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# CYANOBACTERIAL DOMINANCE OF POLAR FRESHWATER ECOSYSTEMS: ARE HIGH-LATITUDE MAT-FORMERS ADAPTED TO LOW TEMPERATURE?[1]

*Evonne P. Y. Tang,*[2] *Roxanne Tremblay, and Warwick F. Vincent*

Département de biologie, Université Laval, Sainte-Foy, Québec, Canada G1K 7P4

ABSTRACT

*Although it is generally believed that cyanobacteria have high temperature optima for growth (> 20° C), mat-forming cyanobacteria are dominant in many types of lakes, streams, and ponds in the Arctic and Antarctic. We studied the effect of temperature on growth (μ) and relative pigment composition of 27 isolates of cyanobacteria (mat-forming Oscillatoriaceae) from the Arctic, subarctic, and Antarctic to investigate whether they are a) adapted to the low temperature (i.e. psychrophilic) or b) tolerant of the low temperature of the polar regions (i.e. psychrotrophic). We also derived a parabolic function that describes both the rise and the decline of cyanobacterial growth rates with increasing temperature. The cyanobacteria were cultured at seven different temperatures (5°–35° C at 5° C intervals), with continuous illumination of 225 μmol photons·$m^{-2}$·$s^{-1}$. The parabolic function fits the μ-temperature data with 90% confidence for 75% of the isolates. Among the 27 isolates of cyanobacteria studied, the temperature optima ($T_{opt}$) for growth ranged from 15° to 35° C, with an average of 19.9° C. These results imply that most polar cyanobacteria are psychrotrophs, not psychrophiles. The cyanobacteria grew over a wide temperature range (typically 20° C) but growth rates were low even at $T_{opt}$ (average $\mu_{max}$ of 0.23 ± 0.069 $d^{-1}$). Extremely slow growth rates at low temperature and the high temperature for optimal growth imply that the cyanobacteria are not adapted genetically to cold temperatures, which characterize their ambient environment. Other competitive advantages such as tolerance to desiccation, freeze–thaw cycles, and bright, continuous solar radiation may contribute to their dominance in polar aquatic ecosystems.*

*Key index words: Antarctic; Arctic; cyanobacteria; growth; low temperature; microbial mats*

The phytoplankton in many temperate freshwater ecosystems is often dominated by cyanobacteria during mid- to late summer (Paerl 1988, Mitchell and Prepas 1990, Stevenson and White 1995). The dominance of cyanobacteria at this time of the year has been variously attributed to their superior light-capturing abilities when self-shading is the greatest (Post et al. 1986, Tilzer 1987), their high affinity for nitrogen and phosphorus when nutrient limitation is the most severe (V. H. Smith 1983, Klemer and Konopka 1989), and their ability to regulate their position in well-stratified water columns (Konopka et al. 1978, Klemer and Konopka 1989, Kromkamp and Walsby 1990). In addition, warm summer temperatures appear to favor bloom-forming cyanobacteria because many species have high temperature optima for growth and photosynthesis (> 20° C; Reynolds 1984). There are numerous studies reporting positive correlations between cyanobacterial abundance and water temperature regardless of whether they are bloom-forming, mat-forming (Varis 1993), or pico-cyanobacteria (Murphy and Haugen 1985, Williams et al. 1994).

Although cyanobacteria are generally assumed to have high temperature optima for growth and photosynthesis (Tilman et al. 1986, Robarts and Zohary 1987, 1992), cyanobacteria are often the major component of autotrophic community biomass and productivity in polar lakes and streams, particularly shallow water ecosystems (Vincent et al. 1993, Hamilton and Edlund 1994, Vézina and Vincent 1997). The predominant species are Oscillatoriaceans, which form mats and films across the benthic substrate in many types of lakes, streams, and ponds in the Arctic as well as in the Antarctic (Vincent 1988, Hawes and Brazier 1991). Their dominance in cold water habitats suggests that either they are psychrophilic or they are psychrotrophic. True psychrophiles have temperature optima of ≤15° C and a maximum growth temperature below 20° C (Morita 1975) such that they are well adapted to cold water environments. Psychrotrophs are tolerant to the cold temperature but they have temperature optima >15° C (Brock et al. 1994). There are suggestions that algae in low temperature environments have lower temperature optima and lower thermal thresholds than those from the temperate zones (Palmisano et al. 1987, Davison 1991). Marine diatoms isolated from the Arctic ocean are indeed psychrophilic (R. E. H. Smith et al. 1994, Suzuki and Takahashi 1995). However, the occurrence of Antarctic algae that are not photosynthetically adapted to the low ambient temperature have also been reported (Davison 1991, Castenholz and Schneider 1993). The purpose of the present study was to determine whether a broad range of mat-forming Oscillatoriaceans isolated from the Arctic, subarctic, and the Antarctic are adapted to the low temperature (psychrophilic) or they are simply cold-tolerant with suboptimal growth at low ambient temperatures (psychrotrophic).

Cyanobacteria in the polar areas may have developed adaptive strategies to help them flourish in the low-temperature environment. For example, cells may allocate resources away from photosynthetic light reaction components toward the enzymes that

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[2] Author for reprint requests.

control dark fixation (Raven and Geider 1988). It is often the dark fixation that limits photosynthesis at low temperatures. Thus, chlorophyll *a* (Chl *a*) content decreases with temperature (Geider 1987, Thompson et al. 1992). Also, algal cells are generally more sensitive to photoinhibition at low temperatures (Falk et al. 1990, Davison 1991), but this may be offset by natural protective mechanisms such as the alteration of pigment ratios (Vincent et al. 1992). Therefore, we also compared the carotenoid to Chl *a* ratios and the *in vivo* absorbance of carotenoids, phycocyanin (PC), and allophycocyanin (APC) relative to Chl *a* for isolates of cyanobacteria grown at different temperatures.

The relationship between biological processes, such as algal growth and temperature, has often been described by $Q_{10}$ or Arrhenius functions (Ahlgren 1987, Regier et al. 1990). However, both of these functions assume continuous acceleration of growth with increasing temperature. In fact, algal growth rates increase up to the optimal temperature ($T_{opt}$), beyond which they decrease (Collins and Boylen 1982, Fan et al. 1994, Suzuki and Takahashi 1995). A second objective of this study was to develop a mathematical function to describe the growth–temperature data with the least possible number of free parameters.

