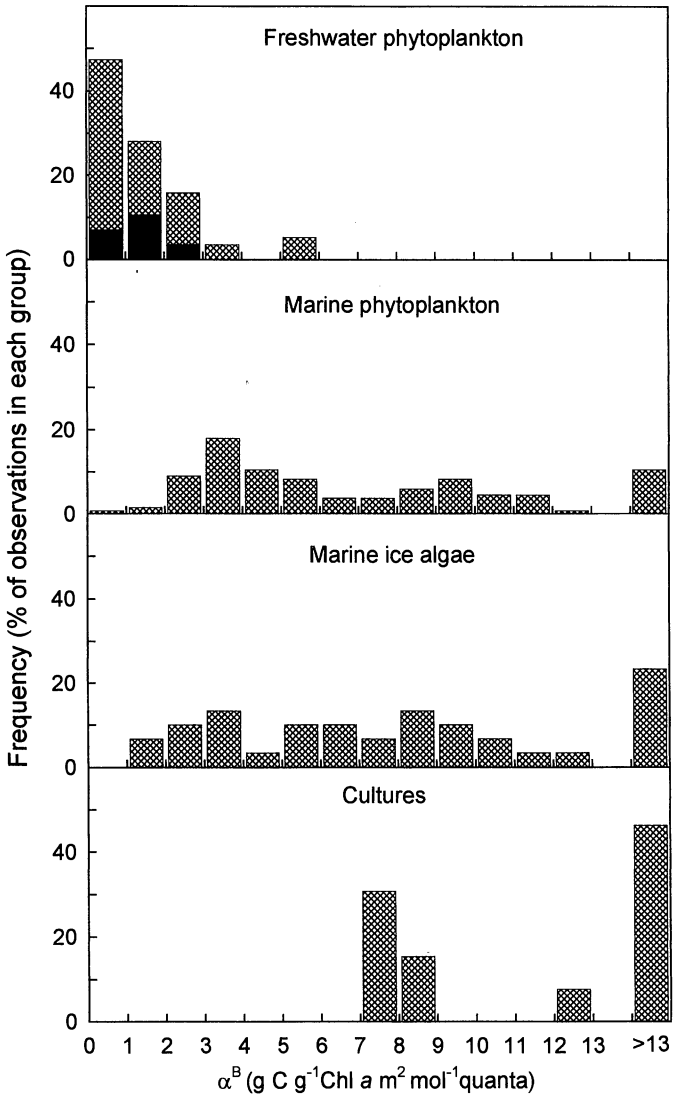

Fig. 7. Frequency distribution of α^B values from the literature at temperatures between −2 and +6°C. Filled bars represent the values from this study. Sources are given in Fig. 6.

ited by ice biota (Vincent 1988 and references therein), and the same is true for culture media. The similar or higher values for these groups, compared to the values from Resolute plankton, despite low light, therefore also suggest a positive effect of nutrients on P_m^B values.

A similar compilation was made for α^B, and the comparisons are given in Fig. 7, Table 4. Consistent with the P_m^B analysis, values from freshwater are significantly ($p < 0.0001$, *t*-test) lower than in other systems (about fourfold) and 10-fold lower than values from cultures. The marine phytoplankton show a double-peaked distribution, with most of the values below 7 g C g^{-1} Chl *a* m^2 mol^{-1} quanta from the Arctic and higher values from the Southern Ocean, consistent with the higher nutrient concentrations in the south polar region. However, our Arctic lake values are similar to those obtained in other studies in cold lakes.

The same literature data sets give an overall mean quan-

tum yield of 35 mmol C mol^{-1} quanta, assuming a mean absorption coefficient of 15 m^2 mg^{-1} Chl *a* for those studies in which the absorption coefficient was not measured. The mean value for a data set from Antarctic ice-covered lakes (Lizotte and Priscu 1994) was 12 mmol C mol^{-1} quanta compared to 6.7 mmol C mol^{-1} quanta in the data set from Resolute. Light-limited ϕ values from warmer water are generally much higher, with highest measured values in temperate and tropical studies of 80–100 mmol C mol^{-1} quanta (Tyler 1975; Kishino et al. 1986; Lewis et al. 1988; Cleveland et al. 1989). High quantum yield values have also been recorded at low temperature; e.g., Robinson et al. (1995) reported a maximum value of 88 mmol C mol^{-1} quanta for benthic algae, and Arrigo et al. (1993) reported maximum values in the range of 80–113 mmol C mol^{-1} quanta for ice algae in McMurdo Sound, Antarctica. Quantum yield values close to the theoretical maximum have also been measured at low temperature (7°C) in growth experiments with macroalgae (Markager 1993). Thus, despite the problems involved in estimating ϕ (Bannister and Weidemann 1984; Bricaud and Stramski 1990), we can conclude that quantum yield values in the range of 80–100 mmol C mol^{-1} quanta are physiologically possible even at low temperature. The question that then arises is, why are values often so low in cold water, sometimes only 2% of the theoretical maximum, and why are ϕ values particularly low in cold freshwater ecosystems. The answer may be methodological, with either underestimation of the carbon uptake or overestimation of the absorption by photosynthetically active pigments. The latter explanation seems especially plausible for cold, nutrient-poor waters such as lakes in the high Arctic.

