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Phytoplankton production in subarctic lake and river ecosystems: development of a photosynthesis–temperature–irradiance model

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Abstract. We investigated the size-dependent temperature response of natural phytoplankton communities from a lake and a river in the Canadian subarctic. Photosynthesis by total, <2 μm and >2 μm size fractions was determined at 11 irradiances (1–109% of ambient solar radiation) and five temperatures (5–25°C) in outdoor solar incubators. Temperature had no effect on photosynthesis at low irradiance, but strongly regulated the photosynthetic response at saturating and inhibiting irradiances. For the river phytoplankton, low temperatures lowered E_K values (onset of light saturation) and shifted photosynthesis in the water column from light dependence to temperature dependence. A photosynthesis–temperature–irradiance (*P–T–E*) model was developed to describe the varied temperature response of photosynthesis across the full range of limiting, saturating and inhibiting irradiances. The *P–T–E* model explained 74–95% of the variation in photosynthesis for all size fractions (total community, >2 μm fraction and <2 μm fraction). Picoplankton (<2 μm) had greater photosynthetic rates (P_{max}) at all temperatures than did the total and >2 μm communities. The picoplankton fraction was also more responsive to increasing temperature than larger cells, implying a greater sensitivity to diurnal or longer term changes in lake water temperature.

Introduction

Lakes and rivers are a dominant feature of the subarctic landscape. In North America, this biogeographical zone lies within a 15° span of latitudes from 52 to 67°N and is characterized by extreme annual variations in air temperature. The influence of the north polar region results in cold winter air temperatures with mean daily minima below –20°C for 4 months each year. The periodic intrusion of warm air masses from temperate latitudes results in summer maxima above 30°C. These effects are reflected in the thermal regime of subarctic lakes and rivers. For 7–9 months each year, these environments are ice covered, and are then likely to experience a rapid rise in temperature immediately following ice-out in June or July, although little information is available. Aquatic organisms may thus experience a wide variation in ambient water temperature. In addition, irradiance levels vary considerably at seasonal, daily and shorter time scales. Phytoplankton are subject to a variable light regime during the frequent mixing events in polymictic subarctic lakes, but diurnal thermoclines can retain phytoplankton near the surface where they encounter prolonged bright light and higher temperatures (Milot-Roy and Vincent, 1994). Large rivers have more stable temperature regimes with reduced seasonal variations in temperature and an absence of diurnal stratification. In these more turbid, well-mixed environments, the phytoplankton are continuously swept through sharp gradients in underwater irradiance.

A number of studies have developed quantitative descriptions of the controlling influence of temperature on physiological processes that can be applied to organisms in aquatic ecosystems. However, the models to date for

photosynthesis–temperature relationships have focused on the light-saturated (P_{max}) region of the photosynthesis versus irradiance (P–E) curve. Photosynthesis in other regions of the curve, specifically the light-limited and light-inhibited portions, is likely to respond to temperature in different ways than P_{max}.

At limiting irradiance (the initial slope of a P–E curve, defined as the α region), photosynthesis is controlled by photochemical reactions that are largely temperature independent (Falkowski and Raven, 1997). Thus, photosynthesis at low irradiance should increase linearly as light increases, irrespective of temperature. Many studies have reported this expected lack of temperature effect on light-limited photosynthesis (Post *et al.*, 1985; Harrison and Platt, 1986; Rey, 1991; Smith *et al.*, 1994), although some evidence of temperature dependency has been found at extreme low temperatures (Tilzer *et al.*, 1986; Palmisano *et al.*, 1987).

At saturating irradiance, biochemical rather than photochemical reactions are the rate-limiting steps for photosynthesis, and these biosynthetic processes are regulated by temperature (Davison, 1991). Increasing P_{max} with increasing temperature has been reported frequently, and is most commonly described as an exponential rise using a Q_{10} temperature coefficient, the ratio of photosynthetic rate change over a 10°C interval (e.g. Tilzer *et al.*, 1986; Henley, 1992; Smith *et al.*, 1994).

Above saturating irradiances, photoinhibition is manifested by an excess of excitation energy that cannot be dissipated through continuing carbon metabolism or through other pathways such as fluorescence and non-radiative quenching (Long *et al.*, 1994). On the P–E curve, photoinhibition is seen as a decline in photosynthetic rate from P_{max} with increasing irradiance (defined as the β region). Photoinhibition is the result of an imbalance between temperature-independent light damage to the photosynthetic machinery and temperature-dependent repair (Greer *et al.*, 1986; Wünschmann and Brand, 1992). The repair process is thought to consist of resynthesis of damaged D1 proteins in photosystem II (Öquist *et al.*, 1995; Sass *et al.*, 1997). Given that photochemical damage is independent of temperature, while biosynthesis is temperature dependent, cells should be less prone to photoinhibition at higher temperatures.

The present study was undertaken to assess the responses to temperature across the P versus E curve of natural communities of phytoplankton from subarctic freshwater environments. The primary objectives were to evaluate the effects of temperature on the α, P_{max} and β regions of the curve, and to develop a model that would describe photosynthesis as a continuous function of irradiance and temperature across all three regions. A further goal was to determine the temperature response of the picoplankton fraction (<2 μm) relative to larger cell constituents of the phytoplankton communities. Picocyanobacteria dominate this fraction, and are a major component of high-latitude freshwater phytoplankton communities (Shortreed and Stockner, 1986; Milot-Roy and Vincent, 1994; Vincent, 1998). Given the strong temperature responsiveness of cyanobacteria in general (Robarts and Zohary, 1987), we hypothesized that photosynthesis by the <2 μm fraction would show a stronger temperature dependence than that by the nanoplankton and microplankton fractions. We addressed these objectives by way of temperature and solar irradiance manipulations with phytoplankton

samples from two contrasting environments: a shallow lake subject to diurnal stratification and mixing, and the turbid downstream reach of a high-order river (i.e., with many tributaries).

Method

Study area

The two study sites are located in the subarctic region of northern Québec (latitude 55°17'N, longitude 77°46'W). The Great Whale River discharges into Hudson Bay after flowing ~300 km from its source at Lac Bienville. The river was sampled in its lowermost freshwater reach at a distance ~3 km upstream of the confluence with Hudson Bay, well above any marine intrusion. The second ecosystem, Lake Kayouk, is a small (~0.04 km^2), shallow (maximum depth ~2.0 m) lake situated in a forest–tundra catchment.