## MATERIALS AND METHODS

Twenty-seven unialgal isolates of cyanobacteria sampled from ice-melt ponds, glacier-fed streams, or nearshore of lakes in the Arctic (Northern Alaska and the Canadian Arctic Archipelago), subarctic (northern Québec), and Antarctic (McMurdo Sound region) were used to examine the relationship between growth and temperature (Table 1). Cyanobacterial mats were collected between 1991 (O-025–O-099 and O-salt) and 1995 (E2–E18). Upon collection, they were transferred to agar plates containing BG-11 culture medium (Castenholz 1988). To obtain monoclonal cultures of cyanobacteria, the field material was streaked onto fresh BG-11 agar plates. Individual filaments were then picked from streaked plates and transferred to separate culture vessels containing small quantities of culture media. Regular, microscopic inspections were performed to ensure that the cultures were unialgal.

All of the isolates were mat-forming filamentous species of the genus *Oscillatoria* or *Phormidium*. The cultures were maintained in sterilized BG-11 medium (Allen 1973, Castenholz 1988) at 13.3 ± 0.1° C under continuous illumination of 45 μmol photons·$m^{-2}$·$s^{-1}$. Cultures were not axenic, but few bacteria were present.

*Experimental conditions.* Each of the 27 isolates was assayed for its growth rates at seven different temperatures ranging from 5° to 35° C at 5° C intervals. The cultures were incubated in temperature-controlled chambers at an irradiance of 225 ± 15 μmol photons·$m^{-2}$·$s^{-1}$, as measured with a QSL 100 photometer (Biospherical Instruments Inc.) equipped with a 4π sensor. Previous studies showed that such an irradiance is high enough to saturate growth in most cyanobacterial species without inducing photoinhibition (Foy 1983, Vézina 1995). Constant illumination was provided by 40W cool-fluorescent tubes.

*Growth measurements.* The growth rate of each isolate at each temperature was estimated as changes in optical density over time (Sorokin 1973). The optical density of an algal culture is correlated positively with cell abundance (Wyman and Fay 1986, Vézina 1995). Fourteen 150-mL Erlenmeyer flasks containing 100-mL of BG-11 medium were inoculated with a uniform inoculum of a cyanobacterial isolate to yield a final turbidity of 0.015 ± 0.005 at 750 nm. Every 2 days, two flasks were chosen haphazardly for turbidity measurement, starting from day 0, for a total of 12 days. All turbidity measurements were performed with a Spectronic 1001 spectrophotometer at 750 nm. The logarithm of turbidity was plotted against time. Growth rate was estimated as changes in turbidity over time from the log-linear portion of the curve using linear regression analysis.

TABLE 1. *A list of the 27 isolates of polar cyanobacteria used in this study, their physical descriptions, and their original habits. NA = not available. All isolates except E17, O-201, and O-salt have been identified to the genus* Phormidium *according to the criteria of Anagnostidis and Komárek (1988). The rest belong to the genus* Oscillatoria. *O-salt has been previously identified as* O. priestleyi *and O-099 as* P. murrayi *in Vincent and Quesada (1994). Isolates O-152 and O-154 were identified as* P. autumnale *in Vézina and Vincent (1997). Temperature data were from [a]pers. observ., [b]Alexander et al. (1989), [c]S. Vézina, pers. commun., and [d]Castenholz and Schneider (1993). The cultures are maintained at the Université Laval culture collection.*

| Isolate | Original habitat | Latitude and longitude | Type of system | Temperature (° C) |
|---|---|---|---|---|
| | | Arctic | | |
| E2 | Char Lake | 74° N, 94° W | Stream | 5[a] |
| E5 | Resolute | 74° N, 94° W | Stream | 5.4[a] |
| E6a | Resolute | 74° N, 94° W | Pond | 5.1[a] |
| E7 | Resolute | 74° N, 94° W | Pond | 4.4[a] |
| E11a | Devon Island | 74.5° N, 89.5° W | Pond | 0.4[a] |
| E11b | Devon Island | 74.5° N, 89.5° W | Pond | 0.4[a] |
| E12 | Devon Island | 74.5° N, 89.5° W | Pond | 7.1[a] |
| E17 | Resolute | 74° N, 94° W | Pond | NA |
| E18 | Meretta Lake | 74° N, 94° W | Lake | 7[a] |
| O-102 | Toolik Lake | 68° N, 148° W | Pond | 6–8[b] |
| O-104 | Toolik Lake | 68° N, 148° W | Pond | 6–8[b] |
| O-120 | Toolik Lake | 68° N, 148° W | Stream | 6–8[b] |
| O-152 | Bylot Island | 73° N, 78° W | Pond | 10–15[c] |
| O-154 | Bylot Island | 73° N, 78° W | Pond | 10–15[c] |
| O-157 | Bylot Island | 73° N, 78° W | Pond | 2–3[c] |
| O-160 | Bylot Island | 73° N, 78° W | Pond | 10–15[c] |
| | | Subarctic | | |
| O-201 | Poste de la Baleine | 55° N, 77° W | Lake | 10–15[c] |
| O-202 | Poste de la Baleine | 55° N, 77° W | Pond | 10–15[c] |
| O-203 | Poste de la Baleine | 55° N, 77° W | Pond | 10–15[c] |
| O-204 | Poste de la Baleine | 56° N, 74° W | Pond | 10–15[c] |
| O-210 | Lac à la l'eau Claire | 56° N, 74° W | Lake | 5–6[c] |
| O-211 | Lac à la l'eau Claire | 56° N, 74° W | Lake | 5–6[c] |
| | | Antarctic | | |
| O-salt | McMurdo Ice Shelf | 78° S, 166° E | Pond | 0–8[d] |
| O-025 | McMurdo Ice Shelf | 78° S, 166° E | Lake | 0–8[d] |
| O-042 | McMurdo Ice Shelf | 78° S, 166° E | Pond | 0–8[d] |
| O-043 | McMurdo Ice Shelf | 78° S, 166° E | Pond | 0–8[d] |
| O-099 | McMurdo Ice Shelf | 78° S, 166° E | Pond | 0–8[d] |

*Pigment analyses.* After 10 days of growth, duplicate samples were taken for extractable Chl *a* and carotenoid analyses. Five to 45 mL of cultures, depending on their optical density, were filtered onto Whatman GF/F filter. The filters were wrapped in aluminum foil and kept frozen until analysis. Chlorophyll *a* and carotenoids were extracted using the methods outlined in Quesada and Vincent (1993). Briefly, the filters were ground with a Teflon pestle and subsequently extracted in 90% acetone. The spectrophotometric absorption was measured at 663 and 480 nm for the determination of Chl *a* (Marker et al. 1980) and carotenoid (Britton 1985), respectively. In some cases, the Chl *a* concentration of the extract was not high enough to produce a reliable measurement on the spectrophotometer. For these samples, the Chl *a* was measured with a Shimadzu RF 5000 spectrofluorometer calibrated with standard Chl *a* (Sigma Chemical Co.).