Although pigments are usually assumed to indicate living cells, incompletely degraded pigments could also be associated with inactive or dead cells. The use of pigments in paleolimnological research shows that pigments derived from the water column can persist for hundreds of years (e.g., Pienitz et al. 1992). The mechanisms that eventually remove the pigments from the water column are chemical decomposition, bacterial degradation, grazing, or sedimentation. However, at low temperature, all of these processes, with the exception of sedimentation, are markedly slowed down, and a lower proportion of living to dead or inactive cells is to be expected. High-latitude lakes are typically dominated by small-cell phytoplankton (e.g., Bergeron and Vincent 1997), which are likely to have slow rates of sinking, even after death.

Grazing by mesozooplankton is strongly dependent on temperature (Huntley and Lopez 1992), and this effect will tend to reduce the loss rate of particles in cold waters. In the polar oceans, perennial overwintering copepods are common (Runge and Ingram 1988) and may result in higher continuous grazing losses compared to freshwater systems, where the summer population of mesozooplankton is established from resting eggs. Furthermore, zooplankton grazing activity may be less effective in high-latitude lakes than in the polar oceans, which contain grazer communities with a broader array of particle-capturing mechanisms; for example, tunicates and choanoflagellates occur in the polar oceans but are absent from lakes. Low-nutrient concentrations might limit bacterial activity and further slow down the degradation process.

Absorption by partially degraded or inactive pigments has previously been suggested as a cause of low quantum yield values (Lewis et al. 1985; Cleveland et al. 1989). Cleveland et al.'s suggestion was based on a significant negative relationship between the ratio $a_{ph}(436)/a_{ph}(676)$ and ϕ, plus the fact that the $a_{ph}(436)/a_{ph}(676)$ ratio often is higher in field samples than in healthy cultures, where values are usually below 2 (Cleveland and Perry, 1987; Cleveland et al. 1989). The same negative relationship was found in this study (Table 3) but for a much lower range of ϕ values (2.2–20.8 compared to 15–80 mmol C mol^{-1} quanta in the Cleveland et al. study). Furthermore, many of the $a_{ph}(436)/a_{ph}(676)$ values in the present study were at or above 2 (Table 2). High-pressure liquid chromatography analysis of the chlorophyllous pigments would provide a more accurate estimate of Chl *a* for these calculations but may still include undegraded Chl *a* that is no longer participating in photosynthesis.

Underestimation of the carbon fixation due to excretion of organic carbon during the experiment is another possible source of error in our study but not in the study by Lizotte and Priscu (1992), because they did not filter their samples. Carbon excretion is unlikely to play a role at low light where ϕ is estimated, but it could lead to an underestimation of P_m^B. This could be pronounced under cold, nutrient-poor conditions where carbon fixation is likely to be in excess of what can be used for growth.

In general, low temperature may exacerbate the effect of nutrient starvation by decreasing the activity of enzymes, thereby reducing the catalytic power per unit enzyme and thus per unit of nutrients invested in them. In addition, low-nutrient concentrations prevent the cells from compensating for low temperature by increasing the concentrations of enzymes. Thus, the negative effect of low-nutrient concentration on photosynthetic performance (Welschmeyer and Lorenzen 1981; Kolber et al. 1988; Cullen et al. 1992; Geider et al. 1993) is likely to be enhanced by low temperature.

In summary, our results from the Arctic and those from high-latitude lakes elsewhere indicate that in cold freshwater ecosystems in general, low temperature and low nutrients act in concert to result in extremely low values of α^B, P_m^B, and ϕ. However, standard assays are likely to exaggerate these effects because of the persistence of inactive or partially degraded photosynthetic pigments in the water column.

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Received: 20 July 1998
Accepted: 14 December 1998
Amended: 14 January 1999