Throughout the field season, temperature and PAR (photosynthetically available radiation) profiles were taken in the water column of both the lake and the river using a PUV-500 profiler (Biospherical Instruments, Inc.). Subsurface (35 cm depth) temperature measurements in Lake Kayouk were taken at 15 min intervals with an Optic Stowaway Temperature Logger (Onset Computer Corp.). Air temperature and incident PAR were measured four times daily between 09:00 and 18:00 h, and every 30 min during experimental incubations, using the PUV-500.

Experimental system

Photosynthesis–irradiance (P–E) curves were developed with the use of white plastic incubation boxes (45 × 10 × 7 cm) that were constructed to hold 11 pairs of inverted scintillation vials in separate compartments. Irradiance was attenuated over the vials with layers of neutral-density screen to give a final light transmission series of 1.0, 1.6, 2.6, 3.6, 5.7, 9.1, 14.0, 25.5, 43.1, 72.7 and 109.2% of ambient irradiance (measured with a Biospherical Instruments, Inc. QSL-100 quantum irradiance probe; >100% of incident irradiance was due to internal reflection). The 20 ml scintillation vials were of borosilicate glass that is transparent to PAR, and which shows slightly increasing absorbance at wavelengths below 400 nm. For example, at 300 nm, 73% of surface irradiance, compared to 100% at 400 nm, is transmitted through the bottom of the scintillation vial, as determined using a Hewlett Packard 8452A Diode Array Spectrophotometer.

Four experiments were conducted, two with Lake Kayouk water and two with Great Whale River water, to obtain P–E curves over five temperatures from 5 to 25°C. These temperatures were chosen to correspond with temperatures likely to be experienced by the plankton over the course of the summer (Figure 1).

For each experiment, water was collected in the early morning and transported immediately to the research station where it was dispensed into pre-rinsed scintillation vials and then inoculated with $[^{14}C]HCO_3^-$ to a final concentration of 0.2 μCi ml^{-1}. The P–E incubators with samples in place were put, in the dark, in controlled-temperature water baths for 30 min prior to the start of an experiment;

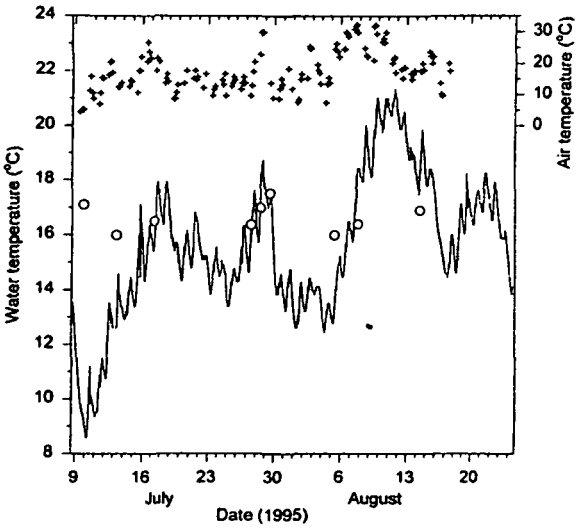

Fig. 1. Water temperature at 35 cm depth in Lake Kayouk (solid line) and the Great Whale River (open circles) and air temperature at the field station in Kuujjuaraapik (crosses) during the study period (9 July–24 August 1995; the temperature logger was deployed 5 days after the first experiment).

20–25 min were found to be sufficient to allow water within the vials to equilibrate to the incubation temperature. Incubations under ambient solar radiation were then conducted for 2–3.5 h between 10:00 and 15:00 h. The endpoints were staggered so that the incubation boxes could be removed one at a time for immediate filtration. Replicate ^{14}C incubations were also held in the dark for each temperature and dark values were subsequently subtracted from the light values. The samples were filtered through GF75 glass fibre filters (equivalent to GF/F) for the total plankton community, and 2 μm Nuclepore membranes to isolate the >2 μm size fraction. All filters were stored frozen until further laboratory analysis, at which time filters were left for 20 h after adding 0.1 ml of 1 N HCl to remove unincorporated $[^{14}C]HCO_3^-$. Ecolite (ICN Biomedicals, Inc.) scintillation cocktail was added and the radioactivity of the samples then measured with a Beckman LS 6500 scintillation counter.

Phytoplankton chlorophyll *a* (Chl *a*; μg l^{-1}) was determined by extracting filtered material in boiling 95% ethanol (Nusch, 1980). Extract fluorescence was then measured with a Sequoia Turner Model 450 fluorometer using NB440 (blue excitation) and SC665 (red emission) filter blocks. Dissolved inorganic carbon was determined by Gran titrations (Wetzel and Likens, 1991).

Curve fitting and statistical analysis

Curves for photosynthesis versus irradiance data were fitted using an iterative non-linear regression (SigmaPlot 3.0) with the equation of Platt *et al.* (1980):

$$P = P_S(1 - \exp{-(\alpha E/P_S)})(\exp{-(\beta E/P_S)}) \quad (1)$$

where P is the photosynthetic rate at irradiance E, P_S is maximum photosynthesis obtained in the absence of photoinhibition, and α and β are parameters describing the initial slope and the photoinhibited portion of the P–E curve, respectively. All photosynthetic rate values were normalized to Chl *a*. The temperature sensitivity of photosynthesis within each of the curve parameter regions (α, P_{max}, β) was first evaluated by examining photosynthesis at a specific irradiance to represent each region: P_{35}, P_{280} and P_{1400} at 35, 280 and 1400 μmol photons m^{-2} s^{-1}, respectively. A fixed irradiance value may not consistently represent one part of the P–E curve (e.g. 280 μmol photons m^{-2} s^{-1} may be in the photoinhibition range rather than P_{max} at low temperature) and we therefore also assessed the effect of temperature on calculated P_{max} and on the photosynthetic rate corresponding to 50% inhibition from P_{max} ($P_{50\%}$). Photosynthesis–temperature (P–T) curves were regressed and the slopes compared by *t*-test for differences. Comparisons using *t*-tests were also made between <2 and >2 μm size fractions, and between the lake and river environments. Using the linear relationship of the P–T curves, a model was developed incorporating both irradiance and temperature as parameters to describe photosynthesis. The P–T–E model was then fitted to the total, <2 μm and >2 μm data sets by non-linear regression.

Results

Physical environment

The thermal regime differed considerably between the two systems. Surface water temperature in Lake Kayouk varied from 8.6 to 21.4°C over the period of July–August 1995 (Figure 1). A diurnal temperature range of 2.5–3.0°C was often observed, and 9°C changes occurred over periods of <10 days. Water temperatures measured on several discrete dates in the Great Whale River were consistently within the narrow range of 16.0–17.5°C.