*In vivo absorbance.* For nine of the strains (E2–E18), an *in vivo* absorption spectrum was measured with a HP-8425A diode array spectrophotometer (Hewlett Packard) connected to a RSA-HP-84

integrating sphere (Labsphere Inc.). The *in vivo* absorbance peaks were recorded at 480 nm for carotenoids, 620 nm for PC, 650 nm for APC, and 680 nm for Chl *a*. All values were corrected for background absorbance by subtracting the absorbance at 750 nm from all values. The absorption of each pigment was expressed relative to that of Chl *a*.

*Curve-fitting.* Prior to modeling the relationship between cyanobacterial growth rates and temperature, we inspected the $\mu$-temperature curves visually, and we observed that this relationship generally took the form of a parabola. Therefore, we attempted to fit a parabolic function expressed in terms of standard growth parameters through the $\mu$ versus temperature data series for each of the 27 isolates. The equation is

$$\mu = \mu_{max} - \mu_{max}[(T_{opt} - T)^2/(0.5\Delta T)^2], \quad (1)$$

where $\mu$ is the observed growth rate at temperature T, $\mu_{max}$ is the maximum growth rate, $T_{opt}$ is the temperature at which $\mu = \mu_{max}$, and $0.5\Delta T$ is the range of temperature over which $\mu$ is increasing with T. Temperatures at which there was no detectable growth were excluded from the curve-fitting. The advantage of fitting the data with this equation is that there are only three estimated parameters. Since the growth experiments were performed at only seven different temperatures, it was essential that the fitted curve had the least number of parameters so as to maximize the degrees of freedom.

For each fitted curve, a Pearson correlation analysis between the observed and the fitted values was performed to evaluate the goodness of fit. In the cases where Equation 1 did not fit the data with 90% confidence, no alternative curve-fitting was attempted. In those cases, we assumed that $\mu_{max}$ was the highest observed $\mu$ and that $T_{opt}$ was the temperature at which $\mu_{max}$ was obtained. The average $Q_{10}$ for growth was calculated between the minimum temperature at which $\mu$ was detectable and $T_{opt}$.

*Statistics.* The mean temperature optima of cyanobacteria isolated from the Arctic, Antarctic, and the subarctic were compared using one-way analysis of variance. To test whether or not the optimal growth temperature of cyanobacteria differs significantly from the temperature of their original habitat, a pairwise *t*-test was performed. Data on temperature optima for cyanobacterial growth in temperate regions were collected from the literature for comparison. In addition to the data collated by Robarts and Zohary (1987), we also did a CD-ROM search (Biological Abstracts) on the 1985–1995 literature for $T_{opt}$ data using the key words cyanobacteria and temperature. When $\mu_{max}$ or $T_{opt}$ were reported in ranges, the midpoints were recorded. These data were used to test for possible differences between temperature optima of polar and temperate cyanobacteria using *t*-tests.

## RESULTS

*Curve-fitting.* All 27 isolates of polar cyanobacteria showed an initial increase of growth with increasing temperature up to a maximum ($\mu_{max}$, $T_{opt}$). Beyond this optimal temperature, growth typically decreased with a more rapid decline at higher temperatures (Fig. 1). The parabolic function (Eq. (1)) fits the $\mu$-temperature data with 90% confidence for 75% of the isolates (Table 2). For the rest of the isolates, there was a marked deviation from the parabolic relationship and no curve-fitting was attempted. For certain isolates, the lack of fit was a result of a continuous increase in $\mu$ with increasing temperature over the full experimental range (isolate O-120; Fig. 1), or it was due to the minimal variations in $\mu$ with changing temperature (isolate O-154; Fig. 1).

*$\mu$-temperature relation.* Only 18 of the isolates displayed detectable growth at 5° C (Fig. 1) despite temperatures of their original habitats at the time of sampling ranging from 0.4° to 15° C (Table 1). The maximum temperature at which growth was observed was 20°–35° C (Fig. 1). The temperature range with observable growth spanned 10° C (isolate O-157) to 30° C (isolate O-120), and the modal range was 20° C (Fig. 1).

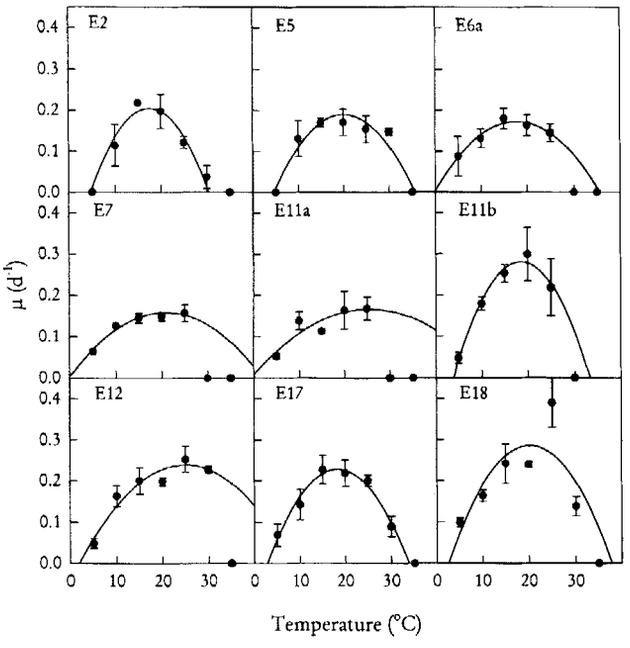
Average $Q_{10}$ values computed for the rising portion of the $\mu$-temperature curve (Table 2) varied from 1.14, which suggests minimal variation of growth with temperature, to 64, a value implying strong inhibition at the lowest temperature beyond simple Arrhenius effects. The mean $Q_{10}$ for the 27 isolates was 4.85 ± 11.7. However, if we exclude the anomalously high value ($Q_{10}$ = 64) for isolate O-042, the mean $Q_{10}$ becomes 2.6 ± 1.46 (Table 2). Our $Q_{10}$ estimates were conservative because $\mu$ increased more rapidly with temperature in the lower temperature range. These values nevertheless suggest high responsiveness to temperature changes.