Diurnal thermoclines were often observed in Lake Kayouk during July and August (Scully and Vincent, 1997). These near-surface thermoclines would form during periods of warm, calm weather and were easily destroyed by wind action. In contrast, fine structure temperature profiles in the Great Whale River always showed isothermal conditions.

Depth profiles of irradiance showed that PAR was attenuated to a slightly greater extent in the Great Whale River (K_d = 1.05 m^{-1}) than in Lake Kayouk (K_d = 0.96 m^{-1}). The average irradiance (E_{av}) to which cells were exposed within the mixed water column was 44% surface PAR in Lake Kayouk and 23% surface PAR in the Great Whale River (equation from Tilzer, 1987).

Phytoplankton communities

Between late June and late August, total Chl *a* in Lake Kayouk ranged from 0.7 to 1.7 μg l^{-1} and in the Great Whale River from 1.2 to 1.6 μg l^{-1}. The <2 μm fraction contributed 20–40% of the total community Chl *a* in Lake Kayouk and

40–50% of the Chl *a* in the Great Whale River. Photosynthetic picocyanobacteria were found in Lake Kayouk at a concentration of 2×10^3 cells ml^{-1} in late June and at 7×10^4 cells ml^{-1} by late July. Picocyanobacterial abundance in the Great Whale River varied less than in Lake Kayouk, from 1.6 to 4×10^4 cells ml^{-1}.

The abundance of >2 μm plankton was similar in the two systems at slightly less than 10^3 cells ml^{-1}. The >2 μm category was comprised of a large diversity of cells including flagellated and ciliated protozoa, green algae and diatoms. Nanoflagellates were a dominant group in both systems, comprising 45–65% of total cells ml^{-1}. With few exceptions, the flagellated cells were in the 2–20 μm size category, including the genera *Ochromonas*, *Chromulina*, *Kephyrion* and *Dinobryon* (Chrysophyceae), *Cryptomonas* and *Chroomonas* (Cryptophyceae) and *Gymnodinium* (Dinophyceae).

Photosynthesis versus irradiance

The four incubation experiments were initially compared at 15°C which is the mid-point of the experimental temperature range 5–25°C, the average temperature in Lake Kayouk during July and August, and 1–2°C lower than temperatures recorded in the Great Whale River. The photosynthesis–irradiance response was well described by the Platt *et al.* (1980) *P* versus *E* model (Figure 2), with r^2 values of 0.87–0.96.

Maximum photosynthetic capacity (P_{max}) by the Lake Kayouk community was 3.8 mg C (mg Chl *a* h)$^{-1}$ in early July and 6.1 mg C (mg Chl *a* h)$^{-1}$ in early August

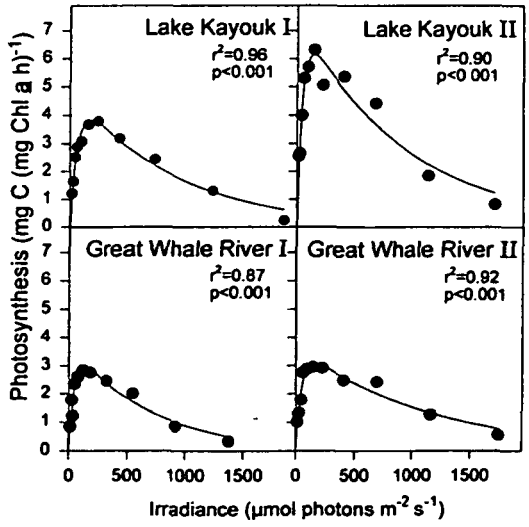

Fig. 2. Photosynthesis–irradiance curves obtained for the total algal community on two separate occasions for each of Lake Kayouk and the Great Whale River. Incubations were held at 15°C. Lake Kayouk I: 4 July 1995; Lake Kayouk II: 4 August 1995; Great Whale River I: 17 July 1995; Great Whale River II: 5 August 1995.

(Table I). P_{max} values were lower [2.9 and 3.1 mg C (mg Chl *a* h)$^{-1}$] in the Great Whale River community.

The initial slope of the *P–E* curve, α, for the Lake Kayouk community doubled over the period between experiments from 0.075 to 0.162 mg C (mg Chl *a* h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$. In contrast, α for the Great Whale River experiments was relatively constant at 0.078 and 0.073 mg C (mg Chl *a* h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$. Photoinhibition was observed at high irradiance (>300 μmol photons m^{-2} s^{-1}) in all experiments (Figure 2). At an irradiance of 1400 μmol photons m^{-2} s^{-1}, the Lake Kayouk community was inhibited by 69 and 71%, and the Great Whale River community by 80 and 63% relative to photosynthesis at 280 μmol photons m^{-2} s^{-1}, in the region of P_{max}.

Temperature effects on P versus E

Temperature exerted a strong effect on the photosynthetic response at mid to high irradiances by phytoplankton in both Lake Kayouk and the Great Whale River, but had little influence on either community at low irradiances (Figure 3). The temperature insensitivity in the initial light-limited portion of the *P* versus *E* curve is seen by the lack of relationship between α values and temperature (Table

Table I. Parameter values obtained by non-linear regression of the photosynthesis–irradiance data for the total algal community in Lake Kayouk and the Great Whale River. SE is given in parentheses for fitted parameters; error was not calculated for the derived parameters, P_{max} and E_K (see Smith *et al.*, 1994)

Experiment (date)	*T*	α	P_S	β	P_{max}	E_K
Lake Kayouk I	5	0.108 (0.012)	2.38 (0.15)	0.005 (0.001)	1.94	18
(04/7/95)	10	0.043 (0.004)	3.30 (0.54)	0.007 (0.002)	2.03	47
	15	0.075 (0.006)	5.04 (0.38)	0.006 (0.001)	3.83	51
	20	0.052 (0.004)	8.63 (1.31)	0.010 (0.003)	5.04	97
	25	0.077 (0.01)	7.21 (0.83)	0.005 (0.002)	5.67	74
Lake Kayouk II	5	0.138 (0.007)	3.75 (0.13)	0.009 (0.001)	2.95	21
(04/8/95)	10	0.154 (0.009)	6.25 (0.32)	0.012 (0.001)	4.76	31
	15	0.162 (0.021)	7.48 (0.67)	0.008 (0.002)	6.14	38
	20	0.137 (0.013)	13.65 (1.63)	0.015 (0.004)	9.53	70
	25	0.148 (0.014)	14.89 (1.57)	0.014 (0.004)	10.81	73
Great Whale River I	5	0.095 (0.006)	1.42 (0.05)	0.005 (0.001)	1.16	12
(17/7/95)	10	0.034 (0.003)	3.97 (1.27)	0.015 (0.008)	1.66	49
	15	0.078 (0.011)	3.80 (0.49)	0.006 (0.002)	2.93	38
	20	0.039 (0.003)	5.85 (0.71)	0.006 (0.002)	3.70	95
	25	0.037 (0.002)	5.99 (0.65)	0.005 (0.001)	3.93	106
Great Whale River II	5	0.087 (0.006)	1.58 (0.05)	0.003 (0.001)	1.35	16
(05/8/95)	10	0.034 (0.004)	3.52 (0.99)	0.010 (0.005)	1.74	51
	15	0.073 (0.008)	3.72 (0.29)	0.003 (0.001)	3.09	42
	20	0.040 (0.003)	7.19 (1.50)	0.011 (0.004)	3.71	93
	25	0.045 (0.003)	5.40 (0.52)	0.005 (0.001)	3.79	84