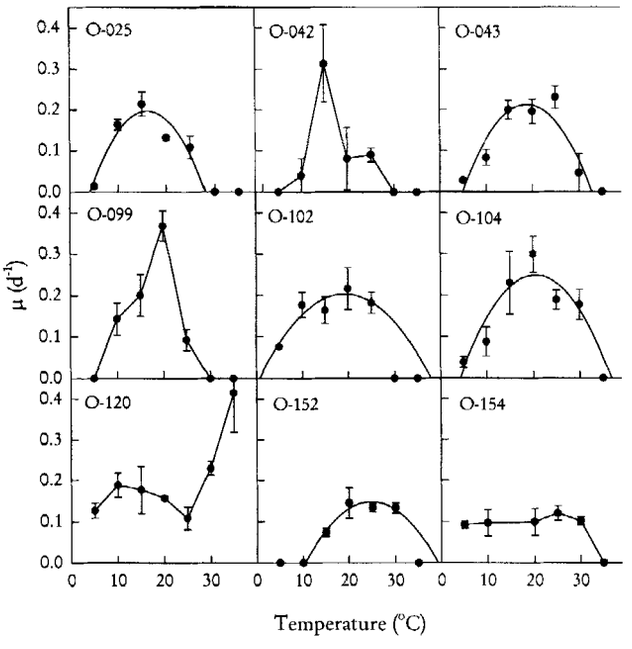
$\mu_{max}$ for the polar cyanobacteria ranged from 0.12 to 0.41 $d^{-1}$, with an average of 0.23 ± 0.069 $d^{-1}$ (Table 2). These growth rates were low compared to the maximum $\mu$ for each temperature found by Eppley's (1972) compilation of data on algal growth. Eppley's relation predicted growth rates to be 0.81–5.41 $d^{-1}$ between 5° and 35° C, but the highest cyanobacterial growth rate obtained in this study was 0.41 $d^{-1}$ at 35° C. The maximum growth rates we measured for polar cyanobacteria were low compared to the $\mu_{max}$ of the temperate cyanobacteria ($t$ = 7.12, $P < 0.001$, n = 39) listed in Robarts and Zohary (1987; Tables 2, 3). The difference between the $\mu_{max}$ of the two groups may reflect the difference in growth potential between the bloom-forming and mat-forming cyanobacteria.

*$T_{opt}$ for growth.* We did not observe significant regional differences between the $T_{opt}$s of cyanobacteria isolated from the Arctic, Antarctic, and subarctic (one-way ANOVA, $F$ = 1.90, $P$ = 0.17, n = 27). The optimal temperature for $\mu$ of all the isolates tested in this study ranged from 15° to 30° C, with a mean of 19.9° C (Table 2), whereas the temperature of their natural habitat ranged from 0.4° to 15° C, with an average of 6.8° C (Table 1). A pairwise comparison revealed that this mean $T_{opt}$ is significantly higher than the mean temperature of the sites from which the cyanobacteria were isolated ($t$ = 13.4, $P < 0.001$, n = 26; Fig. 2).

We compared the mean $T_{opt}$ of the polar cyanobacteria (Table 2) with the mean $T_{opt}$ of the temperate cyanobacteria listed in Table 3, and temperate cyanobacteria have a significantly higher $T_{opt}$ than polar cyanobacteria ($t$ = 2.59, $P$ = 0.012, n = 60), but the two means are close nonetheless (Tables 2, 3).

*Pigment ratio.* The carotenoid : Chl *a* ratio varied from 0.24 to 7.7. In some cases, the Chl *a* and carotenoid concentration at 30° and 35° C were below the limit of detection of the method employed. Some of the isolates showed an increasing carotenoid : Chl *a* ratio with decreasing temperature, es-



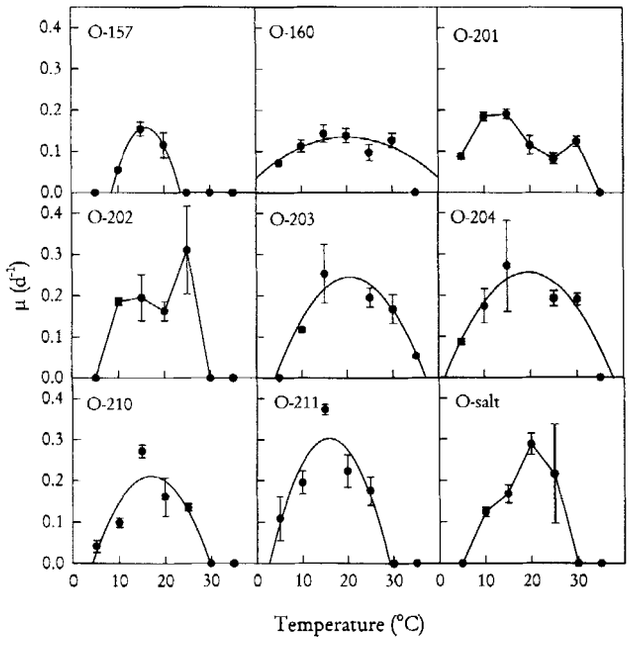




FIG. 1. The relationship between the specific growth rate (μ) and temperature for 27 isolates of polar cyanobacteria. The solid line represents the curve fitted with Equation (1).

pecially at 5° and 10° C (Fig. 3). However, this was not a consistent trend for all of the 27 isolates; for one third of the strains, there was no apparent relationship between the carotenoid : Chl *a* ratio and temperature (Fig. 3).

In vivo *absorption characteristics.* The *in vivo* absorbance of carotenoids relative to Chl *a* plotted against temperature showed a consistent U-shaped pattern among the nine isolates examined (Fig. 4). There was often a gradual decrease in carotenoid : Chl *a* followed by a sharp increase at high temperatures. A similar pattern was obtained for the relationship between the PC : Chl *a* ratio and temperature (Fig. 4) as well as the relationship between APC : Chl *a* and temperature (Fig. 4).

## DISCUSSION

Although various mathematical functions have been used to describe the relation between algal growth and temperature (i.e. Arrhenius function, Regier et al. 1990; $Q_{10}$, van't Hoff rule, Ahlgren 1987; square root function, Ratkowsky et al. 1982), none of these functions depicts the detrimental effect of high temperature on algae, in particular, the decreasing slope of the growth (μ)–temperature relationship near $\mu_{max}$ and the decline in growth rates

TABLE 2. *The maximum specific growth rate ($\mu_{max}d^{-1}$), optimal temperature for growth ($T_{opt}$), and range of temperature at which there is increasing growth with temperature ($0.5\Delta T$) estimated from fitting the data through Equation (1). The correlation coefficients for the relation between observed and fitted growth rates are also listed. No curve-fitting was attempted for the data that do not fit Equation (1) and those isolates are marked with [c]. NA = not available.*

| Isolate | $\mu_{max}$ ($d^{-1}$) | $T_{opt}$ (° C) | $Q_{10}$ | $0.5\Delta T$ (° C) | $R$ |
|---|---|---|---|---|---|
| E2 | 0.20 | 17.9 | 1.82 | 10–17.9 | 0.97[a] |
| E5 | 0.19 | 20.1 | 1.54 | 10–20.1 | 0.88[a] |
| E6a | 0.17 | 17.7 | 1.74 | 5–17.7 | 0.97[a] |
| E7 | 0.16 | 20.8 | 1.69 | 5–20.8 | 0.98[a] |
| E11a | 0.17 | 25.5 | 1.59 | 5–25.5 | 0.89[a] |
| E11b | 0.28 | 18.6 | 3.97 | 5–18.6 | 0.98[a] |
| E12 | 0.24 | 24.9 | 1.98 | 5–24.9 | 0.96[a] |
| E17 | 0.23 | 18.3 | 2.75 | 5–18.3 | 0.98[a] |
| E18 | 0.29 | 20.2 | 2.46 | 5–20.2 | 0.76[b] |
| O-salt[c] | 0.29 | 20.0 | 2.31 | 10–20 | NA |
| O-025 | 0.20 | 16.1 | 6.13 | 5–16.2 | 0.92[a] |
| O-042[c] | 0.31 | 15.0 | 64 | 10–15 | NA |
| O-043 | 0.21 | 18.9 | 1.80 | 10–18.9 | 0.90[a] |
| O-099 | 0.37 | 20.0 | 2.58 | 10–20 | NA |
| O-102 | 0.20 | 19.3 | 1.86 | 5–19.3 | 0.92[a] |
| O-104 | 0.25 | 20.7 | 5.65 | 5–20.7 | 0.92[a] |
| O-120[c] | 0.41 | 35.0 | 1.49 | 5–35 | NA |
| O-152 | 0.15 | 24.9 | 1.90 | 15–24.9 | 0.93[b] |
| O-154[c] | 0.12 | 25.0 | 1.14 | 5–25 | NA |
| O-157 | 0.16 | 16.1 | 5.59 | 10–16.0 | 1.0a |
| O-160 | 0.13 | 20.1 | 1.43 | 5–20.1 | 0.76[b] |
| O-201[c] | 0.19 | 15.0 | 2.18 | 5–15 | NA |
| O-202[c] | 0.31 | 25.0 | 1.41 | 10–25 | NA |
| O-203 | 0.24 | 20.6 | 1.92 | 5–20.6 | 0.83[b] |
| O-204 | 0.26 | 19.6 | 1.73 | 5–19.6 | 0.91[a] |
| O-210 | 0.21 | 17.0 | 5.49 | 5–17.0 | 0.84[b] |
| O-211 | 0.30 | 15.9 | 2.82 | 5–16.0 | 0.86[b] |
| Mean | 0.23 | 19.9 | 4.85 | | |
| SE | 0.069 | 4.2 | 11.7 | | |

[a] Denotes $P < 0.05$.
[b] Denotes $P < 0.1$.
[c] Marks the species where no curve-fitting was attempted.

beyond this maximum. The parabolic function (Eq. (1)) was chosen because it described much of the observed variation with only three estimated growth parameters: maximum growth rate ($\mu_{max}$), optimal temperature for growth ($T_{opt}$), and the range of temperature over which growth increases with temperature ($0.5\Delta T$).

The parabola does not always provide a perfect fit for the $\mu$ and temperature relationship because the change in $\mu$ with temperature may not be symmetrical around $T_{opt}$ (Fig. 1; see also Collins and Boylen 1982). The decline in growth as a result of thermal instability and denaturation of bimolecules is often more rapid than the temperature-dependent increase in $\mu$ associated with increased biochemical activity (McMeekin et al. 1988). However, the parabola gave a reasonable description of the increase and the gradual leveling off of $\mu$ with increasing temperatures (Fig. 1).

Alternatively, we can fit the nonlinear regression model derived by Ratkowsky et al. (1983), which is

$$\sqrt{\mu} = b(T - T_{min})\{1 - \exp[c(T - T_{max})]\}, \quad (2)$$

where $\mu$ is the observed growth rate at temperature T, $T_{min}$ is the suboptimal temperature at which $\mu$ becomes undetectable, $T_{max}$ is the supraoptimal temperature at which $\mu$ becomes undetectable, and b and c are fitted parameters. Although this model takes into account the different slopes of the rising and the declining portion of the $\mu$-temperature relationship, it has four estimated parameters, which further limits the degrees of freedom.

The parabola did not adequately fit the $\mu$-temperature data for 25% of the isolates. Isolate O-120 is a eurythermal strain that has increasing $\mu$ with increasing temperature even at 35° C. Isolate O-154 displayed minimal changes in $\mu$ with temperature. This suggests that O-154 has persistent growth over a wide temperature range despite its low rate of growth (Fig. 1). For the rest of the isolates, the misfit of the parabolic function to the $\mu$-temperature data seemed to be the result of a markedly asymmetrical response of $\mu$ to temperature around $T_{opt}$ (Fig. 1).

The $T_{opt}$ values of the 27 isolates of polar cyanobacteria studied were high (mean $T_{opt}$ = 19.9, SE = 4.85; Table 2), and they all have a $T_{opt} \geq 15°$ C (Table 2, Fig. 2). This survey strongly indicated that they are psychrotrophic (i.e. cold-tolerant) rather than psychrophilic (i.e. cold-adapted). All except two isolates studied have $T_{opt}$ values for growth above 15° C (Table 2). Although the isolates O-042 and O-201 have a $T_{opt}$ of 15° C, they do not fit Morita's (1975) criteria of psychrophily because they can survive at ≥20° C (Fig. 1, Table 2). Our extensive survey shows that the results obtained by Castenholz and Schneider (1993) reflect a general characteristic of Arctic as well as Antarctic Oscillatoriaceae. They found that a strain of *Oscillatoria priestleyi* isolated from the McMurdo Ice Shelf in the Antarctic had an optimal temperature for growth in the range 21°–24° C.