T, temperature (°C); α, initial slope (mg C (mg Chl *a* h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$); P_S, maximum photosynthetic rate obtained in the absence of photoinhibition (mg C (mg Chl *a* h)$^{-1}$); β, photoinhibited region (mg C (mg Chl *a* h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$); P_{max}, maximum photosynthetic rate (mg C (mg Chl *a* h)$^{-1}$); E_K, index of light saturation (P_{max}/α) (μmol photons m^{-2} s^{-1}).

I). In contrast, P_{max} increased with increasing temperature (Figure 3, Table I) as did photosynthesis at inhibiting irradiance (Figure 3). The β parameter remained constant over all temperatures (Table I). Photosynthetic capacity at 1400 μmol photons m^{-2} s^{-1} was inhibited by 50–60% at 25°C (relative to P_{max}), whereas at 5°C, inhibition rose to >90%.

The light saturation parameter (E_K) fell markedly with decreasing temperature in all experiments (Table I). We examined the implications of this temperature effect by calculating how frequently, on average, a phytoplankton cell would be exposed to an irradiance above its E_K for each temperature from daybreak (04:00 h) to sunset (23:00 h). With a seasonal average of 1200 μmol photons m^{-2} s^{-1} for midday incident irradiance (E_{av} = 528 μmol photons m^{-2} s^{-1} for Lake Kayouk), phytoplankton in Lake Kayouk would be exposed through most of the daylight period to an irradiance above their E_K at all depths and at any temperature. In the Great Whale River (E_{av} = 276 μmol photons m^{-2} s^{-1}), phytoplankton at 25°C would experience $E > E_K$ in only the top 25% of the water column throughout an 18 h day, in contrast to $E > E_K$ for 75–85% of the water column at lower temperatures (5–15°C). Therefore, the photosynthetic response of phytoplankton in the lake and at low temperature in the river ecosystem is more often one of temperature dependence than one of light dependence.

To evaluate further the interaction between temperature and irradiance, we plotted photosynthesis as a function of temperature (P–T curve) at a specific irradiance within each of the three P–E regions (Figure 4). In three of four experiments, the P–T slope at 35 μmol photons m^{-2} s^{-1} (α region, P_{35}) did not differ

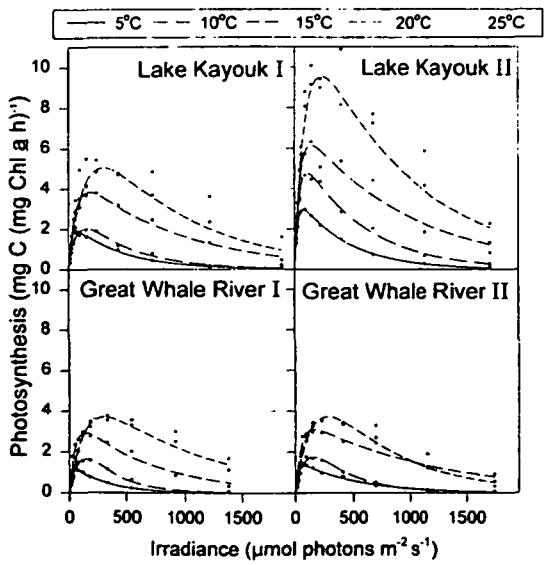

Fig. 3. Photosynthesis–irradiance curves from incubations at five temperatures for the total algal community of Lake Kayouk and the Great Whale River, on two occasions for each location.

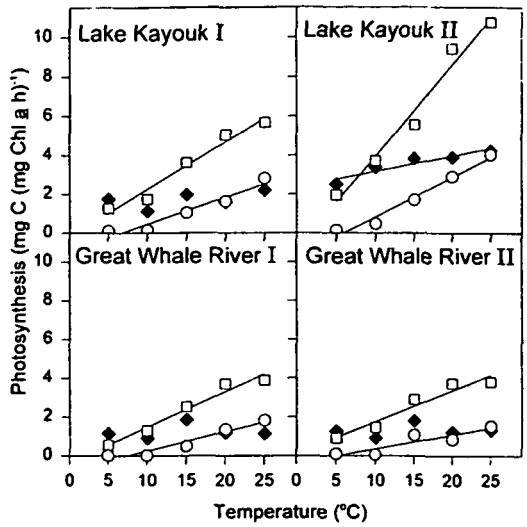

Fig. 4. Photosynthesis of the total algal community as a function of temperature for the three regions of the *P–E* curve. A specific irradiance was chosen to represent each region: ◆ P_{35} = 35 µmol photons m^{-2} s^{-1}; □ P_{280} = 280 µmol photons m^{-2} s^{-1}; ○ P_{1400} = 1400 µmol photons m^{-2} s^{-1}. A regression line has been drawn through those data with a slope significant at a probability of <0.05.

significantly from zero. In one experiment, Lake Kayouk II, photosynthesis at low irradiance did increase with increasing temperature. At irradiances in the P_{max} region (280 µmol photons m^{-2} s^{-1}, P_{280}) and β region (1400 µmol photons m^{-2} s^{-1}, P_{1400}), a strong influence of temperature is seen from the *P–T* curve (Figure 4). Linear regression analysis of the *P–T* plots resulted in highly significant regressions (probability ≤ 0.009) with >90% of the variation in photosynthesis explained by temperature in all but one case (Table II). *P–T* plots of P_{max} and $P_{50\%}$ showed slightly, but not significantly, lower slopes than the P_{280} and P_{1400} versus *T* plots, and similar r^2 and probability values. By fitting linear regressions through this data set, we were then able to compare statistically the slopes of the curves obtained in the P_{max} and β regions. The slope of the P_{280} curve was always significantly greater than that for the P_{1400} curve. Similarly, the slope of estimated P_{max} versus *T* was always higher than for $P_{50\%}$ versus *T* (Table II). Thus, for all of these subarctic populations, temperature had a consistently greater influence on photosynthesis at saturating irradiance than at inhibiting irradiances.