The $\mu$-temperature results obtained here are consistent with field measurements in polar regions. *Phormidium* mats that were freshly collected from Signy Island (maritime Antarctic) and Fryxell Stream (continental Antarctic) displayed maximum photosynthesis at 15° C (Davey 1989) and 25° C (Vincent and Howard-Williams 1989), respectively. These field results imply that high $T_{opt}$ for growth by laboratory cultures is not a result of thermal adaptation to laboratory conditions. Furthermore, our cultures were assayed 6 months (E2–E18) to 5 years (O-025–O-099 and O-salt) after isolation from the field populations, and there was no evidence that the set of older cultures had a higher $T_{opt}$ than the more recently isolated strains ($t = 1.58$, $P = 0.14$, n = 14).

The psychrotrophic nature of polar cyanobacteria contrasts strongly with the psychrophilic nature of polar marine diatoms. Numerous studies have documented that marine algae or sea-ice algae from the

TABLE 3. *A list of $\mu_{max}$ and $T_{opt}$ of temperate cyanobacteria collected from the literature.*

| Species | $\mu_{max}$ | $T_{opt}$ | Location | Reference |
|---|---|---|---|---|
| *Anabaena* sp. | 0.4 | 25 | Lake Mendota, Wisconsin, U.S.A. | Konopka and Brock 1978 |
| *Anabaena* sp. | | 25 | Lake Kasumigaura, Japan | Imamura 1981 |
| *Anabaena* sp. | | 30 | Missouri, U.S.A. | Novak and Brune 1985 |
| *Anabaena flos-aquae* | | 18 | Lough Neagh, Ireland | Foy et al. 1976 |
| *Anabaena flos-aquae* | | 20 | Windemere, England | Foy et al. 1976 |
| *Anabaena flos-aquae* | | 22.5 | Lake Sääskjärvi, Finland | Rapala et al. 1993 |
| *Anabaena flos-aquae* | | 20 | Lake Vanajanselka, Finland | Rapala et al. 1993 |
| *Anabaena mendatae* | | 22.5 | Lake Säyhteenjärvi, Finland | Rapala et al. 1993 |
| *Anabaena oscillarioides* | 0.8 | 28 | Manukau pond, New Zealand | Vincent and Silvester 1979 |
| *Anabaena spiroides* | 0.9 | 24 | Lake Kasumigaura, Japan | Seki et al. 1981 |
| *Anabaena variabilis* | 1.1 | 35 | | Collins and Boylen 1982 |
| *Aphanizomenon* sp. | 0.18 | 25 | Lake Mendota, Wisconsin, U.S.A. | Konopka and Brock 1978 |
| *Aphanizomenon* sp. | | 25 | Lake Kasumigaura, Japan | Imamura 1981 |
| *Aphanizomenon flos-aquae* | 1.2 | 28 | Lake Greifensee | Uehlinger 1981 |
| *Aphanizomenon flos-aquae* | | 15 | Lough Neagh, Ireland | Foy et al. 1976 |
| *Aphanizomenon flos-aquae* | | 25 | Lough Neagh, Ireland | Foy et al. 1976 |
| *Aphanothece stagnina* | | 25 | Southern Baltic Sea | Zhuang et al. 1993 |
| *Microcystis* sp. | 0.5 | 25 | Lake Mendota, Wisconsin, U.S.A. | Konopka and Brock 1978 |
| *Microcystis* sp. | | 32.5 | Lake Kasumigaura, Japan | Imamura 1981 |
| *Microcystis aeruginosa* | 0.8 | 27.5 | | Nicklisch and Kohl 1983 |
| *Microcystis aeruginosa* | 0.59 | 32 | Lake Suwa, Japan | Watanabe and Oishi 1985 |
| *Microcystis aeruginosa* | 0.81 | 32 | Hartbeespoort Dam, South Africa | Van der Westhuizen and Eloff 1985 |
| *Microcystis* sp. | 0.275 | 29.7 | | Kruger and Eloff 1978 |
| *Nodularia sphaeroscarpa* | | 20 | Baltic Sea | Lehtimäki et al. 1994 |
| *Nodularia spumigena* | | 20 | Southern Baltic Sea | Lehtimäki et al. 1994 |
| *Nodularia spumigena* | | 20 | Baltic Sea | Lehtimäki et al. 1994 |
| *Oscillatoria* sp. | | 27 | | Novak and Brune 1985 |
| *Oscillatoria agardhii* | 0.59 | 24 | | Ahlgren 1978 |
| *Oscillatoria agardhii* | | 10 | Lough Neagh, Ireland | Foy et al. 1976 |
| *Oscillatoria agardhii* | | 25 | Loughgall, Ireland | Foy et al. 1976 |
| *Oscillatoria redekei* | | 6 | Lough Neagh, Ireland | Foy et al. 1976 |
| *Oscillatoria redekei* | | 25 | Lough Neagh, Ireland | Foy et al. 1976 |
| *Scytonema ocellatum* | | 20 | | Patterson and Bolis 1993 |
| Mean | 0.68 | 23.9 | | |
| SE | 0.31 | 6.0 | | |
| n | 12 | 33 | | |

Arctic and Antarctic are psychrophiles (Palmisano 1987, R. E. H. Smith et al. 1994, Suzuki and Takahashi 1995). The low $T_{opt}$ of marine algae may reflect the persistently low temperature and stability of the marine environment. The cyanobacteria inhabiting the glacier melt streams and ponds may experience fluctuations in temperature due to solar heating as well as other environmental stresses such as freezing. Tolerance to such variability may contribute to their success in the polar regions.