Environment-related temperature responses

The ensemble of *P–T* curves for each of the two ecosystems was compared by way of *t*-tests of the differences between means and slopes. P_{35} was significantly higher and the slope of the *P–T* curves for P_{280} and P_{1400} was significantly greater for the Lake Kayouk than the Great Whale River phytoplankton (Table III). The relative change in photosynthesis between 5 and 25°C was, however, the same in both environments.

Table II. Slope (SE) and regression characteristics of total community photosynthesis as a function of temperature for a representative irradiance in each region (P_{35}, P_{280} and P_{1400} = photosynthesis at 35, 280 and 1400 μmol photons m^{-2} s^{-1}, respectively; curves shown in Figure 4) and for actual P_{max} and photosynthesis at 50% inhibition from P_{max} ($P_{50\%}$). The *t* statistic indicates the result of a *t*-test for difference between the slopes of P_{280} and P_{1400}, and of P_{max} and $P_{50\%}$

Experiment	*P–E* curve region	Slope	r^2	Regression probability	*t* statistic
Lake Kayouk I	P_{35}	–	0.03	0.4	
	P_{280}	0.24 (0.03)	0.96	0.003	3.11*
	P_{1400}	0.14 (0.02)	0.91	0.008	
	P_{max}	0.21 (0.03)	0.93	0.005	3.26*
	$P_{50\%}$	0.10 (0.01)	0.93	0.005	
Lake Kayouk II	P_{35}	0.08 (0.02)	0.84	0.02	
	P_{280}	0.47 (0.04)	0.97	0.002	5.58*
	P_{1400}	0.20 (0.02)	0.97	0.002	
	P_{max}	0.41 (0.04)	0.97	0.001	2.60*
	$P_{50\%}$	0.20 (0.02)	0.97	0.002	
Great Whale River I	P_{35}	–	0.32	0.86	
	P_{280}	0.18 (0.02)	0.95	0.003	3.12*
	P_{1400}	0.10 (0.02)	0.90	0.009	
	P_{max}	0.15 (0.02)	0.94	0.004	4.94*
	$P_{50\%}$	0.08 (0.01)	0.94	0.004	
Great Whale River II	P_{35}	–	0.27	0.73	
	P_{280}	0.16 (0.03)	0.91	0.008	2.77*
	P_{1400}	0.07 (0.02)	0.77	0.03	
	P_{max}	0.14 (0.02)	0.90	0.01	4.04*
	$P_{50\%}$	0.07 (0.01)	0.89	0.01	

*Indicates significance at a probability of <0.05.

Table III. Results of *t*-tests to determine temperature-related differences in photosynthesis by the total algal community in Lake Kayouk (variable temperature environment) and the Great Whale River (stable temperature environment). For the α region (P_{35}), where the slope of the photosynthesis–temperature curve was found not to differ significantly from zero (i.e. non-significant regression), a *t*-test for difference between means was employed.[a] For the P_{max} and β regions (P_{280} and P_{1400}), where the slope does differ from zero, a *t*-test for difference between slopes was used. ΔP_{280} is the relative increase in P_{280} between 5 and 25°C

P–E curve region	Lake phytoplankton mean or slope (SE)	River phytoplankton mean or slope (SE)	*t* statistic
P_{35}[a]	2.64 (0.20)	1.27 (0.15)	5.45*
P_{280}	0.35 (0.03)	0.17 (0.02)	4.89*
P_{1400}	0.17 (0.02)	0.09 (0.01)	3.68*
ΔP_{280}	3.36	3.08	

*Indicates significance at a probability of <0.05.

Size-dependent temperature responses

Mean photosynthetic rate under conditions of low irradiance was consistently higher for the <2 μm size fraction than for the >2 μm cells, in both the lake and river environments (Table IV). On a relative scale, there was no difference in temperature response at P_{280} between fractions, with a 2.5–4 times increase in

Table IV. Results of *t*-tests to determine temperature-related differences between size categories (<2 μm versus >2 μm) within each region of the photosynthesis–irradiance curve. In cases where the slope of the photosynthesis–temperature curve was found not to differ significantly from zero (i.e. non-significant regression), a *t*-test for difference between means was employed.[a] In those instances where the slope does differ from zero, a *t*-test for difference between slopes was used. ΔP_{280} is the relative increase in P_{280} between 5 and 25°C

Experiment	*P–E* curve region	<2 μm community mean or slope (SE)	>2 μm community mean or slope (SE)	*t* statistic
Lake Kayouk I	P_{35}[a]	2.24 (0.28)	1.35 (0.16)	2.79*
	P_{280}	0.34 (0.05)	0.18 (0.02)	3.13*
	P_{1400}	0.19 (0.03)	0.10 (0.02)	2.30
ΔP_{280}		2.88	2.70	
Lake Kayouk II	P_{35}[a]	5.24 (0.47)	0.14 (0.04)	3.66*
	P_{280}	0.73 (0.11)	0.25 (0.04)	4.10*
	P_{1400}	0.34 (0.03)	0.11 (0.02)	6.84*
ΔP_{280}		3.48	3.71	
Great Whale River I	P_{35}[a]	1.59 (0.21)	0.90 (0.11)	2.96*
	P_{280}	0.26 (0.03)	0.10 (0.01)	4.56*
	P_{1400}	1.19 (0.70)	0.34 (0.20)	1.17
ΔP_{280}		4.0	2.52	
Great Whale River II	P_{35}[a]	1.45 (0.17)	0.83 (0.09)	3.25*
	P_{280}	0.19 (0.02)	0.08 (0.02)	3.45*
	P_{1400}	0.08 (0.02)	0.04 (0.01)	1.68
ΔP_{280}		2.87	2.71	

*Indicates significance at a probability of <0.05.

P_{280} from 5 to 25°C. However, on an absolute scale, the temperature response of P_{280} was significantly different between the two size fractions with a greater slope for the picoplankton. Analysis for P_{1400} yielded a significant difference between slopes in only one of the four experiments.

A striking difference between the picoplankton and larger cell fractions is in the amount of carbon fixed per unit Chl *a*. Regardless of temperature, the <2 μm photosynthetic rate (P_{max}) was consistently double that of larger cells (Figure 5). The picoplankton were, however, more sensitive to bright light than were the >2 μm cells, as can be seen by the larger β parameters and the more rapid decline of photosynthesis from P_{max} by the picoplankton (Figure 5). Under the combination of low temperature (5 and 10°C) and strong inhibiting irradiance (>1000 μmol photons m^{-2} s^{-1}), photosynthesis by both fractions declined to values close to zero.

Photosynthesis versus temperature and irradiance model

Photosynthesis at P_{280} and P_{max} rose linearly with increasing temperature between 5 and 25°C (Figure 4, Table II). We therefore surmised that the equation (1) model of *P* versus *E* could be modified to incorporate temperature by including a linear temperature term as follows:

$$P = (\gamma T)\,(1 - \exp{-(\alpha E/\gamma T)})(\exp{-(\beta E/\gamma T)}) \quad (2)$$

where γ is an estimated parameter describing P_S per degree Celsius and T is temperature in degrees Celsius. Therefore, P_S as a function of temperature (P_{ST}) can be derived as:

$$P_{ST} = \gamma T \tag{3}$$

P_{max} is determined for a specific temperature (P_{maxT}) using the Platt *et al.* (1980) derivation:

$$P_{maxT} = P_{ST}(\alpha/(\alpha + \beta))(\beta/(\alpha + \beta))^{\beta/\alpha} \tag{4}$$

and E_K can be calculated for a specific temperature (E_{KT}) as:

$$E_{KT} = P_{maxT}/\alpha \tag{5}$$

The γT term adequately described both the increase in P_{max} with increasing temperature between 5 and 25°C, and the decrease in photoinhibition over this temperature range. Consistent with our experimental results, the initial slope of the curve was not affected using this formulation. We applied this model to each of the total, >2 μm and <2 μm data sets by non-linear regression analysis. The *P–T–E* model consistently explained ≥74% of the variation in photosynthesis, and for more than half of the data sets explained ≥90% of the variation (Table V), 37–61% more than was explained by irradiance alone.

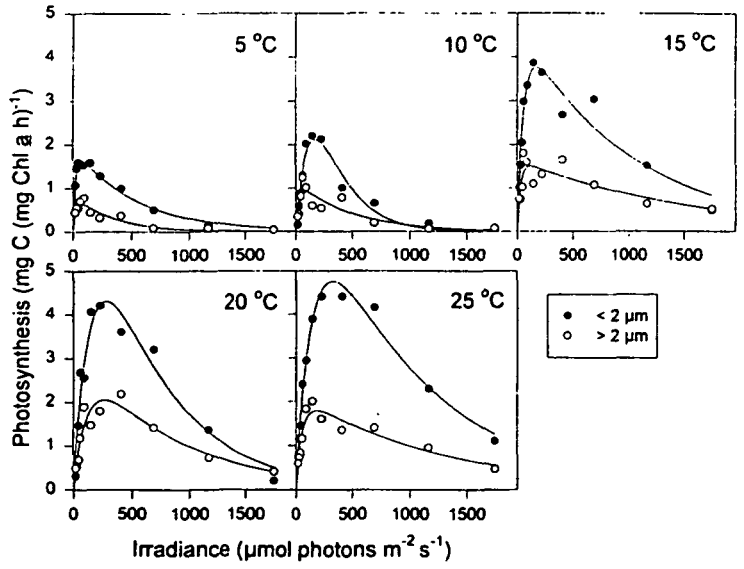

Fig. 5. Representative photosynthesis–irradiance relationships at five temperatures for picoplankton (<2 μm) and larger plankton (>2 μm) (data from experiment Great Whale River II).

Table V. Parameters (SE) obtained from fitting the photosynthesis–temperature–irradiance (*P–T–E*) model by non-linear regression to the data sets. The regression values reported are all significant at a probability of <0.0001

Experiment	Size fraction	α	β	γ	r^2
Lake Kayouk I	Total	0.066 (0.005)	0.006 (0.001)	0.33 (0.03)	0.92
	>2 μm	0.056 (0.004)	0.004 (0.001)	0.22 (0.02)	0.90
	<2 μm	0.082 (0.008)	0.010 (0.003)	0.52 (0.07)	0.83
Lake Kayouk II	Total	0.146 (0.008)	0.012 (0.002)	0.60 (0.03)	0.95
	>2 μm	0.153 (0.020)	0.006 (0.001)	0.28 (0.02)	0.82
	<2 μm	0.192 (0.015)	0.023 (0.005)	1.07 (0.11)	0.89
Great Whale River I	Total	0.043 (0.003)	0.006 (0.001)	0.26 (0.03)	0.91
	>2 μm	0.034 (0.005)	0.003 (0.001)	0.14 (0.02)	0.74
	<2 μm	0.053 (0.004)	0.009 (0.003)	0.42 (0.06)	0.91
Great Whale River II	Total	0.047 (0.004)	0.005 (0.001)	0.25 (0.03)	0.88
	>2 μm	0.036 (0.005)	0.002 (0.001)	0.10 (0.01)	0.79
	<2 μm	0.050 (0.004)	0.008 (0.002)	0.34 (0.05)	0.87

α, initial slope (mg C (mg Chl *a* h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$); β, photoinhibited region (mg C (mg Chl *a* h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$); γ, maximum photosynthesis, per degree Celsius, obtained in the absence of photoinhibition (mg C (mg Chl *a* h)$^{-1}$ °C^{-1}).

To evaluate further the suitability of models, we examined the residuals from application of the *P–E* [equation (1)] and *P–T–E* [equation (2)] models to the subarctic data set. The *P–E* residuals increased with temperature, indicating the need for a linear temperature term (Figure 6A). Residuals from the *P–T–E* equation curve fitting showed an overestimation by the model at highest irradiances (Figure 6B). There also appeared to be a bias at low temperature (5 and 10°C) with an underestimation at 5°C (positive residuals) and an overestimation at 10°C (negative residuals) (Figure 6C). These disparities were minor, however, relative to the overall goodness of fit of the *P–T–E* equation.

Using the model parameters given in Table V, we plotted *P–E* and *P–T* curves in order to examine visually the results of the *P–T–E* model (Figure 7). The *P–E* relationship shows clearly the lack of temperature effect on α, the increase in P_{max} with increasing temperature and the increase in photosynthesis at inhibiting irradiance with no effect on the shape of the curve in the β region (i.e. no temperature effect on the β parameter). The *P–T* curves using the three representative irradiances indicate four elements of the *P–T–E* model that appear to be inherent properties: (i) at 0°C photosynthesis is zero; (ii) at low temperature (<10°C) photosynthesis at limiting irradiance is no longer independent of temperature; (iii) at low temperature (≤8°C) photosynthesis at limiting irradiance is greater than at saturating irradiance; (iv) at low temperature (<10°C) and inhibiting irradiance photosynthesis decreases with decreasing temperature in a non-linear fashion.