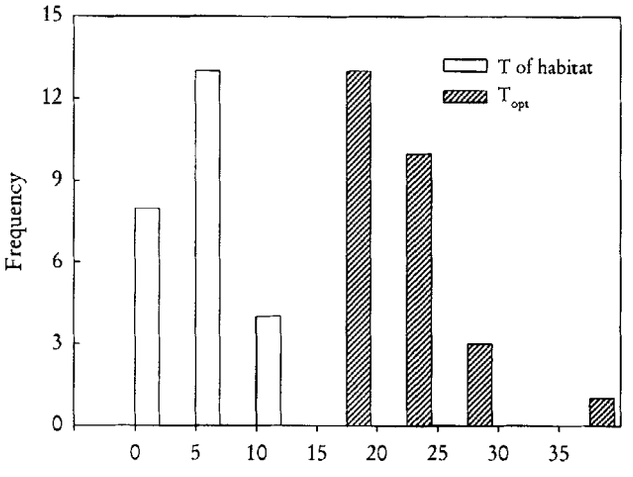
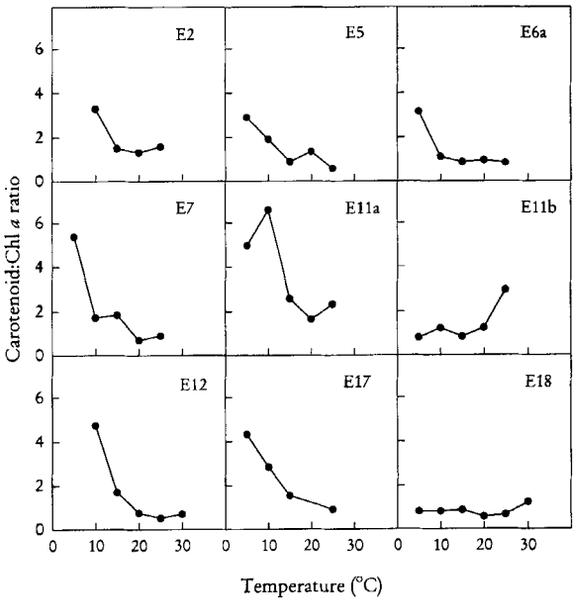
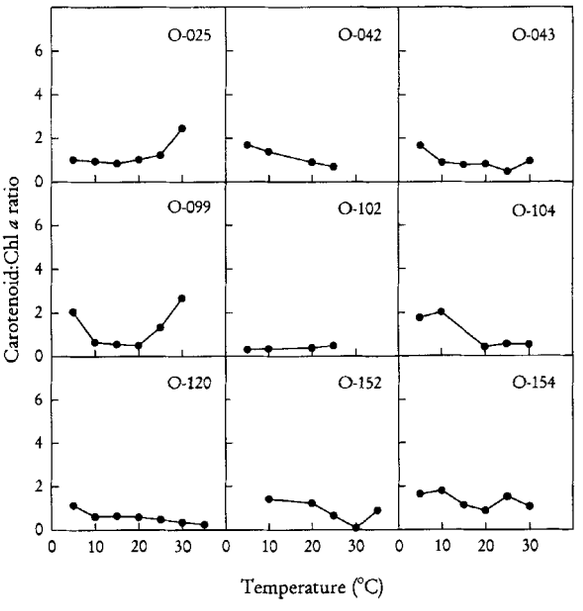



FIG. 2. The frequency distribution of optimal temperature ($T_{opt}$) for growth and the temperature of the habitats of 27 isolates of cyanobacteria.

The temperature optima of polar cyanobacteria are significantly higher than the temperature of their native habitats (Tables 1, 2). These $T_{opt}$s are slightly lower than those of temperate cyanobacteria (Tables 2, 3). This reinforces the speculation that polar cyanobacteria may have evolved in warmer environments and later colonized in cooler environments, such that they are genetically adapted to warm climates (Seaburg et al. 1982). In fact, one-third of the isolates had undetectable growth at 5° C (Fig. 1). Similar findings were reported by Seaburg et al. (1982), who found that several clones of cyanobacteria isolated from Victoria Island, Antarctica, were incapable of growing at ≤5° C. The growth inhibition at low temperature cannot be explained by the lack of temperature acclimation in the present study. Growth at 5° C showed no increase over a 2–3-week period. Similarly, Castenholz



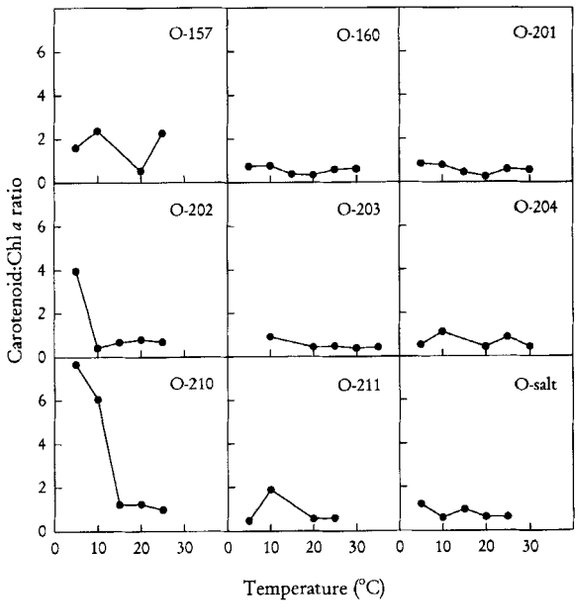




FIG. 3. The change in carotenoid : Chl *a* ratios with increasing temperature for 27 isolates of polar cyanobacteria.

and Schneider (1993) observed undetectable growth of their Antarctic isolate of *Oscillatoria priestleyi* at 4° C, even after 2 weeks of preacclimation to the experimental temperature.

The low or the lack of observable growth at ≤5° C and the responsiveness to temperature changes (Table 2) suggest that cyanobacteria accumulate biomass during the brief periods of warmest summer temperatures. Cyanobacterial growth can generally be observed within a 20° C range (minimum range 10° C, maximum range 30° C; Fig. 1), and these growth ranges are similar to those observed by Seaburg et al. (1982). Therefore, polar cyanobacteria can be considered as eurythermal organisms with broad tolerances to environmental temperature.

Cyanobacterial dominance in temperate aquatic systems has often been attributed to their high temperature optima (Tilman et al. 1986, Varis 1993); however, temperature adaptation or the lack thereof does not explain the dominance of cyanobacteria in polar environments. It may be hypothesized that cyanobacteria have such high growth rates that they can outcompete other algae even at low, suboptimal temperatures. The 27 isolates tested in this study had growth rates ranging from undetectable to 0.13 $d^{-1}$, with a mean of 0.046 $d^{-1}$ ± 0.040 at 5° C. These

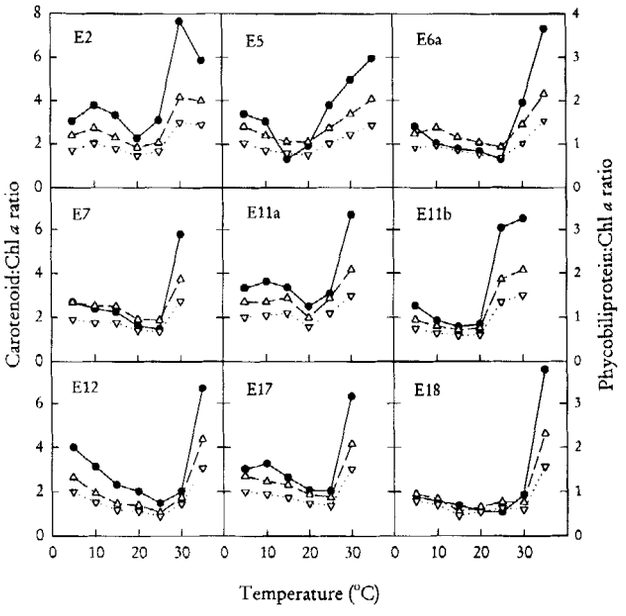



FIG. 4. The relationship between the *in vivo* absorption ratio of carotenoids to Chl *a* (●), phycocyanin to Chl *a* (△), or allophycocyanin to Chl *a* (▽) and temperature.

rates are low compared to the theoretical $\mu_{max}$ derived by Eppley ($\mu_{max}$ = 0.81 $d^{-1}$; Eppley 1972). They are also low in comparison to $\mu_{max}$ of the four clones of Antarctic green algae that Seaburg et al. (1982) studied. For the four species of chlorophytes they studied, average $\mu$ at 5° C was 0.73 $d^{-1} \pm 0.28$, which was significantly higher than the average $\mu$ of the polar cyanobacteria we used in our experiments ($t = 13.0$, $P < 0.001$, n = 31). Thus, the dominance of cyanobacteria cannot be attributed to their superior growth rates at low temperatures even relative to other phototrophs in the polar freshwater environment. The accumulation of cyanobacterial biomass is more likely a result of resistance to mortality rather than a high gain in biomass. Stress factors such as freeze–thaw cycles, desiccation, exposure to ultraviolet (UV) radiation, and continuous irradiance may thus be of overriding importance in determining the community structure of polar freshwater ecosystems (Dodds et al. 1995).

In the winter, polar algae experience a prolonged period of subzero temperatures. Davey (1989) demonstrated that the cyanobacterium *Phormidium* recovers readily from freezing and that photosynthetic and respiratory activity resumes immediately after thawing. The survival of the cyanobacteria throughout the extended winter maintains a large viable inoculum of cyanobacteria for the next growing season.

In the summer, the algae in glacier-fed streams and small ponds are often exposed to diurnal freeze–thaw cycles and periodic desiccation due to the seasonal fluctuation of water level in ponds and streams (Seaburg et al. 1982, Davey 1989). Yet cyanobacteria can withstand prolonged dehydration (Potts 1994). Dried cyanobacterial mats recommence photosynthesis within minutes of rewetting (Vincent and Howard-Williams 1986, Hawes et al. 1992, Dodds et al. 1995).

Elevated UV-B radiation levels have been recorded in the Arctic and Antarctic. Cyanobacteria inhabiting shallow ponds and streams are constantly exposed to UV radiation during the polar summer. Deleterious effects of UV radiation on primary production are well known (Vincent and Roy 1993). Some cyanobacteria possess defense mechanisms, such as UV screening pigments (mycosporin-like amino acids and scytonemin; Garcia-Pichel and Castenholz 1991, 1993, Potts 1994) and avoidance strategies (Vincent and Quesada 1994) that help them reduce the damaging effects of UV radiation and thereby favor their survival in brightly lit habitats in polar, freshwater systems.

The algal community in the polar environment is exposed to continuous high irradiance during the summer. This, in combination with the low temperature, increases the susceptibility to photoinhibition (Jensen and Knutsen 1993, Long et al. 1994). Our results indicate that some cyanobacteria isolates responded to decreasing temperature with an increase in extractable carotenoid : Chl *a* ratio (Fig. 3). Similar responses have been observed in *Dunaliella bardawil* (Ben-Amotz 1996). Carotenoids act as a photoprotectant that quenches excess photochemical energy and thereby protects the photosystems against the synergistic effect of low temperature and high irradiance (Young 1993, Vincent and Quesada 1994). However, some isolates showed no variation in the carotenoid : chlorophyll ratio over the tested temperatures (Fig. 3). Tolerance of irradiances up to 500 μmol photons·$m^{-2}$·$s^{-1}$ or above has been demonstrated in cyanobacteria (Vézina 1995, Roos and Vincent, in prep.). It is possible that the experimental irradiance used in our experiments (225 μmol photons·$m^{-2}$·$s^{-1}$) was not high enough to induce temperature-dependent variations in pigment composition in all isolates.

The U-shaped pattern of the *in vivo* absorption of carotenoid relative to Chl *a* at different temperatures (Fig. 4) further emphasizes the role of carotenoids as a photoprotectant. Algae tend to be more prone to photoinhibition at low temperatures as well as temperatures above the optimum (Graham et al. 1995, Ibelings 1996). The increase in carotenoid : Chl *a* at supraoptimal temperatures may also reflect the faster degradation of Chl *a* relative to carotenoids at high temperatures (Young 1993).

Contrary to expectation, the PC : Chl *a* and APC : Chl *a* ratios followed the same trend with temperature as carotenoid : Chl *a* (Fig. 4). Generally, carbon fixation limits growth and photosynthesis at low temperatures such that algal cells tend to direct resources away from the synthesis of light-harvesting components (Raven and Geider 1988). Thus, we an-

ticipated a concomitant decrease in Chl *a* content, PC, and APC and the absence of a relationship between these pigment ratios and temperature. The consistent decrease in phycobiliproteins: Chl *a* with increasing temperature suggests that all pigment ratios (including carotenoids: Chl *a*) are controlled primarily by variations in cellular Chl *a* biosynthesis. Further studies will be required to understand the influence of decreasing temperature on pigment content and structure of phycobilisomes.

In conclusion, our results show that the cyanobacteria of the Arctic, Antarctic, and subarctic are predominantly psychrotrophic with temperature optima for growth greater than 15° C. Their low growth rates at cold temperatures suggest that the cyanobacterial dominance is achieved by persistent low growth rates and survival under a variety of harsh conditions rather than by thermal adaptation to the ambient environment.

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