Parameters obtained from fitting the *P–T–E* model show clearly the differences between the <2 and >2 μm fractions. In all experiments, the picoplankton had a greater initial slope (α) and higher γ values than for the larger cells (Table V), indicating their higher photosynthetic rates and greater responsiveness to temperature. The greater sensitivity of the smaller cells to inhibiting irradiance is

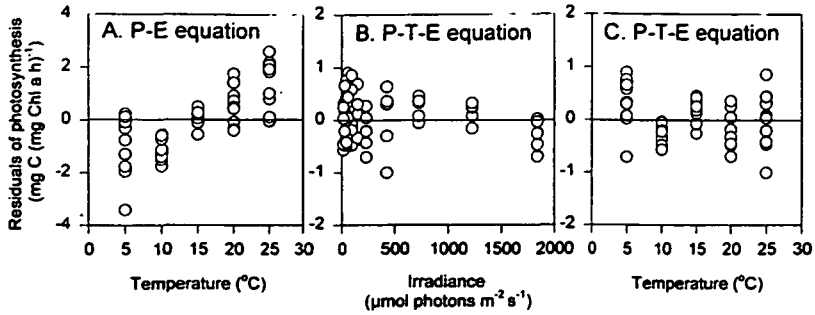

Fig. 6. Representative plots of residuals from non-linear regression analysis of photosynthetic data as a function of the independent variables temperature and irradiance. **(A)** Residuals from running the Platt *et al.* (1980) equation; **(B)** and **(C)** residuals from running the *P–T–E* equation (data for total community, experiment Lake Kayouk I).

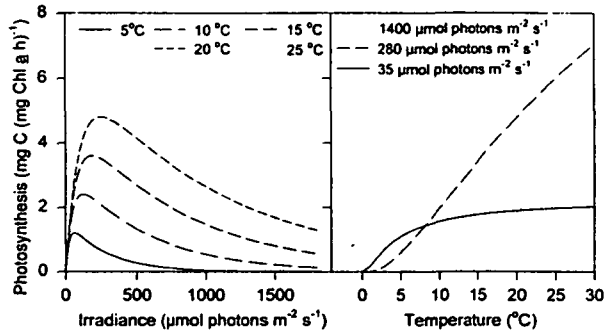

Fig. 7. Representative *P–T* and *P–E* curves plotted using parameters determined by running the *P–T–E* model (data for experiment Lake Kayouk I, see Table V).

seen from the consistently larger β parameter for the picoplankton (Table V). The γ parameter also suggests a greater responsiveness to temperature by the Lake Kayouk phytoplankton in each of the three size groupings as compared with phytoplankton from the Great Whale River (Table V).

Discussion

This study has shown that temperature can substantially affect the short-term photosynthetic performance of phytoplankton in subarctic freshwater environments. As temperature increases over the ambient range of 5–25°C, photosynthetic activity is enhanced at both saturating and inhibiting irradiance. Previous studies examining the temperature response of P_{max} have reported these findings for a wide range of environments and algal species (e.g. Li *et al.*, 1984; Priscu and Goldman, 1984; Tilzer *et al.*, 1986; Smith *et al.*, 1994; Blanchard *et al.*, 1997). The observed temperature effect on P_{max} is consistent with the established view that

temperature-dependent biochemical reactions, e.g. Rubisco activity (Li *et al.*, 1984), are the rate-limiting steps of photosynthesis at light saturation (Davison, 1991).

Increasing per cent photoinhibition (relative to P_{max}) with decreasing temperature is interpretable in terms of the cellular processes occurring at inhibiting irradiance. Firstly, at lower temperature, enzymes within the photosynthetic apparatus are operating at slower rates and so the 'excitation pressure' (*sensu* Maxwell *et al.*, 1994) on photosystem II reaction centres will be higher (Raven and Geider, 1988), resulting in greater damage. Secondly, the low temperatures will impair the balance between photochemical damage and biosynthetic repair.

Light-limited photosynthesis was not affected by temperature, consistent with the view that the rate-limiting steps are photochemical (i.e. electron transport) rather than biochemical (e.g. enzymatic reactions in the Calvin cycle) over the α region of the *P–E* curve (Falkowski and Raven, 1997). In one of four experiments, a positive relationship was observed between photosynthesis at P_{35} and temperature, suggesting that the designation of 35 μmol photons m^{-2} s^{-1} as a representative irradiance for the α region placed the photosynthesis values at or beyond E_K and therefore under the influence of P_{max}.

Increasing E_K with increasing temperature was found in the present study, as elsewhere (Collins and Boylen, 1982; Palmisano *et al.*, 1987; Henley, 1992), and is the direct result of the dependence of E_K on P_{max} (Beardall and Morris, 1976; Henley, 1993). This effect has important implications for total water-column photosynthesis, which do not appear to have been previously considered. Photosynthesis by a cell at depths where $E < E_K$ will be light dependent, whereas photosynthesis at $E > E_K$ will be temperature dependent. Thus, in cold water columns, more of the population will achieve P_{max} than at higher temperatures, because of lower E_K. This is not the case in Lake Kayouk where the entire water column experiences temperature-dependent photosynthetic irradiance levels at any given temperature during daylight hours. However, the deeper water column and greater light attenuation of the Great Whale River means that as temperature decreases from 25 to 5°C, the percentage of the water column that is light dependent for photosynthesis decreases with a corresponding increase in temperature dependency. As a result, photosynthesis in shallow, cold water columns will be operating primarily in the P_{max} and β regions, and thus subject to control by temperature.

The phytoplankton communities from each environment examined in this study differed in their photosynthetic responses to temperature on an absolute scale. The greater responses of the lake community might reflect their greater ability to respond to temperature fluctuations in this thermally more variable environment, relative to the river.

The photosynthetic response to temperature within each region of the *P–E* curve was analysed by linear regression analysis rather than by the more commonly reported Q_{10} value. The Q_{10} approach is often based on only two measurements, but implies a continuous exponential rise with temperature (Ahlgren, 1987) which is unlikely to be achieved in complex biological systems. The Q_{10} function also fails to consider the physiological impairment of cells (e.g.

state transitions of lipid membranes) which occurs at certain high and low temperature thresholds. A more appropriate description of a biological rate response over a large temperature range may be made by a parabolic function, as has recently been developed for use with a cyanobacterial growth data set (Tang *et al.*, 1997). In the present study, photosynthesis increased linearly throughout the temperature range, and we did not achieve temperatures that would impair the cells and cause a reduction in photosynthetic rates. These results imply that subarctic phytoplankton are capable of metabolic activity under a broad range of temperatures, reflecting the highly variable nature of their environment.

The incorporation of a temperature parameter into the *P–E* model of Platt *et al.* (1980) allowed us to describe the photosynthetic response of phytoplankton communities as a continuous function of both irradiance and temperature. Although the analysis of residuals showed some evidence of bias, these effects were small relative to the overall goodness-of-fit. The model was developed for subarctic fresh waters and provided an accurate description of the *P–T–E* relationship for optically and thermally contrasting environments, and is likely to be applicable to other aquatic ecosystems. In its current form, the model would not be appropriate for extreme cold water systems in which photosynthesis is significant at or below 0°C (e.g. Li *et al.*, 1984; Andersson *et al.*, 1994), but can be readily modified to fit such circumstances by expressing temperature as:

$$T = T_p - T_x \tag{6}$$

where T_p is the temperature at which the photosynthetic measurements were made and T_x is the x intercept for the experimental P_{max} versus T relationship. In this way, the T term in the *P–T–E* model can be adjusted to give zero photosynthesis at a specific temperature, above or below 0°C.

Some disparities in the *P–T–E* model, as observed in Figure 7, are evident at low temperatures. From 5 to 25°C, the temperature range with which we developed the model, the curve of photosynthesis at limiting irradiance is not significantly different from zero. However, at very low temperatures, there is a temperature effect. Although this is consistent with some reports in the literature (Tilzer *et al.*, 1986; Palmisano *et al.*, 1987; Raven and Geider, 1988), we are unable to determine whether it is genuine for subarctic lakes. The larger photosynthetic rates at P_{35} in comparison to those at P_{280} when $T \leq 8$°C are due to the fact that the latter irradiance is inhibiting for photosynthesis at low temperature (cf. Figure 3). Therefore, the observed form of the curves is a feature of the data, as well as the model. A third observation is the non-linearity of photosynthesis at inhibiting irradiance as temperature approaches 0°C. This curve gives a better fit to the measured photosynthetic data than the linear regression we originally used (cf. Figure 4) since photosynthetic rates at P_{1400} for both 5 and 10°C were similar and very low.

The three-parameter *P–T–E* model differs from previous attempts to describe the combined influence of irradiance and temperature on photosynthesis. A variety of photosynthesis–temperature equations have been used to describe photosynthetic rate at light saturation with changing temperature (e.g.

Kamykowski, 1985; Li, 1985; Li and Dickie, 1987; Blanchard *et al.*, 1997), but without extension to other regions of the *P–E* curve. The Platt *et al.* (1980) equation has also been modified previously by the replacement of the irradiance term with a temperature function (Knoop and Bate, 1990). Multiple regression analysis incorporating an exponential temperature dependency by P_{max} was used by Keller (1989) to model daily production rates. Similarly, Morel (1991) noted the controversial nature of temperature effects on growth and incorporated a Q_{10} function in a model of daily water column production. The Q_{10} relationship, as shown above, is not appropriate to our subarctic data set. The influence of temperature on the *P–E* response of a cyanobacterium has been modelled using E_K as an exponential function of temperature, allowing the prediction of an increase in P_{max} and a decrease in β region photosynthesis with increasing temperature (Collins and Boylen, 1982). However, a change was also apparent with light-limited photosynthesis whereby α decreased as temperature increased and therefore the model was not applicable to our data set.

Size fractionation into picoplankton (<2 μm) and nano- and microplankton (>2 μm) fractions revealed differences consistent with our hypothesis that the predominantly cyanobacterial picoplankton would show a stronger temperature dependence than larger, mostly eukaryotic, cells. Picocyanobacterial abundance has been found to correlate positively with seasonal temperature in Lake Ontario (Caron *et al.*, 1985), other smaller Ontario lakes (Pick and Agbeti, 1991) and in the St Lawrence River estuary (Bertrand and Vincent, 1994). Recent experiments on filamentous cyanobacteria isolated from subarctic, arctic and Antarctic environments have shown that growth rates are also highly responsive to temperature (Tang *et al.*, 1997). Photosynthesis of picocyanobacteria from the northern Baltic Sea was found to be strongly temperature dependent between 0 and 10°C as opposed to that of nano- and microphytoplankton fractions (Andersson *et al.*, 1994). Shiomoto *et al.* (1997) found that picoplankton productivity corresponded to and sometimes was lower than that of larger cells at temperatures <10°C, while at $T > 10$°C picoplankton were significantly more productive than larger cells. A study conducted in the tropical ocean, however, reported similar variations in P_{max} with temperature for picoplankton and larger phytoplankton (Smith and Platt, 1985).

Size-dependent responses to irradiance have been demonstrated elsewhere, with picoplankton usually exhibiting greater photosynthetic performance than larger cells at low irradiance (e.g. Platt *et al.*, 1983), although results to the contrary have also been reported (Frenette *et al.*, 1996). In the present study, the picoplankton appear to be more efficient at capturing light at low irradiance, resulting in higher photosynthetic rates per unit Chl *a*. The picoplankton had higher α and larger E_K values than the >2 μm cells, which carries implications for the size dependency of temperature effects. With a higher E_K, picoplankton will be exposed to $E < E_K$ (light dependence for photosynthesis) more often than the larger cells, and so picoplanktonic photosynthesis will less often be temperature dependent ($E > E_K$).

Although the relative increase in P_{max} over the 5–25°C range was the same in both fractions, the absolute increase was greater for the picoplankton, implying

that the <2 μm cells will be more responsive to warming or cooling trends. A long-term warming trend has been detected at northern high latitudes (Walsh, 1995). Future climate change scenarios for these regions should consider the implication of size-dependent responses to temperature as observed in the present study. Our findings suggest differential effects that could result in an altered size structure of phytoplankton communities in this area, with implications for food web relationships and the efficiency of carbon transfer to higher trophic levels.

The results of the present study are from small-volume, short-term incubation experiments that provide information on phytoplankton response to a rapid change in irradiance and temperature. As shown in this and other studies, the subarctic freshwater environment is dynamic with short-term changes in both temperature and underwater light environments (Milot-Roy and Vincent, 1994). However, in their natural environment and at time scales longer than in our experiments, the phytoplankton will adjust to changes in their thermal regime via acclimation and adaptation processes (Davison, 1991). Nonetheless, the data show how irradiance and temperature can act in concert over short time intervals to regulate phytoplankton photosynthesis in the northern freshwater environment.

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